Timing Research

interactive metronome

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TIMING RESEARCH

A large body of research studies on mental timing/temporal processing can be viewed at the IQ Brain Clock EWOK (Evolving Web of Knowledge). Visit http://www.iapsych.com/iqclock2/map.htm to view.

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IMPROVEMENTS IN INTERVAL TIME TRACKING AND EFFECTS ON READING ACHIEVEMENT

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This study examined the effect of improvements in timing/rhythmicity on students' reading achievement. 86 participants completed pre- and post-test measures of reading achievement (i.e., Woodcock-Johnson III, Comprehensive Test of Phonological Processing, Test of Word Reading Efficiency, and Test of Silent Word Reading Fluency). Students in the experimental group completed a 4-week intervention designed to improve their timing/rhythmicity by reducing the latency in their response to a synchronized metronome beat, referred to as a synchronized metronome tapping (SMT) intervention. The results from this *non-academic* intervention indicate the experimental group's post-test scores on select measures of reading were significantly higher than the non-treatment control group's scores at the end of 4 weeks. This paper provides a brief overview of domain-general cognitive abilities believed effected by SMT interventions and provides a preliminary hypothesis to explain how this *non-academic* intervention can demonstrate a statistically significant effect on students' reading achievement scores. © 2007 Wiley Periodicals, Inc.

In recent years the role of the school psychologist has expanded to include greater involvement in students' reading acquisition, performance, and curriculum-based evaluation. This increased participation may be attributed to several national initiatives including Reading First under No Child Left Behind (U.S. Department of Education, 2002), the National Reading Panel's (2000) report, the Individuals with Disabilities Education Improvement Act (2004), and the impact of empirical research in reading on district- and state-level policies and procedures (e.g., Daly & McCurdy, 2002; Sheridan, 2004). Recent technological advancements also provided school psychologists with a broader understanding of the process of reading at a physiological level. Results from neuroscience studies (e.g., functional magnetic resonance imaging investigations involving individuals experiencing reading difficulties or diagnosed with dyslexia) have provided new insights into the process of reading at the neural level (e.g., see Katzir & Paré-Blagoev, 2006). This groundbreaking research has demonstrated individual differences in the functions of anatomically similar brain regions of impaired readers and nonimpaired readers (Katzir & Paré-Blagoev, 2006; Shaywitz & Shaywitz, 2005; Shaywitz et al., 1999, 2003).

The integration of our understanding of the process of reading at a physiological level with reading at a behavioral level (i.e., neuroscience-based interventions) may be the next frontier for school psychologists and reading research. One intervention that has received considerable empirical attention, both pro and con, is the FastForWard method (Tallal, Miller, Jenkins, & Merzenich, 1997). A lesser known neuroscience-based intervention is the use of synchronized metronome tapping, which links research on mental interval timekeeping (e.g., see Buhusi & Meck, 2005) and academic achievement. Preliminary results from this research indicate that children diagnosed

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with dyslexia may have deficiencies in their timing and rhythm abilities, as evidenced by their responding within a wider range of times on either side of a metronome beat, when compared to nonimpaired readers (Wolff, 2002). Similarly, McGee, Brodeur, Symons, Andrade, and Fahie (2004) reported children diagnosed with a reading disability differed from children diagnosed with attention-deficit/hyperactivity disorder (ADHD) on retrospective time perception, a finding interpreted as consistent with Barkley's (1997) behavioral inhibition theories. Research also implicated mental or interval timekeeping (time perception) in a number of academic and behavioral disorders (see McGee et al., 2004). Some researchers believe the connection between timing/rhythm and reading may be so robust that a student's mean latency response to a metronome beat may predict performance on standardized reading tests (Waber et al., 2003; Wolff, 2002). Furthermore, a recent study has suggested that elementary timing tasks may represent a form of *temporal g* that is more strongly correlated ($r = .56$) with psychometric g than the standard *reaction time g* ($r = -.34$) approach to measuring the *essence* of general intelligence (Rammsayer & Brandler, in press). Given the growing evidence suggesting a potentially important link between mental interval timekeeping and cognition and learning (Buhusi & Meck, 2005; Rammsayer & Brandler, in press), the connection between timing-based neuroscience interventions (e.g., synchronoized metronome tapping) and academic achievement warrants investigation.

To investigate the relationship between improvements in timing and rhythm (due to synchronized metronome tapping-based intervention) on reading achievement, Taub, McGrew, & Lazarus (2007) administered subtests from the Woodcock-Johnson Tests of Achievement III (WJ-III ACH; Woodcock, Mather, & McGrew, 2001) as pre- and posttest measures of reading. In this study, over 250 high-school-aged participants were randomly assigned to either a control or experimental group. The experimental group participated in a rhythmic synchronization metronome-based assessment and intervention technique (herein after referred to as the Interactive Metronome [IM] method), a *nonacademic* intervention. The IM treatment sessions lasted for approximately 45 minutes each day for total of about 15 hours. (The IM intervention method will be discussed in detail below.) The results from this study indicated, when compared to the control group, the experimental group demonstrated statistically significant improvements on the WJ-III ACH posttest measures of broad reading and reading fluency. Participants who received IM-based interventions also demonstrated statistically significant improvements in domains other than reading.

IM training was also reported to produce positive effects in a number of nonacademic domains. For example, after receiving IM training, participants demonstrated statistically significant improvements in golf performance (Libkuman & Otani, 2002). Shaffer et al. (2001) reported that boys prediagnosed with ADHD demonstrated improved performance, when compared to two ADHD control groups, in the domains of attention, language processing, motor control, reading, and parent report of regulation of aggressive behavior after their participation in an IM-based intervention.

Mental Interval Timing Research and Models

Cognitive psychology's interest in mental timekeeping has spanned decades. For example, cognitive differential psychologists first reported the identification of a *temporal tracking* capability in 1980 (Stankov, Horn, & Roy, 1980). Temporal tracking was identified as being found in various auditorily presented tasks that involved the mental counting or rearrangement of temporal sequential events (e.g., reorder a set of musical tones; Carroll, 1993).

Researchers in cognitive psychology have studied the phenomenon of *interval timing* through a number of research paradigms, one which requires individuals to maintain synchrony (via a bimanual motor response) with auditory tones (e.g., from a metronome), also known as synchronized metronome tapping (SMT). Tapping in synchrony with a metronome requires an individual to correct for asynchronies in their response to a reoccurring beat. The most viable theoretical explanation for SMT behavior can be derived from the pacemaker-accumulator model, which is based on scalar timing/expectancy theory (see Buhusi & Meck, 2005). Briefly, SMT asynchrony corrections are thought to be accomplished through an internal adjustment to the phase of one's underlying master mental time clock (Buhusi & Meck, 2005; Vorberg & Fuchs, 2004). This error correction is triggered when observed temporal deviations (as determined via the accumulation, in a short-term storage *accumulator*, of neural pulses or tics from a cognitive *pacemaker*) are determined to differ from a reference *standard* (which is maintained in a *reference memory*), via performance feedback. This process is referred to as an *automatic phase adjustment*. The allocation of *attentional resources* and the minimization of stimuli that may divert cognitive processing resources away from timing have been hypothesized to play a significant role in mental interval timekeeping and metronome-based synchronization of rhythmic movements (Brown & Bennett, 2006; Buhusi & Meck, 2005). In addition, the quickness and efficiency of the phase adjustment mechanism is believed to eliminate the necessity for, or excessive reliance on, long-term memory (e.g., accessing the reference memory) or learning (Vorberg & Fuchs, 2004).

How SMT-Based IM Training Works

During IM training participants wear a headphone and listen to a reoccurring metronome beat. As they listen to the beat, they engage in physical movements such as clapping hand-to-hand with a sensor on one palm as they match their physical movement to the presentation of the beat (e.g., clap at the beat). The goal of IM training is to reduce the mean negative synchronization error during normal tracking of the regularly occurring metronome beat (clapping prior to or past the beat).

During training, participants receive feedback through an auditory guidance system as they progress through the simple, interactive physical movements. Although feedback is also provided through visual stimuli, the auditory feedback guidance system is the primary feedback method. The auditory feedback system provides tonal stimuli that indicate whether the participant responded *prior to*, *at*, *or past* the regularly occurring auditory metronome beat. The accuracy of participants' expectancy response to the metronome beat is provided in milliseconds (ms), with different tones indicating *far from*, *close to*, or *at* the metronome beat. A visual reading of millisecond latency is also presented on a computer screen.[1] The purpose of IM training is to improve participants' timing/rhythmicity by reducing the latency between the onset of the metronome beat and participant's expectancy response to the beat. After about 3–4 weeks of training, or 15–18 hours, participants are typically able to respond to within approximately 15 ms on either side of the beat. This compares to the average 80–100 ms latency response prior to training. At the completion of training, participants typically have engaged in approximately 25,000 motoric repetitions. These movements are the physical indication of one's expectancy of the onset of the metronome beat. Collectively, results from initial studies suggest that statistically significant improvements in a *domain-specific* SMT-based intervention are associated with statistically significant *domain general* improvements in the areas of academics, ADHD, and sports. How can rhythmic SMT-based interventions result in improved performance across such diverse domains of human performance as academics, ADHD, golf, and tennis?

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[1] Readers are referred to the Interactive Metronome, Inc.'s Web site to view a corporate-sponsored video showing IM training or to obtain additional information: http://www.interactivemetronome.com.

Purpose

Although hypothesized domain-specific cognitive mechanisms are possible, the domain-general or cross-domain SMT training effect is intriguing and argues first for replication of prior studies and second for investigation of potential domain *general* cognitive mechanisms to account for observed cross-domain improvements. Given this assumption, the purpose of this study was twofold.

The first purpose was to replicate an earlier study by examining the impact of improvements in timing/rhythmicity on students' reading achievement. The second purpose was to offer preliminary hypotheses that will contribute to a better understanding of the across-domain general cognitive mechanisms that may explain SMT treatment effects across such diverse human performance domains as academics, ADHD, and sports.

METHOD

Participants

Study participants included 86 students attending a public charter school receiving Title 1 funding located in Central Florida. As a public charter school, the school is a part of the public school system; the key difference between the public charter school and a public school is that the charter school receives funding directly from the State of Florida. The school currently has 133 students and provides education from kindergarten through fifth grade. All students attending the school are African-American, and 83% of the students receive free lunch. The study participants ranged in grade from first to fourth grade. There were 16 first-, 36 second-, 23 third-, and 11 fourth-grade students in the study. A total of 37 participants were male and 48 were female. Participants' ages ranged from 7 years old to 10 years old with a mean of 8.15 years ($SD = 1.0$).

Instruments

The instruments administered to evaluate the effects of IM training on participants' academic achievement and attention/concentration include selected subtests of the Comprehensive Test of Phonological Processing (CTOPP; Wagner, Torgesen, & Rashotte, 1999), Test of Silent Word Reading Fluency (TOSWRF; Mather, Hammill, Allen, & Roberts, 2004), Test of Word Reading Efficiency (TOWRE; Torgesen, Wagner, & Rashotte, 1999), and the WJ-III ACH (Woodcock et al., 2001). Table 1 provides a brief description of each test and identifies the specific subtests administered from each instrument.

Reliability

Most of the reported average internal consistency and alternate form reliability coefficients of the CTOPP exceed .80 and the test–retest coefficients range from .70 to .92 (Wagner, Torgesen, & Rashotte, 1999). The reported average alternate forms' reliability coefficients of the TOWRE all exceed .90 and the test–retest coefficients range from .83 to .96 (Torgesen, Wagner, & Rashotte, 1999). The median reliability coefficients of the tests selected from the WJ-III ACH are all at or above .87 (McGrew & Woodcock, 2001).

A lesser know test was the Test of Silent Word Reading Fluency. This instrument was standardized on 3592 individuals representing demographic characteristics that were similar to the 2001 U.S. Census data in terms of geographic region, gender, race, ethnicity, and parents' educational background. The instrument's normative tables are grouped in 3-month intervals for students ages 6-6 through 7-11, 6-month intervals for students 8-0 through 10-11, and at 1-year intervals for students ranging from 11-0 through 17-11 years of age. Reported test–retest reliabilities

Table 1
Names and Description of the Pretest and Posttests

Test	Description of tests and combinations of tests
Test of Oral Word Reading Efficiency	*Sight Word Efficiency*: A timed test of word recognition and decoding fluency, measures the ability to accurately and quickly recognize familiar words *Phonemic Decoding Efficiency*: A timed test measuring the ability to accurately and quickly read phonetically regular nonsense words. *Total Word Reading Efficiency*: Combines Sight Word Efficiency and Phonemic Decoding Efficiency.
Test of Silent Word Reading Fluency	Students are presented with several rows of words, which increase in difficulty. There are no spaces between the words (e.g., didhimgot). Students are required to draw a line between the boundaries of as many words as possible (e.g., did/him/got) within a 3-min time limit.
The Comprehensive Test of Phonological Processing	*Blending Nonwords*: Phonetic coding synthesis task of nonwords—an auditory processing task that is independent of acquired knowledge (less dependent on students' existing knowledge). *Segmenting Nonwords*: Phonetic coding analysis task of nonwords—an auditory processing task that is independent of acquired knowledge. *Rapid Digit Naming*: Rapid automatized naming test of digits. *Rapid Letter Naming*: Rapid automatized naming test of letters. *Rapid Naming Composite*: Combines Rapid Digit Naming and Rapid Letter Naming. *Alternate Phonological Awareness Composite*: Combines Blending Nonwords and Segmenting Nonwords.
Woodcock-Johnson III Tests of Achievement	*Letter-Word Identification*: Untimed measure of sight-word recognition. *Passage Comprehension*: Measure of reading comprehension and word knowledge. *Reading Fluency*: A timed test measuring reading speed, automaticity and rate of test taking. *Word Attack*: Untimed test requiring pronouncing nonwords that conform to English spelling rules.

for students ranging in age from 7 to 10 years of age, the age range of the present study, were all above .80, and the alternate form reliability coefficients exceeded .85 (Mather et al., 2004).

Procedure

All students completed a pretest battery of psychoeducational instruments (see Table 1). After completing the pretests, students were randomly assigned to either an experimental or control group. The experimental group participated in the IM intervention, at their school, during regular school hours. While the experimental group was participating in the IM intervention, the control group and nonparticipating classmates engaged in recess activities. Students in the experimental group were divided into four groups, one for each grade level. Two certified master trainers worked separately with each of the four grade-level groups. The groups ranged in size from 7 to 12 participants. The students in the experimental group participated in an average of 18 sessions, each lasting approximately 50 minutes. There was one treatment session each day per group. Upon completion of the IM intervention, posttests were administered to all participants. The same tests were used during the pre- and posttest administrations.

Participants completed both individually and group administered tests; however, the TSWRF and WJ-III ACH's Reading Fluency were the only group-administered tests. During the individual assessment each evaluator worked with a student one on one. The individual assessment took approximately 35 minutes to complete. Group administrations were conducted in the students' own classrooms and participants from the experimental and control group completed all group tests together as classmates. Students who were unable to participate and/or who were absent on the day of the group assessments completed the group tests either individually or with other nonclassmate students. During all test administrations the test proctors and administrators were unaware of each student's group assignment. A lead test administrator directed all group assessments. The administrator followed the standardized instructions included in each test's manual. For one test, WJ-III ACH Reading Fluency, minor modifications were made in standardized administration procedures to facilitate group administration of the test. Several steps were followed to ensure that standardized test administration procedures were followed as closely as possible. These steps included (a) a doctoral-level proctor was present during all group administrations, (b) a minimum of one proctor to every four students was maintained during all group administrations, (c) all test proctors were graduate-level school psychology students who either completed or were near completion of their second psychoeducational assessment course, and (d) if a student did not accurately complete a sample item, the group administration was stopped and the proctor followed standardized administration procedures to ensure adequate completion of the sample item. All students progressed through the group test administration at the same time.

Results

Unless otherwise noted, all analyses controlled for pretest scores using the same measure as the posttest (through analysis of covariance). For analyses that did not use developmentally based scores, such as raw or growth scores, age was also controlled in the analyses by entering age as a covariate in the ANCOVA. Given the prediction that statistically significant differences would favor the experimental group, one-tailed tests ($\alpha = .05$) were used to evaluate statistical significance.

Effects on Timing/Rhythm

The initial analysis examined the effect of IM training on timing and rhythm as measured by the IM assessment system. The IM treatment had a statistically significant effect on posttest timing and rhythm scores, with pretest score controlled, $F(1,76) = 107.376$, $p < .001$. Furthermore, the treatment had a large effect (Thompson, 1999) on the posttest outcome ($\eta^2 = .586$, $g = 1.974$). IM training accounted for more than 50% of the variance in IM posttest scores and resulted in close to a two standard deviation increase in those scores (with IM pretest scores controlled).

It seems likely that IM training should be more effective for children who initially showed poor performance (high scores) on the measure of timing and rhythm. Sequential multiple regression was used to evaluate the possibility of a statistically significant interaction between the pretest and treatment. The IM posttest was regressed on the centered IM pretest and group membership in one block, with the centered pretest by group cross-product entered in a second block. As summarized in Table 2, the addition of the cross-product to the regression resulted in a statistically significant increase in R^2, indicating that the Pretest × Treatment Group interaction was statistically significant. The nature of the interaction is demonstrated in Figure 1, which shows separate regression lines for the posttest on the pretest, by treatment group. The lines show that the experimental group performed better on the posttest than did the control group, but that training was indeed most effective for participants with poor initial timing/rhythmicity.

Reading

Multivariate analysis of covariance (MANCOVA) was used to test the effect of IM training on the four measures of reading skill from the WJ-III ACH (Letter-Word Identification (LW-ID),

Table 2
Sequential Multiple Regression to Test Whether IM Training Was More Effective for Those with Initially High (Poor) Scores on Timing/Rhythmicity

Variables entered	ΔR^2	p
IM Pretest (centered), Treatment Group	.707	<.001
Pretest by group cross-product	.082	<.001

Reading Fluency, Passage Comprehension, and Word Attack). Pretest scores on these measures were used as covariates. As recommended by the test authors, *W* scores (a continuous, equal interval growth scale scores) were used for these analyses. The results of this analysis (and subsequent MANCOVA results) are summarized in Table 3. As shown in the table, the IM training did not demonstrate a statistically significant effect on reading achievement as measured by the WJ-III achievement tests.

Table 3 also shows the effects of IM training on measures of reading efficiency, TOWRE (Sight Word, Phonemic Decoding), and fluency, TSWRF. For this set of analyses, standard scores ($M = 100$, $SD = 15$) were used as both pre- and posttest scores; pretest scores and age were the

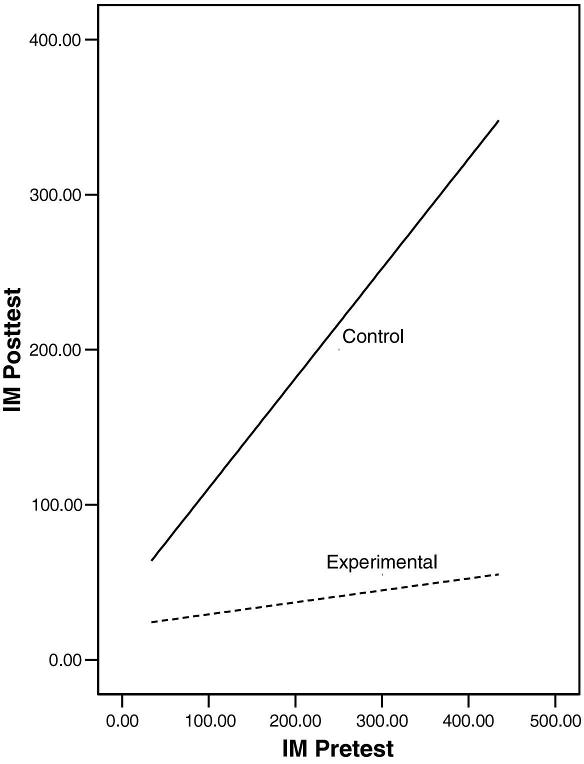

FIGURE 1. Interaction between IM pretest and IM training. The regression lines show that IM training was most effective in improving the timing and rhymicity of children with initial poor performance (low scores represent better performance).

Table 3
MANCOVA Results: Effect of IM Training on Reading

Measures	Hotelling's trace	$F(df)$	p	η^2
WJ Achievement Reading	.045	.842 (4, 75)	$>.05$	.043
Reading Efficiency & Fluency	.098	2.414 (3, 75)	.037	.089
CTOPP Phonological Processing	.205	3.899 (4, 76)	.003	.170

controlled variables. As shown in the table, the IM training produced a statistically significant effect on measures of reading efficiency and fluency. Participants who received IM training scored at a higher level on the multivariate dependent variable. The IM treatment accounted for 8.9% of the variance in reading efficiency and fluency, a small effect size (Keith, 2006, p. 508). Follow-up tests (univariate ANCOVAs) revealed a statistically significant effect for the TOWRE Sight Word Efficiency measure, $F(1,76) = 5.881$, $p = .009$, $\eta^2 = .072$, $g = .481$,[2] but not for the other measures.

Table 3 also shows the results of analyses of the IM effects on phonological processing skills as measured by the CTOPP (digit naming, letter naming, segmenting, and blending). Participants who received IM training demonstrated statistically significantly higher CTOPP scores, and the IM treatment accounted for 17% of the variance in CTOPP scores, a moderate effect. Univariate follow-up statistical analyses revealed statistically significant effects on the letter naming subtest, $F(1,79) = 8.680$, $p = .002$, $\eta^2 = .099$, $g = .536$, but not for the other components of the CTOPP.

Discussion

The current study employed a pre-/posttest evaluation design to investigate the effect of a specific SMT intervention (viz., Interactive Metronome) on reading performance in a sample of 86 first-, second-, third-, and fourth-grade students in a public charter school receiving Title 1 funding. Participants were randomly assigned to either an experimental (IM) or control group. The experimental group participated in a 3–4-week IM intervention designed to improve their timing/rhythmicity. The control group engaged in recess activities with nonparticipating classmates during each of the approximately 50 minute daily intervention sessions. All participants completed the same reading pre- and posttest measures, which were then analyzed via statistical methods that controlled for initial pretest performance levels and age (ANOCOVA, MANOVA).

Timing and Rhythmicity Treatment Findings

The results indicated that the IM treatment produced significant improvements in the timing and rhythmicity of elementary school students (as measured by the IM measurement system). The students in the IM treatment group, when compared to the control group, demonstrated statistically significant improvements, close to a two standard deviation increase in measured timing and rhythmicity scores.

IM treatment transfer effects were evaluated vis-à-vis pre-/posttest changes on standardized measures of reading achievement. The reading-dependent variables sampled four of the five reading skills identified as critical for early reading success by the National Reading Panel (2000). The

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[2] We know of no formula for calculating Hedges' g for overall MANOVA results. Therefore, partial η^2 is reported for MANOVA results and both η^2 and g are reported for the univariate follow-up tests.

reading-dependent variables included standardized measures of phonics, phonological awareness, reading fluency, and comprehension. The fifth key reading skill, vocabulary, was not measured.

Before discussing the IM academic transfer effect findings, it is important to note this intervention did *not* include instruction or training of any kind in phonics, phonological awareness, and/or reading—this was *not* an *academic* intervention. The IM intervention is designed to improve participants' timing and rhythmicity through beeps, tones, tapping, and clapping. In other words, it would not be expected that participants in an intervention designed to improve timing and rhythmicity would demonstrate changes in reading achievement. Furthermore, the experimental IM treatment lasted approximately 3–4 weeks. Developmental *growth* curves based on nationally standardized reading tests (McGrew & Woodcock, 2001) suggest that similarly aged students (8.2 years) typically demonstrate little academic growth (as reflected by norm-referenced tests) over a 3–4-week period.

Reading Achievement Findings

Analysis of the individual reading tests indicated that the IM intervention produced significant transfer effects in phonics, phonological awareness, and reading fluency. Students in the IM experimental group demonstrated statistically significant improvement in their ability to *fluently* recognize familiar words within a *limited timeframe* (TOWRE test). In contrast, no significant treatment effect was demonstrated on an *untimed* word recognition measure (WJ-III LW-ID test). It is important to note that the primary difference between the TOWRE and WJ-III LW-ID tests is that of a *rate fluency* (TOWRE) versus *level* (WJ-III LW-ID) distinction. *Rate fluency* refers to the time taken to work from the beginning of a test to the end of a test. *Level* refers to the difficulty of an item or task (see Carroll, 1993).

Within the context of a rate-fluency/level-ability distinction, the current results suggest the hypothesis that although students did not *learn* to recognize more familiar words in isolation (i.e., their absolute word recognition *level* did not increase), they were able to recognize the words they previously *knew* faster (i.e., the fluency of their level of word recognition skills was improved). It appears that SMT-based IM treatments may demonstrate transfer effects on reading fluency/efficiency of existing word recognition skills, but not increase the overall level of word recognition skills in a student's repertoire.

The IM treatment group also demonstrated statistically significant pre- to posttest improvement accounting for 8.9% of the variance on an equally weighted multivariate reading composite measure (TOWRE and TSWRF). More impressive, however, was the posttest improvement accounting for 17% of the variance on a multivariate composite score that included the CTOPP tests Digit Naming, Letter Naming, Segmenting Nonwords, and Blending Nonwords and accounted for 9.9% of the variance on the CTOPP rapid automatized naming (RAN) test Letter Naming.

An alternative way to examine effect size is Hedges *g* (Howell, 2002). This statistic may be used to explain effect size as a percentage of growth, using a normal curve. Applying Hedge's *g* to the current results, the experimental group experienced a 20% growth on the CTOPP's RAN Letter Naming test and an 18% growth on the TOWER's Sight Word Efficiency. These growth rates compare favorably to the 15% growth identified in a meta-analysis of phonics instruction verses whole-word instruction conducted by the National Reading Panel's Committee on the Prevention of Reading Difficulties in Young Children (National Reading Panel, 2000).

The pre- to posttest reading achievement results suggest that improvements in timing and rhythmicity were associated with statistically significant improvements in three of the five major areas of measured reading: phonics, phonological awareness, and fluency. Yet, the results are not conclusive and must be moderated with a number of cautions. First, the experimental group did not demonstrate statistically significant increases on all the TOWRE's subtests. Second, although a significant improvement was observed on the CTOPP Letter Naming test, participants' performance on a similar test (Digit Naming) was not statistically significant. The key difference between the two tests is that the Letter Naming Test uses 26 letter stimuli, whereas the Digit Naming test's stimuli consist of 9 single-digit numbers. Third, on another measure of fluency (viz., WJ-III Reading Fluency) there was no statistically significant treatment effect. The lack of a significant effect for WJ-III Reading Fluency is at variance from a previous study involving high school students, wherein the experimental group demonstrated a statistically significant, 1-year grade level, improvement on the WJ-III Reading Fluency test (Taub, McGrew, & Lazarus, 2007).

Collectively, the current reading results suggest that students in the experimental IM treatment group demonstrated statistically significant improvements on more *fundamental* early reading skills (i.e., phonics and phonological awareness) and in their speed of processing basic lexical information (e.g., RAN for letters). However, with the exception of fluency of word recognition (i.e., Sight Word Efficiency test), students in the experimental group did not demonstrate statistically significant improvements at the single-word level.

Possible Causal Explanations: A Proposed Explanatory Framework and Preliminary Hypotheses

Previous IM intervention research reported statistically significant improvements in high schools students' performance on measures of reading recognition and reading fluency compared to a nontreatment control group (Taub, McGrew, & Lazarus, 2007). Similarly, IM-treated students with ADHD were reported to demonstrate statistically significant improvements in attention, reading, and language processing (Shaffer et al., 2001). This small collection of academically related studies, investigating direct reading achievement indicators and behaviors that exert an indirect causal influence on achievement (i.e., attention and concentration), are intriguing and suggest the need to focus efforts on understanding *why* improvements in timing and rhythmicity (via SMT interventions) display such far-point transfer effects.

In an effort to jump start efforts directed at understanding the underlying SMT–academic causal mechanisms, it is proposed that SMT-based research needs to be placed in a theoretically sound and empirically based research/conceptual framework. Furthermore, it is argued that the observed positive cross-domain or domain-general effect of SMT-based interventions result from improvements/changes within a domain-general cognitive mechanism (or a small number of domain-general mechanisms). Based on a review of relevant mental interval timekeeping literature, the following preliminary hypotheses are offered.

Master Internal Clock Based on Scalar Timing Theory

To deal with time, organisms (animal and human) have developed multiple timing systems that are active in more than 10 orders of magnitude with various degrees of precision (Buhusi & Meck, 2005). According to Buhusi and Meck, humans have developed three general classes of timing systems (circadian, interval, and millisecond timing), each associated with different behaviors and brain structures/mechanisms. The millisecond timing system, which is involved in a number of classes of human behavior (e.g., speech, music, motor control) and that primarily involves the brain structures of the cerebellum, basal ganglia, and the dorsolateral prefrontal cortex (Buhusi & Meck, 2005; Lewis & Miall, 2006), is most relevant for understanding SMT-based interventions.

Pacemaker-accumulator model. Human behavior based on the perception and timing in the range of seconds to minutes has traditionally been explained by the predominant model of interval timekeeping, namely, the *pacemaker–accumulator model* (PAM). The PAM, which is based on the *scalar expectancy or timing theory* (Church, 1984; Gibbon, Church, & Meck, 1984; Meck, 1983), "is relatively straightforward, and provides powerful explanations of both behavioral and physiological data" (Buhusi & Meck, 2005, p. 755).

Briefly, the PAM model implicates the processing of temporal information via three synchronized *modular information processing systems* (see Buhusi & Meck, 2005). The *clock* system consists of a dopaminergic *pacemaker* that regularly generates or emits neural ticks or pulses that are transferred (via a *gaiting* switch) to the *accumulator*, which accumulates ticks/pulses (neural counting) that correspond to a specific time interval. The raw representation of the stimulus duration in the accumulator is then transferred to working memory, a component of the PAM *memory* system. The contents of working memory are then compared against a *reference standard* in the long-term (reference) memory, the second component of the PAM memory system. Finally, the *decision* level of the PAM is conceptualized to consist of a *comparator* that determines an appropriate response based on a decision rule that involves a comparison between the interval duration value present in working memory and the corresponding duration value in reference memory. In other words, a comparison is made between the contents of reference memory (the standard) and working memory (viz., are they "close?").

Given evidence that supports a domain-general master internal clock central to many complex human behaviors (see Buhusi & Meck, 2005; Lewis & Miall, 2006), it is suggested that the *master internal clock* may be the mechanism that mediates SMT performance and intervention effects. It is hypothesized that SMT training improves human performance across a number of domains (e.g., reading and ADHD) via an increase in the *clock speed* of the master internal clock.

It is beyond the scope of the current study to describe the specific hypothesized brain mechanisms that produce a higher *clock speed* for the internal master clock. What is important to note in the current context is that mental interval timekeeping and temporal processing research has suggested that a *higher mental clock rate* enables individuals to perform specific sequences of mental operations faster and reduces the probability of interfering incidents (i.e., less disinhibition). These two conditions produce superior performance on cognitive tasks as well as more efficient basic information processing skills (Rammsayer & Brandler, in press).

The Master Mental Clock and Cognitive/Neuropsychological Constructs

The major components of PAM-based mental interval timekeeping have strong similarities to a number of domain-general cognitive mechanisms featured in contemporary cognitive information processing and/or neuropsychological research. Working memory, which is pivitol to PAM, is a central concept in major models of information processing. In addition, the PAM long-term (Buhusi & Meck, 2005) memory likely invokes early stages of memory consolidation in long-term memory or storage, another major component of information processing models of cognition. Furthermore, the *if-then* decision-making function of the PAM *comparator* is a function typically associated with skills involved with executive functioning (e.g., monitor, evaluate, change). Finally, research has implicated the important role of *attention* during the cognitively controlled portions of interval timing (Buhusi & Meck, 2005). Therefore, it is hypothesized that a conceptual cross-walk between the major components of the PAM master internal clock and contemporary cognitive information processing theories suggests that SMT performance and SMT transfer effects result in an increased efficiency in the functioning of the domain-general cognitive information processing mechanisms of (a) working memory, (b) executive functioning, and/or (c) controlled or executive attention.

Working Memory, Executive Functioning, and Executive Controlled Attention

Executive functioning (EF), which is also frequently called the *central executive system*, is a term used for a broad construct that represents a cluster of skills necessary for efficient and successful goal-directed behavior (Welsh, 2001). The EF constructs of planning, monitoring, inhibituation, and attention/concentration, elicit a range of basic cognitive processes (e.g., attention, perception, language, and memory) that are coordinated for a very specific purpose: subserving goal-directed behavior.

EF processes are believed to work in symphony to facilitate goal-directed task completion. Timing and processes related to mental timing are believed to be a component of executive function (Welsh, 2001), as is the utilization of executive functions during reading performance (Bull & Scerif, 2001). Because EF is an integration of a constellation of abilities necessary for the planning, self-monitoring/regulating, and evaluation of successful task completion, the area of self-regulated learning has received considerable attention with regard to a variety of cognitive activities (e.g., meta-cognition, pre-attentive processes, sluggish attentional shifting, specific strategy selection and implementation, inhibition, multitasking activities, task switching, maintenance of information under conditions of interference, and resistance to interference; Bull & Scerif, 2001; Borkowski, Carr, & Pressley, 1987; Kane, Bleckley, & Conway, 2001). The central role of EF in the enhancement of selective or controlled attention, the ability to switch between plans and strategies, and the inhibition of task-irrelevant information (intrusions) in working memory (Engle, Tuholski, Laughlin, & Conway, 1999; Passolunghi & Siegel, 2004) is consistent with theoretical and descriptive interpretations of SMT and interval time tracking models.

It is proposed that the *executive controlled attention model* of working memory (Engle, Kane, & Tuholski, 1999; Kane, Bleckley, Conway & Engle, 2001), which invokes the EF system, should be entertained as a potentially useful initial model to explain the domain-general effects of SMT-based interventions. Briefly, the executive controlled attention working memory model hypothesizes that individual differences in task performance are related to EF *controlled attention*. This means that individuals with higher working memory demonstrate better (or more efficient) use of attentional resources and are more able to resist interference during the encoding and retrieval processes than individuals with lower working memory. It is our hypothesis that SMT training does not improve working memory by increasing capacity, rather that SMT training may result in more *efficient* use of an individual's working memory system. The central role that the *general* capability to *efficiently process* information plays in task performance is consistent with a general mechanism explanation for the diversity of across-domain effects of SMT training. Central to the controlled attention working memory model is the role of EF. The alternative working memory view, which argues more for emphasis on underlying *modality-specific* working memory subprocesses (Palladino, Mammarella, & Vecchi, 2003), in contrast to resource-sharing models, presents a much more complex alternative model by which to explain positive SMT training effects across such diverse performance tasks (although it would be inappropriate to completely discard it as a possible explanation at this time). The search for a domain-general mechanism to explain SMT generalized training effects, such as the controlled attention working memory model, represents a more parsimonious approach that is believed to be preferred as formative attempts are made to describe and explain SMT training effects.

Finally, the recent suggestion that *g* or general intelligence (the most enduring and robust domain-general cognitive mechanism in the history of the psychometric study of intelligence) may be more a function of *temporal processing* and not necessarily reaction time (as measured by the traditional Hick paradigm; Rammsayer & Brandler, in press) suggests that mental interval timekeeping models (e.g, PAM) may describe and explain a primary elementary cognitive mechanism involved in most all complex human behavior. If *temporal g* exists, then the across-domain positive treatment effects of SMT training might be explained as the improvement of general neural efficiency via greater resolution of the temporal *g* internal clock.

SUMMARY

This study investigated the effect of a SMT training intervention on elementary-school-age students' reading achievement. The observance of statistically significant improvements in the experimental group's performance on posttest measures of reading, when compared to the control group, is impressive given the nature of the *nonacademic* intervention. Yet, the results are not conclusive and are inconsistent in some cases. For example, the elementary school students scored significantly better on a timed single word recognition test, yet, there was no significant between-group difference on a measure that required reading short simple sentences (WJ-III Reading Fluency). Also, previous research with high school students reported a statistically significant relationship between SMT improvements and reading fluency. One possible explanation for the divergent developmental intervention effect findings is that elementary school students are *learning how to read*, whereas high school students are *reading to learn*. In other words, high school students have mastered or automatized their reading skills, whereas the elementary school students are learning how to read.

Nevertheless, the automatization of critical early reading skills (viz., phonics, phonological awareness skills, and RAN performance), which emerge primarily during the early school grades, are the specific areas where the elementary-aged experimental participants demonstrated the most significant improvements in the current study. It is also possible that studies (the current study, inclusive) that have reported improvements in timing and rhythmicity over short periods (3–4 weeks) may only demonstrate significant effects on the processing of overlearned (automatized) information, in contrast to the more deliberate or controlled learning of new information. This may also explain why golfers, who presumably have overlearned their golf swing, become more accurate with improvements in timing/rhythmicity.

It is believed that subcomponents of the constellation of executive functioning are effected by SMT interventions. Because of the cross-domain influence of working memory on task completion, the executive controlled attention model of working memory, which is heavily dependent on the executive functioning system, was hypothesized as a potentially useful model for conceptualizing SMT research and for interpreting research findings. The executive controlled aspect of working memory was suggested as a possible general cognitive mechanism responsible for the observed positive influence of SMT training across such diverse domains as academics, athletics, and attention/concentration.

Limitations and Future Research

This study may be limited by participants' parents self-selection to have their child attend a public charter school receiving Title 1 funding. Participants may also have been more similar on several demographic variables (e.g., ethnicity, socioeconomic status) than would be found in public school settings.

Because of the relatively small sample size it was not possible to make a distinction between students receiving special education services and those who were not. It is recommended that future studies examine this difference as well as investigate differential SMT training effects with regular education students experiencing academic difficulties. It is also recommended that future studies investigate SMT training effects with students who were unable to graduate or progress to the next grade level because they did not reach a threshold score on high-stakes tests of academic achievement.

Finally, in the present study posttests were administered immediately after SMT training; therefore the stability of the observed positive effects of SMT training on the academic achievement dependent variables is not known. It is recommended that future studies investigate the consistency of the observed positive effects of SMT training on academic achievement over an extended period.

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Improvements in Interval Time Tracking and Effects on Reading Achievement

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Abstract

This paper examines the effect of improvements in timing/rhythmicity on students' reading achievement. A total of 86 participants, attending a Title 1 elementary school completed pre- and post-test measures of reading achievement from the Woodcock-Johnson III Tests of Achievement (Woodcock, McGrew, Mather, 2001), Comprehensive Test of Phonological Processing (Torgesen, Wagner, & Rashotte, 1999a), Test of Word Reading Efficiency (Torgesen, Wagner, & Rashotte, 1999b), and Test of Silent Word Reading Fluency (Mather, Hamil, Allen, & Roberts, 2004). Students in the experimental group participated in a 4 week intervention designed to improve their timing/rhythmicity by reducing the latency in their response to a synchronized metronome beat, referred to as a synchronized metronome tapping (SMT) intervention. The intervention required, on average, 15 daily 50 minute sessions, The results from this *non-academic* intervention indicate the experimental group's post-test scores on select measures of reading were significantly higher than the non-treatment control group's scores at the end of 4 weeks. This paper provides a brief overview of domain-general cognitive abilities believed effected by SMT interventions and provides a preliminary hypothesis to explain how a non-academic intervention designed to improve timing/rhythmicity can demonstrate a statistically significant effect on students' reading achievement scores.

Improvements in Interval Time Tracking and Effects on Reading Achievement

Many jobs and tasks require a critical sense of knowing how much time events or activities should take or how to internally judge intervals of time. This mental operation is often referred to as *mental time keeping or interval timing*. For example, proficient short-order cooks are master mental time/interval timers as they must prepare several different foods concurrently, each of which typically requires a different cooking time interval. To successfully complete each food dish at the same time, short-order cooks rely on their internal clock and a memory of how long it takes to cook a cheeseburger, patty melt, or omelet. Other examples of internally judging intervals of time include walking into a kitchen just when the coffee is finished brewing, noticing when it takes an extra second or two for a call to get connected, or suddenly becoming inpatient when waiting in line (because it seems like the line is not moving *fast enough*). In all of these examples our internal time keeper tacitly is comparing our memory for the typical duration of an event to the period of time that has actually elapsed.

Cognitive psychology's interest in mental time-keeping has spanned decades. For example, cognitive differential psychologists first reported the identification of a *temporal tracking* capability in 1980 (Stankov, Horn & Roy, 1980). Temporal tracking was identified as being found in various auditorily presented tasks which involved the mental counting or rearrangement of temporal sequential events (e.g., reorder a set of musical tones) (Carroll, 1993).

Mental interval timing research and models

More recently, researchers in cognitive psychology studied the phenomenon of *interval timing* through the use of research paradigms that require individuals to maintain synchrony with auditory tones (e.g., from a metronome), also known as Synchronized Metronome Tapping (SMT). Tapping in synchrony with a metronome requires an individual to correct for asynchronies in their response the reoccurring beat. This is thought to be accomplished through an internal adjustment to the phase of one's underlying timekeeper (Vorberg & Fuchs, 2004). This error correction is triggered when temporal deviations from the underlying metronome-based interval (e.g., via performance feedback) occurs. This process is referred to as an *automatic phase adjustment*. The allocation of *attentional resources* and the minimization of stimuli that may divert cognitive processing resources away from timing have been hypothesized to play a significant role in metronome-based synchronization of rhythmic movements (Brown & Bennett, 2005). In addition, the quickness and efficiency of the phase adjustment mechanism is believed to eliminate the necessity for long-term memory or learning (Vorberg & Fuchs, 2004).

The study of the cognitive processes involved in the temporal control of simple rhythmic movements has been dominated by both linear and stochastic *mental time/interval-keeper models* (Engbert, et al., 1997). Alternative models have focused on 1) dynamic qualitative frameworks (i.e., *nonlinear oscillator models* Engbert et al., 1997) or 2) *sensory-motor theories of temporal representation* (i.e., temporal tracking as a form of sensory-guided action that uses the sensory-memory image to drive a movement via a control mechanism) (McAngus, 2005). Engbert et al. (1997) suggested that plausible models of rhythmic motor control may be derived by combining the linear (i.e., to explain the timing processes) and nonlinear or dynamic (to explain nonlinear feedback control and adjustment) mental time-keeper models. Thus, explanations of synchronized tapping behavior may require models that reflect the interaction of both linear (stochastic) and dynamic (oscillator) mental time-keeper models.

Although the advancement of theoretical understanding of the underlying cognitive mechanisms of mental time-keeping is a laudatory scientific goal, recent mental time-keeper research studies have suggested a number of potentially useful applied applications across a diverse array of performance domains. These potential applications include, but are not limited to, the following examples:

- *Neurological disorders*. The observation of small mean negative synchronization errors during normal temporal tracking of a regular auditory metronome has been the focus of recent diagnostic research (O'Byle, 1997). The finding that individuals with Parkinson's disease (PD) tend to tap significantly *further in advance* of the beat than normal neurologically-intact controls (O'Boyle et al., 1995; O'Boyle, 1997) suggests potential applied diagnostic tools for PD or other neurologically based disorders.
- *Children with reading disabilities/dyslexia*. Children identified as dyslexic have demonstrated deficiencies in their timing and rhythm. Specifically, individuals with dyslexia individuals were reported to respond with a wider range of times on either side of a metronome beat compared to normally reading students. A student's mean latency in response to a metronome beat

may also predict performance on standardized reading tests (Waber et al., 2003; Wolff, 2002).

IM Interventions to Improve Human Performance

Several SMT studies have reported that a rhythmic synchronization metronome-based assessment and intervention technique, (hereafter referred to as the Interactive Metronome [IM] method), improved performance across several domains, including golf, tennis, reading, and attention (for individuals with ADHD). IM combines the concept of a musical metronome with a computer-based program that accurately measures and facilitates the improvement of an individual's rhythm and timing.

IM training involves reducing the mean negative synchronization error during normal tracking of a regularly occurring metronome beat. Participants receive feedback through an auditory guidance system as they progress through interactive exercises. Although feedback is provided through both visual and auditory stimuli, the auditory feedback guidance system is the primary feedback method. The auditory feedback system provides tonal stimuli that indicate whether the participant responded *prior to, at, or past* the regularly occurring auditory metronome beat. The accuracy of participants' expectancy response to the metronome beat is provided in milliseconds, with different tones indicating *far from, close to*, or *at* the metronome beat. A visual reading of millisecond latency is also presented on a computer screen.

The purpose of IM training is to improve participants' timing/rhythmicity by reducing the latency between the onset of the metronome beat and participants' expectancy response to the beat. After about three to four weeks of training, or 15-18 one-hour sessions, participants are typically able to respond to within approximately 15 milliseconds on either side of the beat. This compares to the average 80-100 millisecond latency response prior to training. At the completion of training, participants typically have engaged in approximately 25,000 motoric repetitions. These movements are the physical indication of one’s expectancy of the onset of the metronome beat. The various movements incorporated in training include clapping hand-to-hand with a sensor on one palm, taping the palm sensor lightly on the thigh, and taping floor sensors with either the toe or back of the foot. Select intervention/training examples include:

- *Sports: Tennis performance*. A 10-week intervention study designed to improve the rhythmic accuracy and maintenance of rhythm tempos significantly improved the tennis performance of 8-10 year olds (Zachopoulou, Mantis & Psalti, In Press). This study demonstrated that the development of certain perceptual-motor abilities may be influenced by rhythmic ability, which in turn requires an accurate knowledge of time. The relationship between rhythmic ability and skilled motor performance is most important when the coordination of abilities is in the formative stage of development.

  Sports: Golf performance. As a result of 10 hours of IM training, where experimental subjects were trained to tap their hands and feet in synchrony with target sounds,the experimental participants significantly improved the accuracy of their golf swing relative to control participants (Libkuman & Otani, 2002).

- *Children with ADHD*. Shaffer et al. (2001) reported that pre-diagnosed boys with attention-deficit/hyperactivity disorder (ADHD) who received 15 hours of IM training exercises demonstrated improved performance, when compared to two ADHD control groups, in attention, motor control, language processing, reading, and parent report of regulation of aggressive behavior.

- *Students' Reading*. Recently, a statistically significant IM effect on reading achievement was reported. Lazarus and Taub (2005) administered subtests from the Woodcock-Johnson Tests of Achievement III (Woodcock, Mather, & McGrew, 2001) as pre- and post-test measures of reading achievement to over 250 high school-aged participants. Each IM group-based treatment session lasted for approximately 45 minutes each day, four times a week, for three weeks. When compared to the control group, the experimental group demonstrated statistically significant improvements on the post-test measures of broad reading and reading fluency.

Collectively, results form initial SMT-based intervention studies suggest that significant *domain-specific* SMT performance improvement is associated with significant *domain general* improvements in human performance in the areas of sports, academics, and attention/concentration. How can rhythmic SMT-based interventions result in improved performance across such diverse domains of human performance as ADHD, golf, reading, and tennis?

Purpose

Although hypothesized domain-specific cognitive mechanisms are possible, the domain general or cross-domain SMT training effect is intriguing and argues for first investigating potential across-domain *general* cognitive mechanisms and for replication of prior studies. Given this assumption, the purpose of this paper is two-fold.

The first purpose is to replicate earlier studies by examining the impact of improvements in timing/rhythmicity on students' reading achievement. The second purpose is to offer preliminary hypotheses that will contribute to a better understanding of the cognitive mechanisms that may explain SMT treatment effects across such diverse human performance domains

Method

Participants

Study participants included 86 students attending a Title 1 community school located in Central Florida. The participants ranged from first- to fourth-grade. There were 16 first-, 36 second-, 23 third-, and 11 fourth-grade students in the study. A total of 37 participants were male and 48 were female. Participants' ages ranged from 7 years-old to 10 years-old with a mean of 8.15 years (*SD*=1.0).

Instruments

Several tests were administered to evaluate the effects of IM training on participants' academic achievement and attention/concentration. A brief description of each test is presented in Table 1.

Procedure

All students completed a pre-test battery of psychoeducational instruments (see Table 1). After completing the pre-tests, students were randomly assigned to either an experimental or control group. The experimental group participated in the IM intervention, at their school, during regular school hours. While the experimental group was participating in the IM intervention, the control group engaged in their regular classroom activities. Students in the experimental group were divided into four groups, one for each grade-level. Two certified master trainers worked separately with each of the four grade-level groups each day. The groups ranged in size from seven to twelve participants. The students in the experimental group participated in an average of 18 sessions, each lasting approximately 50 minutes. Upon completion of the IM intervention, post-tests were administered to all participants. The same tests were used during the pre- and post-test administrations.

Participants completed both individually and group administered tests. Table 2 identifies which tests were administered either individually and/or in groups. During the individual assessment each evaluator worked with a student one-on-one. The individual assessment took approximately 35 minutes to complete. Group administrations were conducted in the students' own classroom and participants from the experimental and control group completed all tests together as classmates. Students who were unable to participate and/or who were absent on the day of the group assessments, completed the group tests either individually or with other non-classmate students. During all test administrations the test proctors and administrators were unaware of each student's group assignment. A lead test administrator directed all group assessments. The administrator followed the standardized instructions included in each test's manual. For some tests, minor modifications were made in standardized administration procedures to facilitate group administration of the test. Several steps were followed to ensure that standardized test administration procedures were followed as closely as possible. These steps included 1) a doctoral level proctor was present during all group administrations, 2) a minimum of one proctor to every four students was maintained during all group administrations, 3) all test proctors were graduate-level school psychology students who either completed or were near completion of their second psychoeducational assessment course, and 4) if a student did not accurately completed a sample item, the group administration was stopped and the proctor followed standardized administration procedures to ensure adequate completion of the sample item. All students progressed through the group test administration at the same time.

Results

Unless otherwise noted, all analyses controlled for pre-test scores using the same measure as the post-test (through Analysis of Covariance). For analyses that did not use developmentally-based scores, such as raw or growth scores, age was also controlled in the analyses by entering age as a covariate in the ANCOVA. Given the prediction that statistically significant differences would favor the experimental group, one-tailed tests ($\alpha = .05$) were used to evaluate statistical significance.

Effects on Timing/Rhythm

The initial analysis examined the effect of IM training on timing and rhythm as measured by the IM assessment system. The IM treatment had a statistically significant effect on post-test timing and rhythm scores, with pre-test score controlled (F [1, 76] = 107.376, $p < .001$). Furthermore, the treatment had a large effect on the post-test outcome ($\eta^2 = .586$, $g = 1.974$). IM training accounted for more than 50% of the variance in IM post-test scores, and resulted in close to a two standard deviation increase in those scores (with IM pretest scores controlled).

It seems likely that IM training should be more effective for children who initially showed poor performance (high scores) on the measure of timing and rhythm. Sequential multiple regression was used to evaluate the possibility of a statistically significant interaction between the pre-test and treatment. The IM post-test was regressed on the centered IM pre-test and group membership in one block, with the centered pre-test by group cross-product entered in a second block. As summarized in Table 3, the addition of the cross-product to the regression resulted in a statistically significant increase in R^2, indicating that that the pretest-by-treatment group interaction was statistically significant. The nature of the interaction is demonstrated in Figure 1, which shows separate regression lines for the post-test on the pre-test, by treatment group. The lines show that the experimental group performed better on the post-test than did the control group, but that training was indeed most effective for participants with poor initial timing/rhythmicity.

Reading

Multivariate Analysis of Covariance (MANCOVA) was used to test the effect of IM training on the four measures of reading skill from the WJ III (Letter-Word Identification, Reading Fluency, Passage Comprehension, and Word Attack). Pre-test scores on these measures were used as covariates. As recommended by the test authors, W-scores (a continuous, equal interval growth scale score) were used for these analyses. The results of this analysis (and subsequent MANCOVA results) are summarized in Table 4. As shown in the table, the IM training did not demonstrate a statistically significant effect on reading achievement as measured by the WJ III achievement tests.

Table 4 also shows the effects of IM training on measures of reading efficiency, Test of Word Reading Efficiency (TOWRE; Sight Word, TOWRE Phonemic Decoding) and fluency Test of Silent Word Reading Fluency (TSWRF). For this set of analyses, standard scores (*M* =100; *SD* =15) were used as both pre- and post-test scores; pre-test scores and age were the controlled variables. As shown in the Table, the IM training produced a statistically significant effect on measures of reading efficiency and fluency. Participants who received IM training scored at a higher-level on the multivariate dependent variable. The IM treatment accounted for 8.9% of the variance in reading efficiency and fluency, a small effect size (Keith, 2006, p. 508). Follow-up tests (univariate ANCOVAs) revealed a statistically significant effect for the TOWRE Sight Word Efficiency measure (F [1, 76] = 5.881, p = .009, η^2 = .072, g = .481[1]), but not for the other measures.

Table 4 also shows the results of analyses of the IM effects on phonological processing skills as measured by the Comprehensive Test of Phonological Processing (CTOPP; digit naming, letter naming, segmenting, and blending). Participants who received IM training demonstrated statistically significantly higher CTOPP scores, and the IM treatment accounted for 17% of the variance in CTOPP scores, a moderate effect. Univariate follow-up statistical analyses revealed statistically significant effects on the letter naming subtest (F [1, 79] = 8.680, p = .002, η^2 = .099, g = .536) but not for the other components of the CTOPP.

Discussion

The current study employed a pre- post-test evaluation design to investigate the effect of a specific synchronized metronome tapping (SMT) intervention (viz., Interactive Metronome; IM) on reading and mathematics performance in a sample of 86 first-, second-, third- or fourth-grade students in an inner-city charter school. Participants were

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[1] We know of no formula for calculating Hedges' g for overall MANOVA results. Therefore, partial η^2 is reported for MANOVA results and both η^2 and g are reported for the univariate follow-up tests.

randomly assigned to either an experimental (IM) or control group. The experimental group participated in a three-to-four week IM intervention designed to improve their timing/rhythmicity. The control group remained in their traditional classroom during each of the approximately 50 minute daily intervention sessions. All participants completed the same reading pre- and post-test measures which were then analyzed via statistical methods that controlled for initial pre-test performance levels and age (ANOCOVA; MANOVA).

Timing and rhythmicity treatment findings

The results indicated that the IM treatment produced significant improvements in the timing and rhythmicity of elementary school students (as measured by the IM measurement system). The students in the IM treatment group, when compared to the control group, demonstrated statistically significant improvements, close to a two standard deviation increase in measured timing and rhythmicity scores.

IM treatment transfer effects were evaluated vis-à-vis pre-/post-test changes on standardized measures of reading achievement. The reading dependent variables sampled four of the five reading skills identified as critical for early reading success by the National Reading Panel (National Reading Panel (2000). The reading dependent variables included standardized measures of phonics, phonological awareness, reading fluency and comprehension. The fifth key reading skill, vocabulary, was not measured.

Before discussing the IM academic transfer effect findings, it is important to note this intervention did *not* include instruction or training of any kind in phonics, phonological awareness, and/or reading or mathematics—this was *not* an *academic* intervention. The IM intervention is designed to improve participants' timing and rhythmicity through beeps, tones, tapping, and clapping. In other words, it would not be expected that participants in an intervention designed to improve timing and rhythmicity would demonstrate changes in reading achievement. Furthermore, the experimental IM-treatment lasted approximately three-to-four weeks. Developmental *growth* curves based on nationally standardized reading tests (McGrew & Woodcock, 2001) suggest that similarly aged students (8.2 years) typically demonstrate little academic growth (as reflected by norm-referenced tests) over a three-to-four week period.

Reading achievement findings

Analysis of the individual reading tests indicated that the IM intervention produced significant transfer effects in phonics, phonological awareness, and reading fluency. Students in the IM experimental group demonstrated statistically significant improvement in their ability to *fluently* recognize familiar words within a *limited timeframe* (TOWRE test). In contrast, no significant treatment effected was demonstrated on an *untimed* word recognition measure (WJ III LW-ID test). It is important to note that the primary difference between the TOWRE and WJ III LW-ID tests is that of a *rate-fluency* (TOWRE) versus *level* (WJ III LW-ID) distinction. Rate-fluency refers to the time taken to work from the beginning of a test to the end of a test. Level refers to the difficulty of an item or task (see Carroll, 1993). Within the context of a rate-fluency/level ability distinction, the current results suggest the hypothesis that although students did not *learn* to recognize more familiar words in isolation (i.e., their absolute word recognition *level* did not increase), they were able to recognize the words they previously *knew* faster (i.e., the fluency of their level of word recognition skills was improved). It appears that SMT-based IM treatments may demonstrate transfer effects on reading fluency/efficiency of existing word recognition skills, but not increase the overall level of word recognition skills in a student's repertoire.

The IM treatment group also demonstrated statistically significant pre-to-post-test improvement accounting for 8.9% of the variance on an equally weighted multivariate reading composite measure (TOWRE and TSWRF). More impressive, however, was the post-test improvement accounting for 17% of the variance on a multivariate composite score that included the CTOPP tests: Digit Naming, Letter Naming, Segmenting Nonwords, and Blending Nonwords and accounted for 9.9% of the variance on the CTOPP RAN test, Letter Naming.

An alternative way to examine effect size is through Hedges *g* (Howell, 2002). This statistic may be used to explain effect size as a percentage of growth, using a normal curve. Using this conversion of Hedge's *g* for the current results, we find that the experimental group experienced a 20% growth on the CTOPP's RAN Letter Naming test and 18% growth on the TOWER's Sight Word Efficiency. These growth rates compare favorably to the 15% growth identified in a meta-analysis of phonics instruction conducted by the National Reading Panel's Committee on the Prevention of Reading Difficulties in Young Children (National Reading Panel, 2000).

The pre-to-post-test reading achievement results suggest that improvements in timing and rhythmicity were associated with statistically significant improvements in three of the five major areas of measured reading: phonics, phonological awareness, and fluency. Yet, the results are not conclusive and must be moderated with a number of cautions. First, the experimental group did not demonstrate statistically significant increases on all the TOWRE's subtests. Second, although a significant improvement was observed on the CTOPP Letter Naming test, participants' performance on a similar test (Digit Naming) was not statistically significant. The key difference between the two tests is the Letter Naming Test uses letter stimuli, whereas the Digit Naming test's stimuli consist of single-digit numbers. Third, on another measure of fluency (viz., WJ III Reading Fluency) there was no statistically significant treatment effect. The lack of a significant effect for WJ III Reading Fluency is at variance from a previous study involving high school students, where the experimental group demonstrated a statistically significant, one-year grade-level, improvement on the WJ III Reading Fluency test (Lazarus & Taub, 2005).

Collectively, the current reading results suggest that students in the experimental IM-treatment group demonstrated statistically significant improvements on the more *fundamental* early reading skills (i.e., phonics and phonological awareness) and in their speed of processing basic lexical information (e.g., RAN or rapid automatized naming for letters). However, at the single word level, students in the experimental group did not demonstrate statistically significant improvements, with the exception of fluency of word recognition (i.e., Sight Word Efficiency test).

Possible causal explanations: A proposed explanatory framework and preliminary hypotheses

Previous IM intervention research has reported statistically significant improvements in high schools students' performance on measures of reading recognition, reading fluency, and mathematics when compared to a non-treatment control group (Lazarus & Taub, 2005; Taub, McGrew, & Lazarus, 2005). Similarly, IM treated students with ADHD were reported to demonstrate statistically significant improvements in attention, reading, and language processing (Shaffer, et al. 2001). This small collection of academically-related studies investigating direct reading and mathematics achievement or behaviors believed to exert an indirect causal influence on achievement (i.e., attention and concentration) are intriguing and, in our opinion, suggest a need to focus efforts on developing and understanding *why* improvements in timing and rhythmicity can display such far-point transfer effects.

In an effort to "jump start" efforts directed at understanding the underlying SMT-academic causal mechanisms, we propose that SMT-based research needs to be placed in a theoretically sound and empirically based research/conceptual framework. It is our position that the SMT relevant literature would benefit from being organized within the context of an existing and empirically valid taxonomy of human cognitive abilities, as would most research that involves human cognitive ability assessment and performance.

Cattell-Horn-Carroll (CHC) Theory of Cognitive Abilities

The Cattell-Horn-Carroll (CHC) Theory of Cognitive Abilities is generally accepted as the most evidenced-based empirical taxonomy of human cognitive abilities (see overview by McGrew, 2005). Consisting of 8 to10 broad cognitive ability domains (e.g., Gf-Fluid Intelligence, Gc-Crystallized Intelligence, Gv-Visual-Spatial Processing, etc.), which in turn subsume 70+ more narrow or specialized abilities, the CHC framework is generally believed to be the best available lens from which to identify and conceptualize human cognitive abilities (McGrew, 2005), such as those involved in the diagnostic and training components of IM and other SMT methods. Using the CHC framework, we have tentatively identified a handful of broad cognitive abilities that appear relevant to understanding SMT effects. This section begins with a brief review of these abilities and concludes with the preliminary identification of a hypothesized general cognitive mechanism which may account for the across-domain treatment effects of SMT training.

Auditory Processing

Auditory processing (Ga) is the perception of auditory information (Gustafsson & Undheim, 1996) which involves a wide range of abilities necessary for discriminating patterns in sounds and musical structure. The narrow ability areas subsumed within the broad domain of auditory processing include the ability to analyze, comprehend, discriminate, manipulate, and synthesize sound patterns and group of sounds. Although tapping aspects of phonological properties, such as sounds being signaled by the acoustical/phonemic properties of speech (Ramus et al., 2000), auditory processing abilities do not require the comprehension of language (McGrew & Woodcock, 2001). More important to understanding the impact of SMT training effects is the relationship between auditory processing and timing and rhythm as exemplified in studies of tonal patterns in music, beat induction, attentional selectivity, taping in time with music, interaction between motor skills and rhythmicity, and the effect of these subdomains on measurable areas of real-world performance. Specific areas that appear to be impacted by the attending and filtering mechanisms of auditory processing include individuals' motor skill performance and academic achievement.

Broad short-term & working memory (Gsm)

The *Gsm* domain is defined as the ability to apprehend and maintain awareness of elements of information in the immediate situation (events that occurred in the last minute or so). *Gsm* is a limited-capacity/resource system that loses information quickly through the decay of memory traces, unless an individual activates other cognitive resources to maintain the information in immediate awareness. Within the broad area of Gsm, *Memory span* (MS) and *Working memory* (MW)[2] would appear to be the two narrow abilities most often associated with rhythm perception and temporal/interval time keeping.

Memory span (MS). MS, or what is commonly called short-term auditory memory, is the ability to attend to, register, and immediately recall (after only one presentation) temporally ordered elements and then reproduce the series of elements in correct order. Remembering the digits of a phone number is a common exemplar of MS. The successful processing of auditory temporal information requires individuals to maintain perceived stimuli for a certain period of time in short-term memory (MS). Thus, short-term memory span (MS) is believed to play an important role in rhythm perception and performance (Franek, in press).

Working memory. Working memory (MW) is the process of temporarily storing relevant information and performing a set of cognitive operations for problem solution. MW is often recognized as the mind's "scratchpad." This complex cognitive ability involves concomitant cognitive task and management strategies including divided or controlled attention, allocation of limited short-term memory resources, monitoring, and self-evaluation. The extant research suggests that MW, and related information

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[2] The MW abbreviation, rather than the intuitive WM abbreviation, is used to be consistent with contemporary CHC terminology where memory abilities typically start with the letter "M" (for memory) and are followed by a differentiating second letter (e.g., W = working; V = visual; A = associative, etc.). See McGrew (2005) for further discussion.

processing mechanisms (e.g., executive functions)[3], may represent a potentially important cognitive construct for understanding the diagnostic and training effects of IM training.

Researchers have typically divided MW component of information processing models into two to four subcomponents. We propose that the most important SMT-related MW subcomponents are the *phonological loop*[4] and the management of attentional resources (of the limited capacity resource-constrained MW system) by the *central executive or executive function system* (Baddeley, 2002). The *visuospatial sketchpad* has been hypothesized to be a visual analogue of the phonological loop and serves the function of integrating spatial, visual, and possibly kinesthetic information into a unified representation that may be temporarily stored and manipulated. This is in contrast to the central executive mechanism, which coordinates and manages the activities and processes involved in MW tasks, including attention resource management.

Two major theoretical approaches (*multiple-resource* and *resource-sharing*) have been postulated to explain the functioning of MW (Bayliss, Jarrold, Gunn, & Baddeley, 2003). Multiple-resource models assume that task performance is supported by a number of subsystems dedicated to specific processes or domains (Baddeley, 1986; Shah & Miyake, 1996). In contrast, resource-sharing models assume that processing and storage operations compete for a limited pool of working memory resources (Daneman &

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[3] It is important to recognize that MW is a central component of contemporary cognitive information processing (IP) models and research. In general, Kyllonen's (1996) four-source consensus IP model (Kyllonen, 1996) is a sufficient framework for this paper According to Kyllonen (1996), the four primary components or sources of IP models are procedural and declarative knowledge, processing speed (Gs), and working memory (MW). Another typical description of information processing models makes the distinction between: (1) memory systems—short-term/working and long-term memory, (2) types of knowledge-declarative and procedural, and (3) types of processing-controlled and automatic (Lohman, 2000).

[4] Often also referred to as the "articulatory loop."

Carpenter, 1980; Just & Carpenter, 1992). Mental or interval time tracking appears to share the core requirement, which is also pivotal to the construct of working memory performance, of being able to efficiently utilize and manage information within a system constrained by the amount of cognitive resources that can be manipulated at any one time. It is therefore believed that the resource-sharing MW models may offer a useful lens for understanding the effects of SMT related interventions.

Broad cognitive processing speed (Gs)

Another potentially important IM-related finding is the demonstrated link between the cognitive processing speed (Gs; including the increased fluency or automaticity of task performance with repeated practice) and MW. Gs abilities are typically defined as the ability to automatically and fluently perform relatively easy or over-learned (automatized) cognitive tasks, especially when high mental efficiency (i.e., attention and focused concentration) is required.

The influence of Gs on MW should not be underestimated. Contemporary research has suggested that Gs influences the development of MW capacity and efficiency, and thus, represents a critical causal mechanism in successful task completion across a variety of cognitive and human performance domains (Conway, Kane, & Engle, 2003; Kail, 1991; Kail & Hall, 1999; Lohman, 1989). Specifically, the more complex a task, the stronger the relationship may be between speed and working memory (Jensen, 1998). SMT tasks were previously described as being dependent on the *quickness* and *efficiency* of the phase adjustment mechanism which eliminates or reduces the need for utilization or necessity of long term memory (Vorberg & Fuchs, 2004).

Executive functioning abilities

As just described, the CHC taxonomy may provide a sound theoretical framework to begin to identify and understand the broad cognitive abilities positively effected by SMT training. Although the broad cognitive abilities of Ga, Gsm (WM), and Gs are conceptually viewed as individual cognitive constructs, they also may share variance and contribute to an important cognitive performance construct that has emerged primarily from the neuropsychological literature—executive functioning.

Executive functioning (EF), which is also frequently called the *central executive system*, is a term used for a broad construct which represents a cluster of skills necessary for efficient and successful goal directed behavior (Welsh, 2001). The EF constructs of planning, monitoring, inhibituation, and attention/concentration, elicit a range of basic cognitive processes (e.g., attention, perception, language, and memory) which are coordinated for the very specific purpose: of subserving goal-directed behavior.

EF processes are believed to work in symphony to facilitate goal-directed task completion. Timing and processes related to mental timing are believed to be a component of executive function (Welsh, 2001) as is the utilization of executive functions during mathematics and reading performance (Bull & Scerif, 2001). Since EF is an integration of a constellation of abilities necessary for the planning, self-monitoring/regulating, and evaluation of successful task completion, the area of self-regulated learning has received considerable attention with regard to a variety of cognitive activities (e.g., meta-cognition, pre-attentive processes, sluggish attentional shifting, specific strategy selection and implementation, inhibition, multitasking activities, task switching, maintenance of information under conditions of interference and resistance to interference) (Bull & Scerif, 2001; Borkowski., Carr, & Pressley, 1987; Kane, Bleckley, & Conway, 2001; Schwizer, 2001). The central role of EF in the enhancement of selective or controlled attention, the ability to switch between plans and strategies, and the inhibition of task-irrelevant information (intrusions) in working memory (Engle et al., 1999; Passolunghi & Siegel, 2004) is consistent with theoretical and descriptive interpretations of SMT and interval time tracking models.

Executive attention and the domain-general model of Working Memory (MW) functioning

Central to a primary goal of this paper is the identification of a *general* cognitive mechanism that might account for the positive impact of IM-type training across such diverse domains as sports (e.g., golf, tennis), school achievement, and behavior (e.g., ADHD). We propose that the *executive controlled attention model* of working memory (Engle, Kane, and Tuholski, 1999; Kane, Bleckley, Conway & Engle, 2001), which invokes the EF system, should be entertained as a potentially useful initial model to explain the domain-general effects of SMT-based interventions

In brief, the executive controlled attention working memory model hypothesizes that individual differences in task performance is related to EF *controlled attention.* This means that individuals with higher working memory demonstrate better (or more efficient) use of attentional resources and are more able to resist interference during the encoding and retrieval processes than lower working memory individuals. The central role that the *general capability* to maintain information, in a highly active state, in many *different contexts*, particularly under conditions of distraction or interference, plays is consistent with a general mechanism explanation for the diversity of across-domain effects of SMT training. Central to the controlled attention working memory model is the role of EF. The alternative working memory view, which argues more for emphasis on underlying *modality-specific* working memory subprocesses (Palladino, Mammarella & Vecchi, 2003), in contrast to resource sharing models, presents a much more complex alternative model by which to explain positive SMT training effects across such diverse performance tasks (although it would be inappropriate to completely discard as a possible explanation at this time). The search for a domain-general mechanism to explain SMT generalized training effects, such as the controlled attention working memory model, represents a more parsimonious approach which we believe is necessary as formative attempts are made to describe and explain SMT training effects.

Summary

This study investigated the effect of a SMT training intervention on elementary school-age students' reading and mathematics achievement. The observance of statistically significant improvements in the experimental group's performance on post-test measures of reading and mathematics, when compared to the control group, is impressive given the nature of the *non-academic* intervention. Yet, the results are not conclusive and are inconsistent in some cases. For example, the elementary school students scored significantly better on a timed single word recognition test, yet, there was no significant between-group difference on a measure that required reading short simple sentences (WJ III Reading Fluency). Also, previous research with high school students reported a statistically significant relationship between SMT improvements and reading fluency. One possible explanation for the divergent developmental intervention effect findings is that elementary school students are *learning how to read*, whereas high school students are *reading to learn.* In other words, high school students have mastered or automatized their reading skills, whereas the elementary school students are still acquiring reading skills requiring more controlled or deliberate cognitive processing.

On the other hand, the automatization of critical early reading skills (viz., phonics, phonological awareness skills, and RAN performance), which emerge primarily during the early school grades, are the specific areas where the elementary-aged experimental participants demonstrated the most significant improvements in the current study. It is also possible that studies (the current study, inclusive) that have reported improvements in timing and rhythmicity over short periods (three- to-four weeks) may only demonstrate significant effects on the processing of over-learned (automatized) information, in contrast to the more deliberate or controlled learning of new information. This may also explain why golfers, who presumable have over-learned their golf swing, become more accurate with improvements in timing/rhythmicity.

We have proposed three Cattell-Horn-Caroll (CHC) broad cognitive ability constructs that may be useful in understanding the positive effects of SMT training across a variety of human performance domains. The attending and filtering mechanisms of auditory processing (Ga) are believed to play an important role in participants' motor skill performance. Within the broad cognitive ability of short-term memory (Gsm), both memory span and working memory are hypothesized to play key roles in rhythm perception and performance and attentional resource management. The quickness and efficiency of the broad cognitive ability processing speed (Gs) is also proposed as a key component in the nonlinear phase adjustment activities involved in SMT tasks. Short-term memory, processing speed, and to a lesser extent auditory processing, are also subcomponents of the constellation of executive functioning abilities that we believe are effected by SMT intervention. Because of the cross-domain influence of working memory on task completion, the executive controlled attention model of working memory, which is heavily dependent on the executive functioning system, is hypothesized as a potentially useful model for conceptualizing SMT research and for interpreting research findings. The executive controlled aspect of working memory is suggested as a possible general cognitive mechanism responsible for the observed positive influence of SMT training across such diverse domains as academics, athletics, and attention/concentration.

Limitations and Future Research

This study may be limited by participants' parents self-selection to have their child attend an inner-city Title 1 charter school. Participants may also have been more similar on several demographic variables (e.g., ethnicity, socio-economic status) than would be found in public school settings.

Because of the relatively small sample size it was not possible to make a distinction between students receiving special education services and those who were not. It is recommended that future studies examine this difference as well as investigate differential SMT training effects with regular education students experiencing academic difficulties. It is also recommended that future studies investigate SMT training effects with students who were unable to graduate or progress to the next grade-level because they did not reach a threshold score on high-stakes tests of academic achievement.

Finally, in the present study post-tests were administered immediately after SMT training, therefore the stability of the observed positive effects of SMT training on the academic achievement dependent variables is not known. It is recommended that future studies investigate the consistency of the observed positive effects of SMT training on academic achievement over an extended period.

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Table 1. Names and Description of the Pre-Test and Post-Tests.

Test	***Description of Tests and Combinations of T***
Test of Oral Word Reading Efficiency	*Sight Word Efficiency*: A timed test of word r decoding fluency, measures the ability to recognize familiar *Phonemic Decoding Efficiency*: A timed test accurately and quickly read phonetically r *Total Word Reading Efficiency*: Combines Sig and Phonemic Decoding Efficiency
Test of Silent Word Reading Fluency	Students are presented with several rows of w difficulty. There are no spaces between th didhimgot). Students are required to draw boundaries of as many words as possible (a 3 minute time limit.
The Comprehensive Test of Phonological Processing	*Blending Nonwords*: Phonetic coding synthes an auditory processing task that is indepen knowledge (less dependent on students' e *Segmenting Nonwords*: Phonetic coding analy an auditory processing task that is indepen knowledge. *Rapid Digit Naming*: Rapid automatized nami *Rapid Letter Naming*: Rapid automatized nam *Rapid Naming Composite*: Combines Rapid D Rapid Letter Naming *Alternate Phonological Awareness Composit* Nonwords and Segmenting Nonwords
Woodcock-Johnson Tests of Achievement III	*Letter-Word Identification*: Untimed measure recognition *Passage Comprehension*: Measure of reading word knowledge *Reading Fluency*: A timed test measuring rea and rate of test taking

Table 2. Group and Individually Administered Tests

Group Administered Tests	Individually Administered Tests
Test of Silent Word Reading Fluency	Sight Word Efficiency
Reading Fluency	Phonemic Decoding Efficiency
	Blending Nonwords
	Segmenting Nonwords
	Letter-Word Identification
	Passage Comprehension

Table 3

Sequential Multiple Regression to Test whether IM Training was More Effective for those with Initially High (Poor) Scores on Timing/Rhythm

Variables Entered	ΔR^2	p
IM Pretest (centered), Treatment Group	.707	<.001
Pretest by Group Crossproduct	.082	<.001

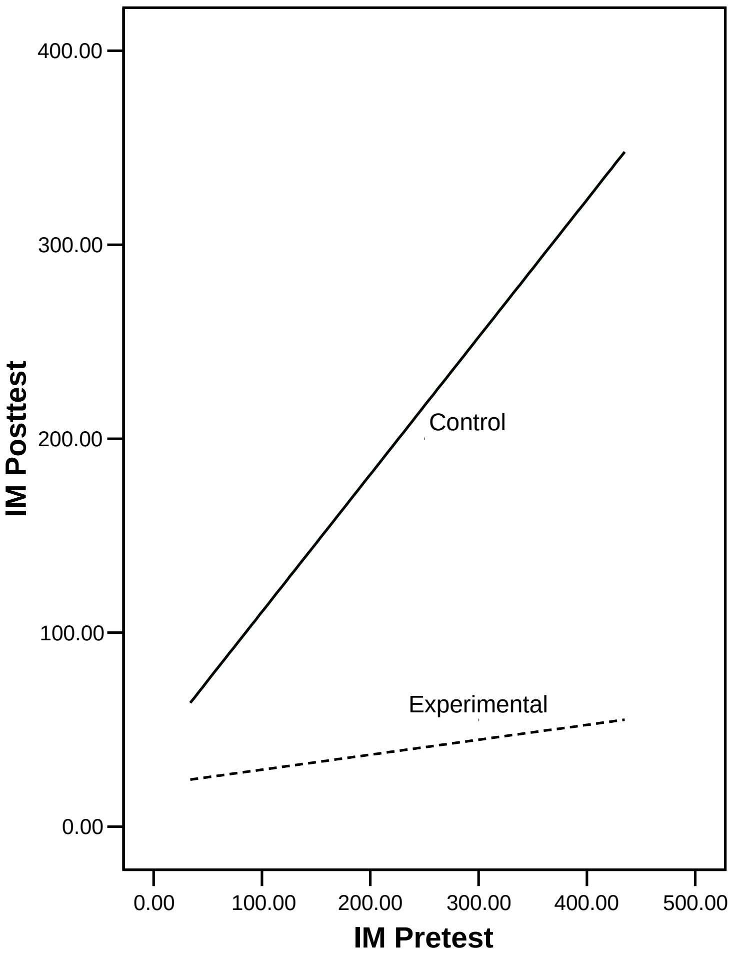
Table 4

MANCOVA Results: Effect of IM Training on Reading and Mathematics

Measures	Hotelling's Trace	*F (df)*	*p*	η^2
WJ Achievement Reading	.045	.842 (4, 75)	> .05	.043
Reading Efficiency & Fluency	.098	2.414 (3, 74)	.037	.089
CTOPP Phonological Processing	.205	3.899 (4, 76)	.003	.170

Figure Caption

Figure 1. Interaction between IM pretest and IM training. The regression lines show that IM training was most effective in improving the timing and rhymicity of children with initial poor performance (low scores represent better performance).


400.00
300.00
200.00
100.00
0.00
IM Posttest
Control
Experimental
0.00
100.00
200.00
300.00
400.00
500.00
IM Pretest

Running Head: EFFECT OF IMPROVEMENTS IN INTERVAL TIMING ON MATHEMATICS

Integrating Cattell-Horn-Carroll and Information Processing Theories to Explain the Positive Effects of Improvements in Interval Timing on Mathematics Achievement

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Abstract

This paper examines the effect of improvements in timing/rhythmicity on mathematics achievement. A total of 259 participants, attending high school, completed pre- and post-test measures of mathematics achievement from the Woodcock-Johnson III Tests of Achievement (Woodcock, McGrew, Mather, 2001). Students in the experimental group participated in a 4 week intervention designed to improve their timing/rhythmicity by reducing latency response to a synchronized metronome beat, referred to as the Interactive Metronome method. The intervention required, on average, 15 daily 45-minute sessions. The results from this *non-academic* intervention indicate the experimental group's post-test scores on the measures of mathematics were significantly higher than the non-treatment control group's scores. This paper proposes an integration of the Cattell-Horn-Carroll theory of cognitive ability and contemporary information processing theory to provide a context from which to develop preliminary hypotheses to explain how a non-academic intervention designed to improve timing/rhythmicity can demonstrate a statistically significant effect on students' mathematics achievement scores.

Integrating Cattell-Horn-Carroll and Information Processing Theories to Explain the Positive Effects of Improvements in Interval Timing on Mathematics Achievement

Mathematics competency is importance in both academic and real-world environments. The skills necessary for mathematical success in K-12 schools include number correspondence, addition, subtraction, problem solving, and fluency (Mullis et al., 2001; Rivera-Batiz, 1992; Rourke & Conway, 1997). With the exception of simple arithmetic (Bull & Johnston, 1997; Bull, Johnston, & Roy, 1999; Geary, 1993; Rourke & Conway, 1997), relatively little is known about the development of mathematics skills and/or the underlying cognitive abilities that contribute to mathematics achievement and performance.

Research examining the cognitive processes involved in mathematics performance has typically reported laboratory-based investigations of the basic cognitive tasks and strategies individuals use to solve mathematical problems, such as mental algorithms, components, and strategies (Ashcraft, 1995; Geary, 1994). Much of the mathematics research is domain specific. The domains investigated include exploring the development of number sense (i.e., the implicit awareness of quantitative concepts and relationships; Gersten & Chard, 1999), the development of algorithms (Geary, 1993), and other domain-specific competencies that are necessary for arithmetical success (Bryant & Rivera, 1997; Hoard, Geary, & Hamson, 1999).

The state-of-the-art of mathematics performance research has recently benefited from an expanded focus on the breadth of cognitive constructs included in research studies (e.g., Bull & Johnston, 1997; Bull et al., 1999) and the marriage of psychometric and cognitive information processing theories of intellectual functioning.

It is our position that research involving psychometric and cognitive information processing (IP) theories, human cognitive ability assessment, and academic performance would benefit from being organized within an existing comprehensive, empirically sound taxonomy of cognitive abilities. It is believed an integration of contemporary IP theories and psychometric research, within the framework of a well-validated taxonomy of human cognitive performance may advance our understanding of academic achievement and performance.

Cattell-Horn-Carroll Theory of Human Cognitive Ability

The contemporary psychometric Cattell-Horn-Carroll (CHC) theory, which is grounded in more than half a century of structural evidence derived from the factor analytic tradition (Carroll, 1993; 1997), is generally accepted as the most comprehensive and empirically based structural model of human cognitive abilities (see McGrew, 2005). Recent CHC-grounded research has added important information to understanding the general cognitive mechanisms that contribute to the development of mathematical skills and knowledge.

The CHC framework is a hierarchical model of intelligence consisting of three-levels or strata. The first level includes over 70 narrow cognitive abilities, which in turn are subsumed by 9 to 10 broad abilities. At the apex of the model is a third-order general factor (i.e., Spearman's *g*). The broad cognitive abilities articulated in CHC theory include: Fluid Reasoning (Gf), Comprehension-Knowledge (Gc), Short-term Memory (Gsm), Visual Processing (Gv), Auditory Processing (Ga), Long-term Retrieval (Glr), and Processing Speed (Gs; McGrew & Flanagan, 1998). CHC provides a solid theoretical and empirical foundation, as well as a comprehensive model to identify the range of potentially important broad cognitive abilities that may contribute to the development and acquisition of mathematics skills and knowledge. Conceptualizing research within the CHC taxonomy also provides a common nomenclature and model to investigate and understand achievement, whether from a componential approach in mathematics or a working memory model (Baddeley, 1986; Geary & Widaman, 1987; 1992).

Information Processing Models and Mathematics Achievement

Information Processing Models Defined

The recent integration of psychometric research (i.e., CHC theory) with contemporary information processing (IP) theories has resulted in important strides in understanding human intelligence and cognitive and academic performance (Kyllonen, 1996; McGrew, 2005). Although slightly different IP models have been hypothesized and researched, the four-source consensus model (Kyllonen, 1996) will be used in the current context. Within Kyllonen's (1996) model, the four primary components contributing to IP performance are *procedural knowledge*, *declarative knowledge*, *processing speed* (*Gs*), and *working memory* (MW)[1].

One of the most intriguing findings from the marriage of psychometric and IP models, first reported by Kyllonen and Christal (1990), is that "individual differences in working memory capacity may be […] responsible for individual differences in general ability" (Kyllonen, 1996, p. 61). Kyllonen's hypothesis was based on very high latent factor correlations (.80 to mid .90's) between measures of working memory and fluid reasoning (*Gf)* in a variety of adult samples (Kyllonen, 1996; Kyllonen & Christal, 1990). Since 1990, working memory (Baddeley, 1996a, 1996b; Baddeley & Hitch, 1974) has played a central role in research attempting to explain individual differences in higher-level cognitive abilities such as 1) language comprehension (*Gc*; Engle, Cantor, & Carullo, 1992; Just & Carpenter, 1992), 2) reading and mathematics (*Grw* and *Gq*; Hitch, Towse, & Hutton, 2001; Leather & Henry, 1994), 3) reasoning or general intelligence (*Gf* and *g*; Ackerman, Beier, & Boyle, 2002; Conway, Cowan, Bunting, Themault, & Minkoff, 2002; Engle, Tuholski, Laughlin, & Conway, 1999; Fry & Hale, 1996, 2000; Kyllonen

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[1] Another typical description of information processing models makes a distinction between: (1) memory systems—short-term and long-term memory, (2) types of knowledge-declarative and procedural, and (3) types of processing-controlled and automatic (Lohman, 2000).

& Christal, 1990; Süß, Oberauer, Wittmann, Wilhelm, & Schulze, 2002), and 4) long-term memory performance (Park, et al., 1996; Süß, et al., 2002).

The theoretical explanations for the consistently strong working memory→criterion relations differ primarily in the cognitive resources proposed to underlie working memory performance (Lohman, 2000). A sample of resources hypothesized to influence cognitive/academic performance vis-à-vis working memory are storage capacity, processing efficiency, the central executive, domain-specific processes, and controlled attention (Bayliss, Jarrold, Gunn, & Baddeley, 2003; Engle, et al., 1999). Researchers have hypothesized that working memory is strongly associated with complex cognitive performances (e.g., fluid reasoning, reading, and mathematics) because of the considerable amount of information that must be actively maintained within the limited resources of working memory. This is most evident when active transformation of the information in working memory is required.

An interesting and frequently investigated set of CHC/IP model relationships are those that suggesting that working memory (part of CHC Gsm), and to some extent Gs (as a facilitator of working memory) may be isomorphic with *g* (general intelligence) and/or the CHC ability domain (Gf), which is often claimed to be "the most important […] aspect of intelligence" (Stankov, 2000, p. 38). According to Stankov (2000), working memory is a critical aspect of Gf. As articulated by Kyllonen (1996),

> the remarkable finding is the consistency with which the working memory capacity factor has proven to be the central factor in cognition abilities[…] that working memory capacity is more highly related to performance on other cognitive tests, and is more highly related to learning, both short-term and long-term, than is any other cognitive factor (p. 72-73).

The important conclusion here is that contemporary CHC and IP research both converge on the critical importance of working memory (a Gsm ability) and fluid intelligence (Gf) in a wide variety of cognitive/academic performances, including mathematics. These results highlight the importance of increasing our understanding of the relationship between select CHC/IP cognitive constructs (working memory in particular) and mathematics achievement, and, more importantly, determining if interventions/treatments that promote efficient working memory performance also improve academic performance.

IP Models and Mathematics Performance Research

IP research has consistently suggested a significant causal relationship between working memory[2] and mathematics performance (Geary, 1993; Passolunghi & Siegel, 2004). Several authors have found that working memory plays a crucial role in calculation and in solving arithmetic word problems (Furst & Hitch, 2000; Geary, 1993; Geary, Hamson, & Hoard, 2000; McLean & Hitch, 1999; Passolunghi, Cornoldi, & De Liberto, 1999; Passolunghi & Pazzaglia, 2004; Passolunghi & Siegel, 2004; Swanson, 1993).

The central executive function component of Baddeley's (1996a) domain-general working memory system is hypothesized to allow for improvement in performance via the enhancement of selective or controlled attention— the flexibility to switch between retrieval plans, and the inhibition of task-irrelevant information (intrusions) in working memory (Engle et al., 1999; Passolunghi & Siegel, 2004). For example, computational word problems require the ability to reduce the accessibility of memories of nontarget and irrelevant information, which often can produce “intrusion errors” (Passolunghi & Siegel, 2004). To adequately construct a representation of a math word problem representation, information must be examined for relevance, selected or inhibited, and then integrated with other information (Passolunghi et al., 1999; Passolunghi & Pazzaglia, 2004). Barrouillet et al. (1997) have noted that even during the most elementary math operations (e.g., association of two operands with a response) a number of incorrect response competitors are activated and must be inhibited (Geary, 1993; Geary et al., 2000).

The phonological (articulatory) loop (Baddeley, 1986, 1996), the component of the working memory system that specializes in the storage and rehearsal of auditory/verbal information (Passolunghi & Siegel, 2004), has been reported to provide support to the counting processes in math performance. The phonological loop has been classified within the auditory processing (Ga) CHC domain (Flanagan, McGrew & Ortiz, 2000),

Finally, processing speed (Gs) has been implicated in efficient performance across cognitive and academic performance domains (Kail, 1991; Kail, Hall & Caskey, 1999; Lohman, 1989). A pivotal concept in IP models is that human cognition is constrained by a limited amount of processing resources, particularly in working memory. Many cognitive activities require a person's deliberate efforts, however, people are limited in the amount of mental effort they can allocate to a specific activity. In the face of our limited processing resources, the speed of processing becomes critical because processing speed determines in part how rapidly limited resources can be reallocated to other cognitive tasks (Kail, 1991). In addition to more efficient working memory processing, the fluency of retrieval of numerical information from long-term memory may also be associated with Gs (Case & Toronto, 1982).

Although it is widely accepted that working-memory capacity is an important limited resource for complex cognitive and academic performance (e.g., mathematics), exactly how

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[2] Working memory is subsumed under the CHC broad domain of Gsm (McGrew, 2005).

working memory influences specific components of cognitive processing and criterion related performance (in a given task) is not well understood. This is why more fine-grained causal and intervention-based research and analyses are needed (Süß et al., 2002).

Results of CHC→Math Achievement Studies

A number of recent studies have examined the validity of CHC measures in predicting mathematics performance (e.g., Floyd, Evans, & McGrew, 2003; Hale, Fiorello, Kavanagh, Hoeppner, & Gaither, 2001; McGrew & Hessler, 1995; McGrew, Flanagan, Keith, and Vanderwood, 1997; Williams, McCallum, and Reed, 1996). Collectively, these studies are suggestive of important cognitive ability domains that might, via assessment and/or intervention, contribute to a better understanding of, and intervention in, mathematics achievement.

Using multiple regression, McGrew and Hessler (1995) identified the broad CHC factor Comprehension Knowledge (Gc), which is analogous to crystallized intelligence or one's acquired knowledge, as demonstrating the strongest relationship with mathematics achievement from age 5 through late adulthood. Another broad CHC factor, Fluid Reasoning (Gf), defined as problem-solving requiring deductive and inductive thinking, also demonstrated a statistically significant relationship with mathematics achievement across the lifespan. The broad CHC factor Processing Speed (Gs), or speed of mental processing, also was related to mathematics achievement through age 40. Interestingly, Short-term Memory (Gsm) demonstrated significant associations with mathematics only in the 5-to-10-year-old and 40-to-60-year-old age groups. Visual-Spatial Thinking (Gv) had few significant associations with mathematics achievement when included together with a relatively complete range of CHC abilities in the prediction model.

McGrew, et al., (1997) replicated McGrew and Hessler's (1995) study using structural equation modeling (SEM). In this study, the broad CHC factors of Fluid Reasoning (Gf), Comprehension-Knowledge (Gc), and Processing Speed (Gs) remained strong predictors of Mathematics Reasoning *after the influence of general intelligence (g)* was accounted for in the CHC→Math causal models. Most recently, Floyd, Evans and McGrew (2003) used SEM to investigate the relative contribution of broad CHC factors on mathematics achievement in the nationally representative standardization sample of the Woodcock-Johnson Psychoeducational Battery III (Woodcock, McGrew, & Mather, 2001). Floyd et al (2003) reported that Fluid Reasoning (Gf), Comprehension-Knowledge (Gc), Processing Speed (Gs), and in contrast to earlier studies, Short-term Memory (Gsm) and Working Memory demonstrated statistically significant relationships with mathematics achievement from ages 6 through adulthood, with the exception of Short-term Memory at age 6.

Interestingly, across all the recent CHC→Math achievement studies reviewed here, Auditory Processing (Ga), Long-term Retrieval (Glr) and Visual-Spatial (Gv) abilities failed to demonstrate significant associations with mathematics performance. It is important to keep in mind, however, that these broad CHC factors were found to be nonsignificant only when included in models containing a relatively complete set of broad CHC domain ability measures (e.g., a model containing four additional broad CHC factors).

Working Memory—IP—Mental/Interval Timing—Mathematics Link?

We believe that a potentially important (and often overlooked) historical CHC/IP link may exist that could account for the importance of working memory in mathematics and other cognitive performance situations. According to Stankov (2000), one of the earliest recorded descriptions of a psychometric factor that captures a critical essence of working memory is the *temporal tracking* ability factor first reported by Stankov and Horn (1980) in the CHC Ga ability domain. Temporal tracking is defined as “being found in various auditorily presented [tasks] involving the mental counting or rearrangement of temporal [sequential] events” (Carroll, 1993; p. 386).

More recently, cognitive psychology has studied the phenomenon of *interval timing* through the use of research paradigms that require individuals to maintain synchrony with auditory tones (e.g., from a metronome). Tapping in synchrony with a metronome has been described as a “linear error correction mechanism that compensates for asynchronies by locally adjusting the phase of the underlying timekeeper” (Vorberg & Fuchs, 2004). When temporal deviations from the underlying metronome-based interval are realized (e.g., via performance feedback) an *automatic phase adjustment* is triggered. The allocation of *attentional resources* and the minimization of stimuli that may divert cognitive processing resources away from timing have been hypothesized to play a significant role in metronome-based synchronization of rhythmic movements (Brown & Bennett, in Press). In addition, the quickness and efficiency of the phase adjustment mechanism is believed to eliminate the necessity for long-term memory or learning (Vorberg & Fuchs, 2004). Thus, it is reasonable to hypothesize that synchronizing rhythmic movements to a metronome occurs primarily within the short-term, immediate resource-limited cognitive mechanism of *working memory*, which requires temporal tracking ability.

The study of the cognitive processes involved in the temporal control of simple rhythmic movements has been dominated by linear and stochastic *mental time/interval-keeper models* (Engbert, Scheffczyk, Krampe, Rosenblum, Kurths & Kliegel, 1997). Alternative models have focused on dynamic qualitative frameworks (i.e., *nonlinear oscillator models*; Engbert et al.,

1997) or *sensory-motor theories of temporal representation* (i.e., temporal tracking as a form of sensory-guided action that uses the sensory-memory image to drive a movement via a control mechanism; McAngus, 2005). Engbert et al. (1997) suggested that plausible models of rhythmic motor control may be derived by combining the linear (i.e., to explain the timing processes) and nonlinear or dynamic (to explain nonlinear feedback control and adjustment) mental time-keeper models. Thus, explanations of synchronized tapping behavior may require models that reflect the interaction of both linear (stochastic) and dynamic (oscillator) mental time-keeper models.

Timing/Rhythm and Academic Achievement

A primary working hypothesis in the current investigation is that research across different subdisciplines in cognitive psychology, which often use different terminology and measures, have identified important links between central theoretical cognitive constructs and a variety of human performance outcomes (e.g., academics). It is our opinion that much of this research may actually be focusing on related, if not the same, cognitive constructs, many of which are important for mathematical success. Working memory has clearly been identified as a central theoretical explanatory construct for many complex cognitive performances. Temporal tracking, an ability first identified in the domain of auditory processing (Ga), may have been a precursor of working memory, or, may represent an important facilitator of human cognitive performance that occurs within working memory, most likely guided and supported by the executive function and phonological loop subcomponents. The advancement of this hypothesis comes from recent studies which have demonstrated that interventions focusing on improving the ability to judge and maintain rhythmicity (temporal or mental time keeping or tracking) produced improvements across a diverse array of outcome domains.

Several behaviors important to school success demonstrated statistically significant relationships with timing/rhythm including academic achievement, attention, motor planning, and sequencing (Barkley, 1997a, 1997b; Greenspan, 1992; Wolff, 2002; Wolff, Michel, Ovrut, & Drake, 1990). Areas of academic achievement reported to be affected by timing/rhythm included language, mathematics, reading, and overall academic achievement (Ellis, 1992; Lazarus & Taub, 2005; Mitchell, 1994**;** Weikart, Schweinhart & Larner, 1987).

Recent research has also highlighted the potentially important role of timing precision and rhythm in the diagnosis of students with disabilities and developmental dyslexia (Wolff, 2002). Typically, children are able to tap their finger, repeat a beat, or a single syllable within about 50 milliseconds on either side of a pacing signal (Fraisse, 1982; Poeppel, Ruhnau, Schill & Steinbuechel,1990; Radiloka et al., 1997). In contrast, for students with dyslexia their latency of anticipation of a metronome beat was in the range of 150-200 milliseconds (Wolff, 2002). This finding led Wolff to hypothesize that an underlying deficit of temporal information processing may contribute to dyslexia.

Most recently, Lazarus and Taub (2005) reported a statistically significant effect for improvement in timing/rhythmicity on a number of reading achievement outcomes including reading decoding, reading fluency, and a measure of total reading. This study used a rhythmic synchronization metronome-based assessment and intervention technique, called the Interactive Metronome (IM®) method, to improve participants' latency response to a reoccurring metronome beat. Other studies using the IM method report significant effects for improvements in tennis performance (Zachopoulou, Mantis, & Psalti, 2005), golf accuracy (Libkuman & Otani, 2002), attention, motor control, language processing, and decreased aggressive behavior in children with ADHD (Shaffer, et al., 2001).

Collectively, these diverse studies indicate that improvements in the latency response to a reoccurring metronome-based intervention, which is hypothesized to improve mental/interval/temporal tracking within the working memory system, may produce domain *general* effects across a number of human performance domains. More specifically, and most relevant to the present study, is the area of mathematics.

Purpose

The cross-domain effects of the rhythmic synchronization metronome-based assessment and intervention argues for further investigation. This includes an exploration of *across*-domain general effect of IM intervention on academic achievement. Based on the above literature review, we offer the preliminary hypothesis that the ability of a metronome-based assessment and intervention system, hereafter referred to as synchronized metronome tapping (SMT), to produce improvements across a variety of human performance domains is most consistent with the positing of improvement in some type of domain-general cognitive IP mechanism.

The benefit of SMT intervention methods, which focus primarily on maintaining and judging rhythm, may enhance working memory performance through a number of possible mechanisms either alone or in combination (e.g., increased selective controlled attention; better inhibition of irrelevant information in working memory; enhanced use of the phonological loop via verbal mediation; refinement of executive function monitoring strategies). The demonstration of the positive impact of SMT methods in other human performance domains (i.e., mathematics performance) would provide additional indirect support for the hypothesis that SMT methods may be mediated by changes in functioning of a domain-general cognitive mechanism (which we hypothesize to be working memory).

The purpose of this paper is two-fold. The first purpose of the paper is to investigate the effect of the SMT method on mathematics achievement. The second purpose is to generate hypotheses that might contribute to understanding and explaining the diagnostic and training effects of SMT by examining the across-domain general cognitive mechanisms involved in mathematics performance.

Method

Participants

Participants attended a large suburban high school in South Florida. A total of 259 participants were included in the study. The participants' ages ranged from 13 to 19 years of age with a mean of 15.44 years of age. There were 191 -ninth, 43- tenth, 51- eleventh, and 12 – twelfth grade students in the study. A total of 171 students were male and 126 were female.

Pre-Post Dependent Variable Measures

The Woodcock-Johnson Tests of Achievement III (WJ III; Woodcock, McGrew, & Mather, 2001) served as a pre- and post-test measure of participants' mathematics achievement. As described in the WJ III technical manual (McGrew & Woodcock, 2001), the entire sample was stratified according to race, gender, geographic region, education, and age to mirror the population characteristics of the US Census projections for the year 2000. The entire WJ III was standardized on 8,818 individuals.

All participants completed two tests of mathematics from the WJ III. The two tests contributing to the Math Calculation Skills cluster, Calculation and Math Fluency, were administered to all participants. The Calculation test measures mathematics computation skills by requiring examinees to write numbers and complete basic to complex mathematical operations. The Math Fluency test is a measure of automaticity of basic mathematics calculation skills and requires examinees to complete a combination of simple addition, subtraction, and multiplication problems within a three-minute period.

Procedure

All participants were randomly assigned to either an experimental or control group after they completed the WJ III mathematics pre-test. A total of 119 participants comprised the treatment group and 140 participants were in the control group. The IM intervention took place during the students' physical education (PE) class period. While the experimental group participated in the intervention, the control group was engaged in regularly scheduled PE activities. A certified master trainer conducted all IM trainings. The students in the experimental group participated in an average of 15 sessions, each lasting approximately 45 minutes.

After the experimental group completed the IM intervention, the selected WJ III math pre-tests were again administered to all participants. Participants from the experimental and control group completed all tests together. All test proctors and supervisors were unaware of each students' group assignment. Standardized administration procedures were followed during the administration of each test, with the exception that the tests were administered in groups, rather than individually. Several steps were followed to ensure that standardized test administration procedures were followed as closely as possible. These steps included 1) a doctoral level supervisor was present during all group administrations, 2) a minimum of 1 proctor to every 4 students was maintained during all group administrations, and 3) all students progressed through the group test administration at the same time. If a student did not accurately completed a sample item, the group administration was stopped and the proctor followed standardized administration procedures to ensure adequate completion of the sample item.

The Intervention

Timing and rhythm was measured by the IM, a SMT based intervention. During the intervention, participants listened to a metronome beat through earphones and were instructed to make rhythmic movements that coincided with the exact beat of the metronome. Low scores indicated that the participant was clapping or making movements at or near the synchronized metronome beat, whereas high scores indicated the participant was far from the beat. The SMT method may be considered a technological way of measuring, to the nearest millisecond, timing and rhythm (aka, mental or interval timing or temporal tracking). The goal of training was to reduce participants' latency scores from about 50 milliseconds on either side of the metronome beat to approximately 15 milliseconds.

Results

This study investigated the relationship between improvement in students' timing/ rhythmicity and mathematics achievement. Participants' pre- and post-test scores were obtained from the administration of two mathematics tests from the WJ III. The IM method was used to measure and improve participants' latency response to a synchronized metronome beat. The Analysis of Covariance (ANCOVA) statistical procedure was used for all analyses. To control for the effect of initial level of performance on the subsequent post-tests, participants' standard scores on the WJ III pre-test measures of mathematics served as the covariate(s) in all analyses.

The results reported in Table 2 indicate a statistically significant effect for improvements from IM training on the Math Calculations Skills cluster F (1, 256) = 4.654, $p = .03$. The IM treatment had a small effect on Math Calculation Skills post-test scores ($\eta^2 = .018$; $g = .184$). Analyses of the individual test scores that contribute to the Math Calculation Skills cluster are also presented in Table 2. These results indicate that participants who received IM training scored statistically significantly higher on the Math Fluency and Calculation tests than did control group participants, although the effect size was small.

Discussion

The purpose of this pilot study was to determine if a short-term non-academic treatment designed to improve the timing/rhythmicity abilities of high school students would generalize to increased performance in mathematics achievement test scores. We hypothesized that if significant SMT treatment effects were found on math achievement dependent variables for such a short-term intervention, this finding, when combined with similar significant treatment effects on other academic outcomes, would collectively suggest the need to begin to hypothesize and investigate possible domain-general mechanisms that could account for the broad generalization of the SMT intervention method. In particular, results from previous studies investigating the effect of improvement in timing/rhythmicity, using the SMT method, have reported statistically significant improvements (when compared to a non-treatment control group) on standardized measures of reading recognition and reading fluency (Lazarus & Taub, 2005). Similarly, students with ADHD have been reported to demonstrate statistically significant improvements in attention, reading, and language processing (Shaffer et al. 2001) after SMT training.

The present study included 259 participants attending either ninth-, tenth-, eleventh- or twelfth-grade in a suburban high school. Participants were randomly assigned to either an experimental or control group. The IM method, an SMT based intervention was used to improve the experimental group's timing/rhythmicity during, on the average, fifteen 45 minute daily SMT treatment sessions (a total treatment of slightly more than 11 cumulative hours). The control group participated in traditional PE class activities during the same time period. Neither group received academic instruction during the IM treatments or PE class activities. Pre- and post-test performance on two WJ III mathematics achievement tests (Calculation and Math Fluency), were used as the dependent variables in the analyses. The ANCOVA statistical procedure was used to analyze all scores, with the participants' pre-test mathematics scores serving as the covariant.

The results indicated that the SMT method had, on average, a statistically significant effect on the experimental subjects' math achievement scores, above and beyond the typically expected growth demonstrated on math achievement during the same time frame (i.e., the change in math scores for the control group subjects). As measured by the WJ III Calculation and Math Fluency tests, participants in the experimental group were found to have completed, on average, more mathematics problems, were more accurate in their math problem solving, and completed the mathematics problems faster than the control group.

Although IM training had a statistically significant effect on mathematic achievement scores, the magnitude of the effect was small and accounted for approximately 2% of the variance in the test scores. An alternative way to examine effect size is through Hedges *g*. Table 1 also presents the effect size for Hedges *g* on Calculation, Math Fluency, and Math Calculation Skills. This statistic may be used to explain effect size as a percentage of growth, using a normal curve. Using this conversion of Hedge's *g* for the current results we find that the experimental group experienced a 12% growth on the Calculation test and a 10% growth on the Math Fluency test, when compared to the control group. The question is then raised whether potentially larger effects on average math achievement scores might be possible with lengthier STM treatment periods (across more days, weeks, and/or months). The detection of significant changes in math achievement scores from a non-academic intervention after only 15-45 minute treatment sessions, is at a minimum, a significant finding for an initial pilot study on a small sample. This positive finding is worthy of further exploration.

Preliminary Working Hypothesis and Areas to Investigate

Given the limitations of the current study (i.e., small sample size, no other variables administered to measure changes in potentially important domain-general basic cognitive processes, the need for replication in additional samples, the possibility of a placebo effect), any hypotheses advanced regarding possible explanatory mechanisms are at best, informed scholarly speculations needing further investigation. Nevertheless, the finding of significant SMT effects in this study, when combined with similar positive findings in behavior (ADHD), reading, language, and overall academic achievement for school age subjects (Lazarus & Taub, 2005; Shaffer et al., 2002; Weikart, Schwienart, & Larner, 1987) argues for the advancement of preliminary hypothesis to *jump start* more detailed and varied investigations in an attempt to discover: (a) whether these preliminary findings can be replicated in other samples and populations, (b) whether the IM training effects are greater or less with different types of students (e.g., those with and without specific types, and degrees, of different disabilities; those with higher or lower specific cognitive abilities such as working memory and processing speed), (c) whether varying the intensity and duration of the IM intervention produces systematic and quantifiable relations between treatment parameters and levels of achievement outcome changes, and (d) to ascertain what may be happening *under the hood* (i.e., what cognitive mechanisms are mediating the transfer of IM treatments to academic achievement domains?).

Based on the assumption that the across academic/behavior domain IM treatment effects are more parsimoniously accounted for (explained) by changes in a domain-general cognitive mechanism(s), and that the mature and rich cognitive ability CHC and information processing literature (reviewed and summarized in the introduction of this paper) is the best initial source of research and theory to draw upon at this time, we offer the following preliminary explanations as possible hypotheses for further investigation.

- SMT training may increase the efficiency of the cognitive processes that produce increased automatization and efficient performance on complex cognitive tasks. Changes in processing speed (Gs) and the efficiency of working memory (Gsm-MW), the latter reflecting changes in increased executive control (specifically better controlled attention and inhibition of irrelevant task information), are considered the most likely domain-general CHC/IP cognitive mechanisms. As previously reviewed in this paper Gs and working memory abilities have consistently associated with increased performance proficiency in a wide range of complex cognitive performance situations (fluid reasoning, general intelligence, language acquisition, long-term memory storage, reading, and mathematics).
- Research is needed that would investigate SMT effects at the neurological level (e.g., fMRI studies), which would help identify the location(s) of SMT training effects, which, in turn, would help identify relevant cognitive abilities vis-à-vis known brain-behavior relationships.
- The design of future SMT academic intervention studies should be expanded to include markers of hypothesized cognitive mechanisms (e.g., Gs, working memory, executive functions, controlled attention) to ascertain which cognitive abilities may be modified via the SMT intervention, and, more importantly, which cognitive abilities may mediate the changes in academic outcomes. Longitudinal studies are

particularly necessary to establish possible underlying domain-general causal mechanisms.

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Table 1

ANCOVA Results: Effect of SMT Training on Mathematics

Measures	*(df)* *F*	*p*	η^2	Hedges *g*
Calculation	(1, 257) 5.523	.020	.021	.175
Math Fluency	(1, 256) 4.942	.027	.019	.165
Math Calculation Skills	(1, 256) 7.955	.005	.030	.184

Running Head: TIMING AND RHYTHM

The Effects of Training in Timing and Rhythm on Reading Achievement

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Abstract

This study investigated the relationship between improvement in students' timing and rhythm and academic achievement in reading. Improvements in students' timing and rhythm were measured by the Interactive Metronome (IM) and academic achievement was measured by these tests of the Woodcock Johnson III Achievement (WJ III ACH): Letter-Word Identification, Passage Comprehension, and Reading Fluency as well as Broad Reading. This research used a pre-test post-test control group design. A timing and rhythm experimental group (using IM training) was compared to a traditional control group which received no intervention. A total of 280 high school students in grades 9-12 (130 in the treatment group and 150 in the control group) completed the study. All analyses of participants' pre- and post-test performance were conducted using the Analysis of Covariance (ANCOVA) statistical procedure. The results from this analysis indicate that there was a main effect for the treatment group on the post-test Broad Reading variable, with pre-test scores being controlled. Analyses of the individual scores that contribute to the calculation of the Broad Reading score reveal that the treatment group's Reading Fluency post-test scores are also significantly higher than the control group's post-test Reading Fluency scores. These results are surprising due to two factors. First, the treatment lasted only three weeks and it was not an "academically oriented" intervention. Second, developmental growth curves based on the tests used in this study indicate that very little academic growth takes place over short periods of time for a population averaging 15.5 years of age.

The Effects of Training in Timing and Rhythm on Reading Achievement

Many researchers believe that timing and rhythm play an important role in a variety of behaviors important to school success including motor planning, sequencing and cognitive functions such as academic achievement, adaptive behavior, and attention (Barkley, 1997a, 1997b; Greenspan, 1992). Bloom (1993) found that sensitivity to timing necessarily involves sensitivity to affective and cognitive information important for school and social success. Other research has found that improvement in timing and rhythm was significantly related to students' ability to monitor and control their behavior and outcome measures of motor skill (Gubay, 1979, 1985; Peterlin, 1991; Williams, Woollacott & Ivry, 1992). Investigations in timing and rhythm have also found significant relationships between the constructs and outcome measures of students' academic success (Wolff, 2002; Wolff, Michel, Ovrut, & Drake, 1990).

Research has identified significant relationships between timing and rhythm and student improvements in mathematics, reading, and measures of overall academic achievement (Weikart, Schweinhart & Larner, 1987; Ellis, 1992). These findings were further enhanced by studies of rhythm, which was significantly related to improvements in reading achievement in first and second grade, as well as test scores in language, mathematics, and reading in first, second, and third grade (Weikart et al., 1987; Mitchell, 1994).

Timing and rhythm has a significant relationship to cognitive development and this relationship starts early in life. In studies investigating language, newborns have been found to discriminate between the speech rhythms of different cultures; this innate ability is also believed to play a vital role in organizing and categorizing language as the child develops (Merzenich et al., 1996; Ramus, Hauser, Miller, Morris & Mehler, 2000). One-month old infants are sensitive to auditory duration changes of 20 milliseconds, which progresses at four to five-months of age to the ability to discriminate duration, rate, and rhythm (Lawson, 1980; Lewkowicz, 2000). Several investigators have found repetition, rhythm and interpersonal coordination of rhythms were a central means by which the infant acquires cognitive experiences and creates order and predictability in the world (Lewis & Goldberg, 1969; Stern, Beebe, Jaffee, & Bennett, 1977; Stern & Gibbon, 1979). Timing and rhythm are also involved in parent-child interactions. Studies investigating timing and rhythm interactions of mother-infant relationships have found that this interaction accounts for a significant portion of variance in the *prediction* of childrens' early cognitive ability and affective behaviors (Jaffe, Beebe, Feldstein, Crown & Jasnow, 2001).

The capacity for sequencing and timing movement has been shown to support adaptive motor performance as well (Keele, 1981; Libkuman, Otani & Steger, 2002). Conversely, poor sequencing and timing is significantly related to motor and attentional problems (Gubay, 1985; Keele, 1981; Schmidt, 1992; Williams, Woollacott & Ivry, 1992). Self-control is also related to timing and sequencing capacities (Peterlin, 1991; Rubia, Overmeyer, Taylor, Brammer, Williams, Simmons, & Bullmore, 1999).

Timing and rhythm difficulties in children have been associated with reading problems. Recent research has highlighted the role of timing precision and rhythm in handicapped students and developmental dyslexia. Using an isochronic pacing metronome, Wolff (2002) compared the performance of dyslexic students to those of matched normal readers or normal adults. The findings indicated that dyslexic students anticipated the signal of the metronome by intervals that were two or three times as long as their normal counterparts. The group differences were significant when participants tapped with their preferred index finger alone or with both fingers in unison. Dyslexic students also took significantly longer than normal readers to recalibrate their tapping responses when the metronome rate was experimentally changed in the middle of a trial. In addition, dyslexic students in contrast to normal readers had inordinate difficulty reproducing simple motor rhythms by finger tapping, and had similar difficulty reproducing the appropriate speech rhythm of linguistically neutral nonsense syllables. Furthermore, these difficulties were exaggerated when participants had to synchronize their performance to an external pacing metronome.

Fraisse (1982), Poeppel et al. (1990) and Radiloka et al. (1997) have reported that when normal children tap their finger or repeat a single syllable at a specified rate, they will consistently anticipate an external pacing signal within 50 milliseconds (range 30-50 milliseconds). Based on these findings Poeppel and his colleagues hypothesized that 50 milliseconds might represent the basic time unit by which the synchronization among collectives of neurons regulates the timing of coordinated behavior.

This finding is noteworthy in that Wolff (2002) found that dyslexic students anticipated the signal in the range of 150 to 200 milliseconds. He hypothesized that the clocking mechanism of dyslexic students that mediates between central nervous system function and coordinated behavior is dysfunctional within a restricted time window (Llinas, 1993). He further suggested that this dysfunction may identify the underlying deficit of temporal information processing in dyslexia.

Inaccuracy of timing is also increasingly being implicated in language processing disorders (Harnadek & Rourke, 1994). Merzenich et al. (1996) found that both language impaired students and normal students were able to discriminate and sequence tones. The normal group only required tens of milliseconds whereas the language disabled group required hundreds of milliseconds.

Waber et al (2000) found that disabled readers exhibit motor timing control deficits relative to average readers. In their study the authors generated three main findings. First, children referred for assessment of school problems performed with greater variability of timing precision in coordinated bimanual finger tapping than did non-referred children. Second, motor control deficits do not appear to be restricted to children who are poor readers. Motor control variables predicted numeric calculation as well as reading and spelling. Third and most related to our present study, motor timing control predicted performance on standardized measures of reading across the full range of skill. This means that the association between timing precision and reading does not appear to be limited to developmental dyslexia but extends across the full range of ability. It also has a relationship to children for whom there is no expressed concern about academic performance. The authors caution that although the associations between motor timing control and academic achievement scores, including reading, were statistically significant, the effect sizes were modest. This means that whatever underlying process motor timing represents it is one of the many factors that influence reading skills.

In the Waber et al (2000) study the child was to first listen to a metronome for 10 seconds without responding. On command from the examiner, the child tapped in synchrony with the metronome signal for 10 seconds and then continued to tap for another 20 seconds after the metronome stopped. There were 10 tapping patterns. The researchers believe that the tapping tasks may serve as an indicator of the neuropsychological integrity of the functional network that is relevant to reading. It may also be indicative of the effectiveness by which information is integrated by the brain. Consequently it would be expected to have implications for the fluent and effective integration of underlying behavioral and cognitive processes. They note that reading may be particularly sensitive to such inefficiencies because of the requirement for fluency, integration, and precision over and above that required for phonological processing.

If reading is particularly sensitive to inefficiencies in timing and rhythm, then what might happen if individuals could be trained to be more efficient? That is, if they significantly improved their timing and rhythm, could they then become more efficient readers? Important in the public school setting are the encouraging results from initial studies investigating the relationship between timing and rhythm with academic achievement. Results from these studies identified significant relationships between timing and rhythm and improvements on important outcome measures of student success, including tests of reading and mathematics (Shaffer et al., 2000). Consequently, the purpose of this current study was to explore the relationship between timing and rhythm and reading achievement in normal high school students. The intent was to determine if improvement in skills in timing and rhythm had an effect on various components of reading.

Method

Design

This research used an experimental pretest-posttest design. A timing and rhythm experimental group was compared to a traditional control group which received no intervention.

Participants

Participants were recruited from Flanagan High School in Broward County, Florida. This high school is one of the largest high schools in Florida and enrolls more than 5000 students in grades 9 through 12. This high school is situated on two campuses. There is one annex devoted exclusively to ninth grades students and there is a main campus that is home to students in grades 10 through 12. The school serves a multicultural suburban community.

Students were recruited from those enrolled in physical education/health education at the time of the study. Students were on a block schedule where they took only four courses each marking period. If one of their four courses was in physical education/health education, then they were eligible to participate. All pre-testing, treatment, and post-testing occurred during this class. Permission slips were received from parents of 318 students. Though their parents singed informed consent forms, some students decided that they did not want to miss physical education/health education and declined to participate, whereas two students had English language skills that were too limited to participate.

Students were first administered the pre-test measures then placed in either the treatment or control group based on a computer program that generated random numbers. A total of 280 students (130 in the treatment group and 150 in the control group) completed the study.

The study was approved by the Human Subjects Review Board of the University of Central Florida, the Human Subjects Review Board of Florida International University, Research Services of the School Board of Broward County, Florida and the Principal of Flanagan High School. Moreover, all researchers and research assistants passed the Human Participants Protection Education for Research Teams online course, sponsored by the National Institutes of Health (NIH). During the study, participants were treated in accordance with the "Ethical Principles of Psychologists and Code of Conduct" (American Psychological Association, 1992). Parents of all participating students signed a Parent Permission Form (which was available in both English and Spanish). All participants also signed an assent to participate.

Instruments

The WJ III ACH has 22 tests that are organized into five areas; reading, mathematics, written language, knowledge and oral language. The kindergarten to 12th grade sample was composed of 1,143 individuals. Individuals were randomly selected with a stratified sampling design that controlled for 10 specific community and subject variables. These included census region, community size, sex, race, Hispanic origin, and others related to colleges and universities and occupation status of adults. In addition to region and size, 13 socioeconomic variables were considered in order to avoid a bias toward any specific type of community.

For this study, the reading tests from the WJ III ACH were administered to all subjects. These included:

Test 1: Letter Word Identification. This task requires identifying and pronouncing isolated letters and words. The median reliability for this test is .94

Test 2: Reading Fluency (timed). This task requires rapidly reading and comprehending simple sentences. The individual is required to circle whether or not each sentence is true or false within a three minute time period. (Examples: The sky is green. You can sit on a chair. A bird has four wings.) The median reliability for this test is .90

Test 9: Passage Comprehension. This task requires reading a short passage silently and then supplying a key missing word. (Example: The boy ______ off his bike. Correct: fell, jumped, etc.). The median reliability for this test is .88.

In addition, a broad reading score was calculated. This is a cluster score that includes Test 1: Letter Word Identification, Test 2: Reading Fluency, and Test 9: Passage Comprehension. The reliability for this cluster score is .94.

The WJ III ACH uses *W* scores. The *W* score is a special transformation of the Rasch ability scale (Rasch, 1960; Wright & Stone, 1979). The *W* for each test is centered on a value of 500, which is set to approximate the average performance of a child at age 10-0. Cluster scores such as Broad Reading are the average (arithmetic mean) *W* score of the tests included in that cluster. The *W* score is not visible to examiners and the software converts raw scores into *W* scores.

Training of research assistants

Research assistants were all graduate students currently enrolled in the Ed.S. degree program in school psychology at Florida International University. They received five hours of specialized training in administering the Woodcock-Johnson III (WJ III ACH) from the primary researchers and were always supervised in administration procedures.

The apparatus

Timing and rhythm was measured by Interactive Metronome© (IM) which is an apparatus that includes a computer, the IM software, headphones, and two contact sensing triggers. One of the computer connected electronic triggers is a glove with the contact sensor on the palm side that is attached to a person's hand. The other trigger is a flat plastic pad that is activated by tapping on it either by the toe or the heel (Cassily, 1996). The participant listens to a metronome beat that is heard through earphones. The object is for the individual to make rhythmic movements that coincide with the exact beat of the metronome. These movements consist of clapping both hands, clapping one hand at a time on the side of the body, alternate toe tapping and alternate heel tapping, single toe and heel tapping, alternate toes tapping and hand clapping, and balancing on one leg with toe tapping using the other leg.

For example, in one exercise when the participant claps his or her hands together this activates the trigger. Or in another exercise, when a participant taps his or her foot this activates the other trigger. This is turn, sends a signal to the PC based metronome program, which then analyzes how early or late the participant's movement is relative to the metronome beat. The program computes a millisecond difference score between the metronome beat (zero milliseconds) minus the milliseconds either before or after the metronome beat. For example, a score of 80 milliseconds would mean the participant was 80 milliseconds away from the beat.

As part of the technology, IM analyzes exactly when in time the tap occurs in relation to the guidance beat. It then instantaneously transposes this precise information into guidance sounds that participants hear in their headphones. Both the pitch and left-to-right headphone locations change according to the accuracy of each tap. For example, if the participant taps before the reference beat then the guidance sound is heard on the left side. Consequently, when the participant taps after the beat the sound is heard on the right side. With practice, this audio guidance enables the participant to improve his or her scores. For example, when a participant learns through the guidance sounds that their taps are preceding the reference beat then the participant can briefly slow down to catch the beat.

In addition to the guidance sounds, the participant also receives feedback about their performance by looking at the computer monitor. When a participant taps before the reference beat, this score is visually indicated to the left of the center and when the taps come after the beat, this is indicated to the right of center.

In measuring performance, the absolute values of the millisecond scores are averaged to produce a mean millisecond deviation for each exercise. These are then averaged to produce an overall millisecond deviation score. The lower the score, the more accurate the performance, that is, the participant’s goal is to lower the score to make the movements coincide with the metronome. Low scores indicate that the participant is clapping or making movements to the rhythm; whereas high scores mean the participant is off rhythm. The use of IM technology may be seen as an electronic way of measuring, to the nearest millisecond, timing and rhythm.

Training Procedure

Training was conducted by competent IM Trainers. Each IM Trainer met all the standards established by IM and was certified as an IM Trainer. The training was conducted in a large classroom in groups of 10 to 20 and each participant had their own IM equipment to use during the session.

Each participant underwent 12 45 minute to 60 minute IM treatment sessions over a course of three to five weeks. Ninth grade students attended school only four days per week whereas 10th, 11th and 12th grade students attended school every day. Ninth grade students were on a rotating block schedule. Due to overcrowding, all ninth grade students were assigned at the beginning of the school year to one day of the week where they did not attend school and instead attended an extended school day four days per week.

Once treatment began, it was set up for students to receive the training every school day. Students were limited to receiving one session daily. However, holidays, campus activities, and absences meant that training was not provided to every student every day. One student may have been working on session five while another student in the same classroom was working on session six. However, each participant in the experimental group needed to complete all 12 sessions to be included in the study.

Each session consisted of eight to twelve tasks using four to eight different exercises that were prescribed in the treatment guide and were repeated a specified number of times. Exercises were done at a preset tempo of 54 repetitions per minute and the number of repetitions per exercise increased from 30 to a maximum of 2000. The exercises included clapping both hands together, tapping one hand alone against the upper thigh, tapping one toe or heel alone on the floor, alternating toe taps on the floor, alternating heel taps on the floor, alternating between tapping one hand on the upper thigh and the toe on the opposite side of the body on the floor, and balancing on one foot and tapping the toe on the opposite side of the body. The IM computer program and guide sounds systematically guided each participant through the learning process. Through the 12 sessions participants progressively learned to do these tasks.

- Focus on one thing without being interrupted by things around them or by their own internal thoughts.
- Recognize that there is a repeating pattern to the reference beat.
- Use the guide sounds to synchronize (plan and sequence) his/her own simple hand or foot taps so that they align with the external beat pattern.
- Recognize when his/her own actions are deviating from the external beat pattern.
- Recognize and correct his/her own timing and focus related habits and tendencies.
- Progressively improve his/her ability to monitor mental and physical actions as they are occurring.
- Minimize the degree of his or her planning and sequencing deviations.
- Make corrections rapidly.
- Quickly and accurately learn and create new planned sequences (Interactive Metronome, 1999).

Each student had an ID number that they used to access the computer and the program that recorded their millisecond scores for each exercise. The initial IM sessions were devoted to teaching participants how to discriminate the sounds triggered by their own actions and the metronome beat. Participants were taught to make smooth rhythmic hand motions and foot motions. They were instructed to focus on the metronome beat and not be distracted by the sounds around them or other students. Also during the first session participants took the “Initial Long Form Assessment Tasks” which measured the accuracy of their performance in milliseconds on all the tasks in the training regimen prior to engaging in the training. This assessment established a base line for each participant.

From session to session, participants increased the length of time they engaged in the exercises. Also they first completed the easier clapping exercises before engaging in the more difficult exercises. During each session participants also were given a brief assessment called the “Daily Pre-Test and Post-Test Short Form” that measured how accurate was their performance on the both hands task both without guide sounds (Task 1) and with guide sounds (Task 2) for 54 repetitions per task. The Pre-Test was given at the beginning of each session and the Post-Test was administered at the conclusion of each session.

Half-way through the 12 sessions, participants took the “Mid-Term Long Assessment Tasks” which was identical to the first assessment. This gauged improvement in timing and rhythm for each participant. During the last training session, participants took the “Final Long Form Assessment Task.” This evaluated their overall progress on the 14 tasks (and was identical to the previous two assessments).

In order to increase motivation, participants received a computerized score regarding their daily performance. In addition, the most accurate scores (i.e., low scores) were written on the blackboard and participants competed against each other, as well as themselves, to increase performance in each session.

The researchers did not conduct any training sessions. However, we randomly monitored the sessions in order to make sure that the training protocol was accurately followed.

Results

This study investigated the relationship between improvement in students' timing/ rhythm and academic achievement. Improvements in students' timing and rhythm were measured by the IM and academic achievement was measured by the WJ III ACH. Prior to participating in the intervention, students completed several pre-test measures of academic achievement. After completing the pre-test assessments students were randomly assigned to either a control or treatment group. After the treatment group completed the three week intervention, students from both the control and treatment group completed post-tests measures. The method of data collection and assignment of participants was consistent with a pre-test post-test control group design. Scores on the pre- and post-test measures were compiled after the completion of the study.

All analyses of participants' pre- and post-test performance were conducted using the Analysis of Covariance (ANCOVA) statistical procedure. Students' scores on the pre-test measure of academic achievement served as the covariant in all analyses. For example, in an analysis of the post-test dependent variable Reading Fluency, participants' pre-test scores on the Reading Fluency test from the WJ III ACH served as the controlling variable. As discussed above, participants' pre-test standard scores on the WJ III ACH served as the covariant in all analyses. The dependent variable was participants' post-test Ref-W scores. The same tests from Form A of the WJ III ACH were used as pre- and post-test measures.

Descriptive statistics of participants' pre- and post-test Ref-W scores are presented in Table 1. As expected, both the control and experimental group demonstrated gains on the post-test measures. To determine if there was a statistically significant between group difference in participants' post-test scores, all dependent variables were analyzed using a one-way ANCOVA. The results from these analyses are presented in Table 2 and Table 3. Table 2 presents the results of a one-way ANOVA with one between subjects variable (group), three covariant variables (Letter-Word Identification, Passage Comprehension, and Reading Fluency), and one Dependent variable, post-test scores on Broad Reading. Surprisingly, the results from this analysis indicate that there was a main effect for the treatment group on the post-test Broad Reading variable, with pre-test scores being controlled. These data indicate the treatment groups' post-test scores were higher than the control groups' post-test scores on the Broad Reading dependent variable and that the observed difference between the two groups score was statistically significant F (1, 29494.53) = 7.86, *p* = .005. Analyses of the individual scores that contribute to the calculation of the Broad Reading score reveals that the treatment group's Reading Fluency post-test scores are also significantly higher than the control group's post-test Reading Fluency scores F (1, 164141.350) = 8.19, *p* = .005. As identified in Table 3, participants' Reading Fluency pre-test scores were the only controlling variable in this analysis. In contrast to participants' Broad Reading and Reading Fluency post-test scores, the results for the dependent post-test variables Letter-Word Identification and Passage Comprehension did not indicate a statistically significant difference between the two groups' post-test scores F (1, 481.270) = 2.874, *p* = .091 and F (1, 18818.973) = .980, *p* = .32 respectively.

Although not all dependant variables were statistically significant. The observance of statistically significant increases in both Broad Reading and Reading Fluency were surprising. This is due to two factors, first the treatment lasted only three weeks and it was not an "academically oriented" intervention. Second, developmental growth curves based on the tests used in this study (McGrew & Woodcock, 2001) indicate that very little academic growth takes place over short periods of time for a population averaging 15.5 years of age. This is in contrast to younger or even primary school-age students who experience rapid academic growth over short periods of time.

In an effort to determine if ninth grade students performed differently on the post-test dependent variables, as compared to ninth, tenth, eleventh, and twelfth grade students additional analyses were conducted. In this set of analyses, ninth grade students' performance on the dependent variables identified as statistically significant in the previous set of analyses was investigated. The mean age of the ninth-grade only group was 14.88 years-of-age, with a range of 13 to 17 years-of-age. There were a total of 191 ninth grade students in the control and treatment groups. The results of the ninth-grade only groups' performance on the dependent variables are presented in Table 4 and Table 5. Table 4 contains the results of an analysis using post-test Broad Reading scores as the dependent variable. A visual comparison between Table 2 and Table 4 indicates that there was a slight increase in variance accounted for by the ninth-grade only group, in addition to a decrease in the F statistic. This indicates that the ninth-grade only group performed somewhat better on the dependent variable. Table 5 presents the results of a one-way ANCOVA. The ninth-grade only control and treatment group served as the single between subjects variable and post-test Reading Fluency scores was the single dependent variable. A visual comparison between Table 3 and Table 5 indicates that there was a decrease in F for the ninth-grade only group. More important, however, was the difference in the portion of variance accounted for. This was an increase in effect size, for the ninth-grade only group from 3.1 percent to 4.5 percent. Although these results are impressive, the portion of variance accounted for by the ninth-grade only group is still below the 6 percent threshold for an effect size to be considered medium in magnitude (Cohen, 1977). Additionally, it is not known if the observed difference in the ninth-grade only groups' scores and was due to their being younger. Which, based on the aforementioned developmental growth curves, may indicate they experienced more academic growth as a result of the treatment than their high school peers or if the observed increase in effect size was due to another, yet, unidentified variable on which the ninth-grade only group was different.

Discussion

Students in the treatment group reported in post-training interviews that they felt more focused and attentive following training in timing and rhythm. However, the statistically significant academic gains as measured by the treatment groups' post-test scores on Reading Fluency and Broad Reading in comparison to the control groups' post-test scores on these same variables were unexpected. First, students received no direct training in pronouncing words, reading fluency, or passage comprehension. This was not an "academically oriented" intervention. Without direct training it would not be expected that increases in reading achievement would occur. Second, the treatment lasted only three weeks and developmental growth curves based on the WJ III ACH (McGrew & Woodcock, 2001) indicate that for students averaging 15.5 years of age, very little academic growth takes place over short periods of time.

Of the three measures of Broad Reading, scores on Reading Fluency were most affected by the treatment. Reading Fluency does not require new learning but may best be seen as the ability to rapidly read and comprehend sentences. It is hypothesized that due to the limited time frame of the training that the academic changes were primarily related to more efficient cognitive processing. For example, for a high school student to circle as quickly as possible Yes or No to sentences such as, “A fish lives on land” does not require new learning but instead requires efficient mental processing

There are two major theories regarding fluency contribution to a reader’s understanding of text. Both theories emphasize the component parts of fluency. One theory emphasizes the contribution of automaticity and the other stresses the role of prosody (Kuhn & Stahl, 2003). However, there appears to be some consensus regarding the primary components of fluency. These include: (a) accuracy in decoding, (b) automaticity in word recognition, and (c) the appropriate use of prosodic features such as stress, pitch and text phrasing.

In understanding the role of automaticity, efficient readers read both accurately and automatically. Given the fact that an individual only has limited attention available for any given task, attention expended in one activity is not available for another. In the case of reading, an individual must determine what words comprise the text while simultaneously constructing meaning. On the Reading Fluency test on the WJ III ACH, the student must also evaluate the statement to determine if it is true or not. The more efficient the reader, the more accurately, automatically and rapidly the student will perform the task.

Although the automaticity theory accounts for the accurate and effortless decoding that fluent readers demonstrate, it does not account for the role that prosody plays in reading. According to linguists, prosodic aspects of language include rhythm and expression (Kuhn & Stahl, 2003). Prosody comprises a series of features including timing or duration, pitch or intonation, stress or loudness, all of which contribute to reading text (Allington, 1983; Dowhower, 1991; Schreiber, 1987, 1991). Additionally, prosodic reading includes appropriately chunking groups of words into phrases or meaningful units in accordance with the syntactic structure of the text. Kuhn and Stahl (2003) believe that taken together these features are classified as suprasegmental because they extend over more than one speech sound and contribute to the construction of meaning from a text. Prosody may also provide a link between fluency and comprehension. It has been speculated (Chafe, 1988) that to read a sentence, one must assign syntactic roles to the words. Appropriate intonation, phrasing and stress are all indicators of fluent readers. Both timing and rhythm play an important role in the reading process.

Children that have deficits in timing and rhythm are often poor readers. In fact, many children with these deficits are learning disabled in reading. Perhaps by significantly improving a student's skill in timing and rhythm, this may have the effect of reducing the reading disabilities of handicapped readers and improving the reading fluency and broad reading skills of average readers.

Recent syntheses of research on reading have highlighted the importance of including fluency building as part of daily instruction (Chard, Simmons, & Kameénui, 1998; National Reading Panel, 2000; Snow, Burns, & Griffin, 1998). However, in a review of effective interventions for building reading fluency (Chard, Vaughn, & Tyler, 2002), researchers concluded that building fluency includes an explicit model of fluent reading, multiple opportunities to read familiar text independently and with corrective feedback, and established performance criteria for increasing text difficulty.

Improving fluency is particularly important as previous research has shown that direct measures of reading rate are highly correlated with measures of more complex reading outcomes (Hudson, Mercer, & Lane, 2000; Torgesen, Rashotte, & Alexander, 2004). The most widely used method to increase reading speed is the repeated reading technique (Meyer & Felton, 1999). Using this approach, the student repeatedly reads letters, words, phrases, or passages a specific number of times, or until fluency has reached a pre-established level. The National Reading Panel (2000) noted that the repeated reading technique was the only method reviewed for which there is consistent, positive support for increasing reading fluency. None of the studies reviewed included using an indirect approach such as explicit training in timing and rhythm. However, result of this present study support the premise that this is a promising line of future inquiry.

Research examining the role of timing and rhythm in reading may have an important impact on programs that are aimed at the remediation of reading failure. Many of the current reading programs are based on the assumption that impaired phonological processing at the segmental level is the core deficit of dyslexia. Findings from programs in phonics for dyslexic students suggest that the ability to decode single words and non words improves but there are questions regarding the long term effects (Wolff, 2002). In fact, many of the children who improve in their phonological decoding skills later encounter failure in reading as they get older when performance is assessed in terms of reading automaticity, reading fluency and reading comprehension (Bruck, 1989; Wise, Olson, Ring, & Johnson, 1998). Greenspan (1992) believes that the relationship between motor regulation, attention, and executive functions suggest that technologies aimed at improving sequencing, motor planning, timing and rhythm may have a role in helping children learn.

The study of the relationship between timing and rhythm and reading is just beginning. The technological advances made in the measurement of timing and rhythm and the development of a treatment program that increases an individual’s ability in this area can move this line of inquiry forward. The science is such that we can now accurately measure (to the millisecond) and improve timing and rhythm.

There are a number of unanswered questions based on this study that require further inquiry. A limitation of this study is that longitudinal research is necessary to determine the long-term effects of training in timing and rhythm. Some questions include: Will the results of this increase in Reading Fluency and Broad Reading in the treatment group hold up months or years after the training has been completed. ? Will the treatment group’s Reading Fluency and Broad Reading Skills continue to increase relative to their non-trained peers? That is, will the training enable the treatment group to make even larger gains in Reading Fluency and Broad Reading in comparison to their non-trained peers? Will the absence of additional training or booster sessions in timing and rhythm result in the Reading Fluency and Broad Reading gains of the treatment group to regress back to scores comparable to the controls? Also after a period of time will improvement occur in the treatment group relative to the control group in areas directly related to new learning? That is, do those treated students who have improved skills in timing and rhythm now have a better capacity to learn new knowledge than their non-treated peers?

In conclusion, the results of this study demonstrate that training in timing and rhythm can have a positive impact on Reading Fluency and Reading Comprehension in high school age students. With a confluence of forces focusing in on improving children's reading (National Reading Panel, 2000), recent brain research that has explored the neuropsychology of reading ability and disability (Shaywitz, 2003; Shaywitz & Shaywitz, 1999), and the emphasis on accountability in the No Child Left Behind legislation, it is time to research new technologies that hold promise for increasing the educational competence of our nation's youth.

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Table 1

Descriptive statistics of participants' pre- and post-test achievement scores.

Variable/Group	n	Pre-Test M	Pre-Test SD	Post-Test M	Post-Test SD
Broad Reading					
Control Group	145	537.05	20.98	543.78	22.34
Experimental Group	127	538.82	20.90	549.62	20.82
Letter Word Identification					
Control Group	148	536.77	17.84	539.57	19.53
Experimental Group	129	538.32	15.60	542.95	17.45
Reading Fluency					
Control Group	150	562.42	42.23	578.86	45.34
Experimental Group	130	562.93	43.22	588.50	43.76
Passage Comprehension					
Control Group	149	512.31	13.35	513.94	13.25
Experimental Group	129	514.11	12.73	516.51	11.69

Table 2.

Results for the Post-Test Broad Reading Dependent Variable.

Source	SS	df	MS	F	Sig.	Eta Squared
Pre-Test Letter Word Identification	4939.03	1	4939.03	40.86	.000	.143
Pre-Test Passage Comprehension	3008.44	1	3008.44	24.89	.000	.093
Pre-Test Reading Fluency	23773.51	1	23773.51	196.67	.000	.446
Group	950.08	1	950.08	7.86	.005	.031
Error	29494.53	249				
Total	74560057.00	249				

Table 3.

Results for the Post-Test Reading Fluency Dependent Variable.

Source	SS	df	MS	F	Sig.	Eta Squared
Pre-Test Reading Fluency	346278.01	1	346278.01	544.285	.000	.678
Group	5210.60	1	5210.60	8.19	.005	.031
Error	164141.50	258				
Total	89528472.00	261				

Table 4.

Results for the Post-Test Broad Reading Dependent Variable for the Ninth-Grade Only Group.

Source	SS	df	MS	F	Sig.	Eta Squared
Pre-Test Letter Word Identification	3408.19	1	3408.19	39.12	.000	.193
Pre-Test Passage Comprehension	1518.62	1	1518.62	17.34	.000	.096
Pre-Test Reading Fluency	17156.77	1	17156.77	196.94	.000	.546
Group	484.58	1	484.58	5.56	.020	.033
Error	49998392.00	169				
Total	76558.25	168				

Table 5.

Results for the Post-Test Reading Fluency Dependent Variable for the Ninth Grade Only Group.

Source	SS	df	MS	F	Sig.	Eta Squared
Pre-Test Reading Fluency	231227.86	1	231227.86	517.44	.000	.749
Group	3616.81	1	3616.81	8.09	.005	.045
Error	77292.79	173				
Total	58898758.00	176				

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THE NEURAL BASIS OF TEMPORAL PROCESSING

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Key Words timing, cerebellum, cortex, dynamics, interval, conditioning

■ **Abstract** A complete understanding of sensory and motor processing requires characterization of how the nervous system processes time in the range of tens to hundreds of milliseconds (ms). Temporal processing on this scale is required for simple sensory problems, such as interval, duration, and motion discrimination, as well as complex forms of sensory processing, such as speech recognition. Timing is also required for a wide range of motor tasks from eyelid conditioning to playing the piano. Here we review the behavioral, electrophysiological, and theoretical literature on the neural basis of temporal processing. These data suggest that temporal processing is likely to be distributed among different structures, rather than relying on a centralized timing area, as has been suggested in internal clock models. We also discuss whether temporal processing relies on specialized neural mechanisms, which perform temporal computations independent of spatial ones. We suggest that, given the intricate link between temporal and spatial information in most sensory and motor tasks, timing and spatial processing are intrinsic properties of neural function, and specialized timing mechanisms such as delay lines, oscillators, or a spectrum of different time constants are not required. Rather temporal processing may rely on state-dependent changes in network dynamics.

INTRODUCTION

In his chapter "The Problem of Serial Order in Behavior," Karl Lashley (1951) was among the first neurophysiologists to broach the issue of temporal processing.

> Temporal integration is not found exclusively in language; the coordination of leg movements in insects, the song of birds, the control of trotting and pacing in a gaited horse, the rat running the maze, the architect designing a house, and the carpenter sawing a board present a problem of sequences of action which cannot be explained in terms of succession of external stimuli.

Lashley emphasized the inherently temporal nature of our environment. He explains that without an understanding of the neural mechanisms underlying our ability to process the order, interval, and duration of sensory and motor events, it is not possible to gain insight into how the brain processes complex real-world stimuli.

All sensory and motor processing ultimately relies on spatial-temporal patterns of action potentials. For the purpose of this review it is useful to draw clear distinctions between spatial and temporal processing. We use the former term to refer to the processing of stimuli defined by which sensory neurons are activated. For example, in the visual domain the orientation of a bar of light can be determined based on a static snapshot of active retinal ganglion neurons. Similarly, the discrimination of the pitch of two high-frequency tones (that activate different populations of hair cells in the cochlea), or the color of a bar of light, or the position of a needle prick to the skin, can be discriminated solely upon the spatial patterns of activation, that is, by which afferent fibers are active. In contrast, other stimuli, such as the duration of a flashed bar of light or the interval between two tones, cannot be characterized by a snapshot of neural activity. These stimuli require the nervous system to process the temporal pattern of incoming action potentials. We refer to the analysis of these stimuli as temporal processing. In contrast to these simple examples, most sensory stimuli are not purely spatial or temporal but, like speech and motion processing, require analysis of the spatial-temporal patterns of activity produced at the sensory layers.

In the 50 years since Lashley's chapter, much progress has been made on understanding the neural basis of sensory and motor processing; however, much of this progress has been made regarding the spatial components of processing. Hebb's postulate, published two years before Lashley's chapter on temporal integration, plays a fundamental role in our understanding of spatial processing. Hebbian or associative synaptic plasticity presents a means by which neurons can develop selectivity to spatial input patterns, and it provides the underlying basis for the emergence of self-organizing maps (e.g., von der Malsburg 1973, Bienenstock et al. 1982, Miller et al. 1989, Buonomano & Merzenich 1998a). In contrast, associative plasticity alone cannot underlie the discrimination of a 100- or 125-ms presentation of a vertical bar or a 2-kHz tone.

Here we review the behavioral, electrophysiological, and theoretical data on temporal processing. We first define the different timescales over which the brain processes information and then focus on temporal processing in the range of a few milliseconds (ms) up to a second.

SCALES AND TYPES OF TEMPORAL PROCESSING

The terms temporal processing, temporal integration, and timing are used to describe a number of different phenomena. One source of ambiguity is that these terms are used to refer to a wide range of timescales over which animals process time or generate timed responses. This range spans at least 12 orders of magnitude—from microseconds to circadian rhythms. Based on the relevant timescales and the presumed underlying neural mechanisms, we categorize

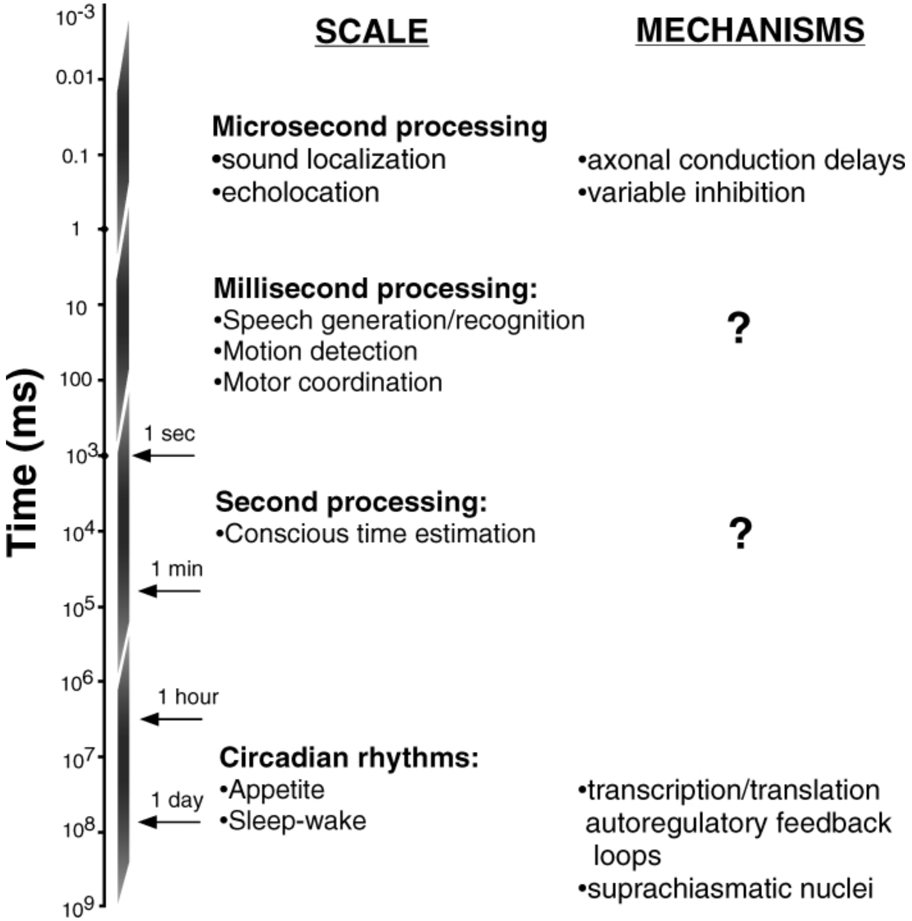

Figure 1 Timescales of temporal processing. Humans process temporal information over a scale of at least 12 orders of magnitude. On one extreme we detect the delay required for sound to travel from one ear to the other. These delays are on the order of tens to hundreds of microseconds. On the other extreme, we exhibit daily physiological oscillations, such as our sleep-wake cycle. These circadian rhythms are controlled by molecular/biochemical oscillators. Temporal processing on the scale of tens and hundreds of ms is probably the most sophisticated and complex form of temporal processing and is fundamental for speech processing and fine motor coordination. Time estimation refers to processing in the range of seconds and minutes and is generally seen as the conscious perception of time.

temporal processing into four different time scales (Figure 1): microseconds (Carr 1993, Covey & Casseday 1999), milliseconds (Buonomano & Karmarkar 2002), seconds (Gibbon et al. 1997), and circadian rhythms (King & Takahashi 2000). These general classes are not meant to represent purely nonoverlapping types of processing or indivisible categories. Rather, they probably reflect the minimal set of categories that serve different functions and rely on different mechanisms yet, nevertheless, exhibit significant overlap. Although there are numerous issues of interest at all these scales, here we focus on temporal processing on the scale of tens to hundreds of ms.

Temporal Processing Versus Temporal Coding

Another important distinction and source of confusion is the difference between temporal coding and temporal processing (Figure 2). We refer to temporal processing as the decoding of temporal information or the generation of timed motor responses. In its simplest form, temporal processing may consist of neurons that respond selectively to the interval between two events. By definition, to process temporal information, one must start with spike patterns in which information is encoded in the temporal domain. In the sensory domain we focus on cases in which the temporally encoded information arises directly from external stimuli (e.g., duration discrimination, Morse code, rhythm perception, etc.). In addition to these external temporal codes, theoretical and experimental data suggest that temporal

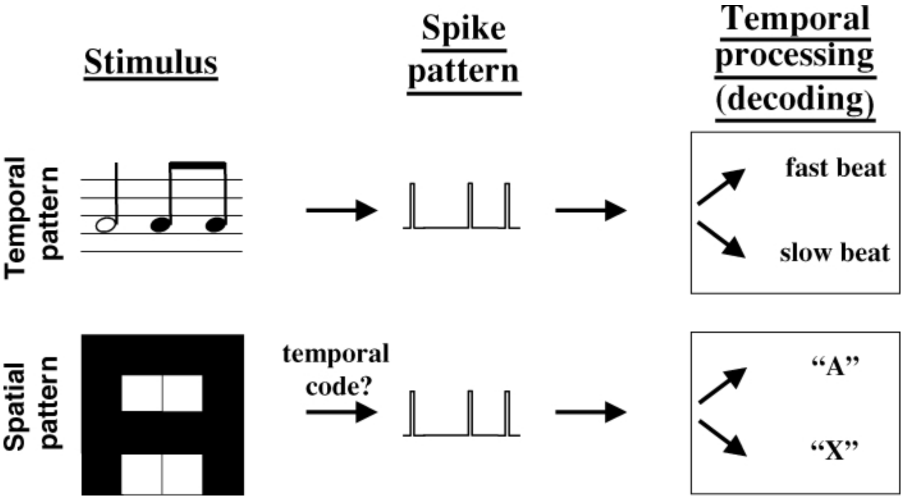

Figure 2 Temporal processing and temporal coding. (*Upper panel*) Temporal processing refers to decoding of temporal information arriving from environmental stimuli such as music (*left*). A stimulus such as a piece of music will generate temporal patterns of action potentials that follow the beat of the music (*middle*). These action potential patterns must be decoded in order to decide whether the stimulus was played at a fast or slow tempo (*right*). (*Lower panel*) Spatial stimuli such as a statically flashed image of a letter (*left*) generate spatial patterns of action potentials. Even in response to a rapid spatial stimulus, all neurons will not fire in synchrony, and it is possible that temporal codes for spatial stimuli may be generated at early states of sensory processing (*middle*). In principle, this temporal encoding of spatial stimuli might be used by the brain for stimulus processing. However, the temporal code would also have to be decoded (*right*) as with stimuli that are inherently temporal in nature.

codes may also be internally generated. That is, static or steady-state stimuli may be partially encoded in the temporal patterns of spikes (e.g., Richmond et al. 1990, McClurkin et al. 1991, Middlebrooks et al. 1994, Laurent et al. 1996, Rieke et al. 1996, Mechler et al. 1998, Prut et al. 1998). For example, by taking into account the temporal structure of neuronal responses to static Walsh patterns there is more information about the stimuli than there is in the firing rate alone (McClurkin et al. 1991). Mechler et al. (1998) have shown that there is significant information about the contrast of transient stimuli in the temporal pattern of V1 neuron firing. Internally generated temporal codes may provide a means to increase the bandwidth (Rieke et al. 1996) or to perform computations such as invariant pattern recognition (Buonomano & Merzenich 1999, Wyss et al. 2003).

Although the studies above suggest that in some cases there is information in the temporal pattern of action potentials generated internally, there are few data showing that the brain uses this information (see, however, Stopfer et al. 1997). If internal temporal codes are generated by the brain, they must be decoded or processed, like the external temporal patterns discussed here.

SENSORY TIMING

Temporal information in the range of tens to hundreds of ms is fundamental to many forms of sensory processing. Motion processing is a ubiquitous example in the auditory, somatosensory, and visual domains of a task that requires temporal information. However, it is arguably in the auditory domain that timing is most prominent, owing to its importance in vocalization and speech recognition.

A good example of the ability of the auditory system to process temporal signals is Morse code, in which language is reduced to temporal code. First, Morse code requires discriminating the duration of single tones (short versus long) and the interval between them (element, letter, and word pauses). Second, it requires perception of a sequence of tones, which represent auditory objects (letters and words). Third, the timing of the stimuli is not absolute but rather a function of the speed of transmission. At 15 words per minute (wpm), each dot and dash and interelement and intercharacter pause are 80, 240, 80, and 240 ms, respectively. Experts can understand Morse code at rates of 40–80 wpm; at 40 wpm the above elements' values are 30, 90, 30, and 90 ms, respectively. Thus, Morse code requires discrimination of continuous streams of sounds and discrimination of the duration, interval, number, and sequence of elements, as well as temporal invariance. The complexity of this analysis provides an example of the sophistication of temporal processing on the timescale of tens to hundreds of ms.

Speech Recognition

To nonexperts, Morse code at high speed sounds much like noise, and considerable training is required to understand it. However, in many ways it is a simpler task than speech recognition, which shares much of the temporal richness of Morse code but exhibits additional features such as prosody, spectral information, and speaker-specific recognition. During continuous speech, syllables are generated every 200–400 ms. The sequential arrangement of syllables is important in speech recognition (e.g., "la-dy" × "de-lay"). The pauses between syllables or words are also critical for parsing, as in "black bird" × "blackbird," or for example, the ambiguity in the mondegreen "kiss the sky" × "kiss this guy" can be decreased by longer interword intervals. The temporal structure within each syllable and phoneme also contributes to speech recognition. Specifically, temporal features are fundamental for phoneme discrimination. These features include voice-onset time (the time between air release and vocal cord vibration), which contributes to the "ba" × "pa" discrimination (Lisker & Abramson 1964), the duration of frequency transitions (e.g., "ba" × "wa"; Liberman et al. 1956), and the silent time between consonants and vowels (e.g., "sa" × "sta"; Dorman et al. 1979). Additionally, prosodic cues such as pauses and duration of speech segments are used to determine semantic content (Lehiste et al. 1976).

Owing to the multiple levels and scales of temporal information in addition to spatial information, speech is one of the most complex forms of pattern recognition and requires both spatial and temporal processing (Shannon et al. 1995, Tallal 1994, Doupe & Kuhl 1999). Various lines of evidence have revealed the degree to which speech recognition relies on temporal information. Indeed, in some cases it can rely primarily on the temporal structure. For example, experiments with cochlear implants show it is possible to achieve good levels of speech comprehension with 2–4 electrodes (Dorman et al. 1989, Dorman et al. 1997). Additionally, Shannon et al. (1995) showed that speech recognition could be achieved with relatively little spectral information. Near-perfect recognition of vowels, consonants, and sentences was observed with four broad spectral bands, and significant recognition of consonants and vowels was seen with a single band, in which only temporal and amplitude information was available.

Given the importance of temporal information in speech and language it would be expected that deficits in temporal processing would produce language deficits. Indeed, it has been suggested that certain forms of language-based learning disabilities may be caused by generalized sensory deficits in temporal processing (Livingstone et al. 1991, Eden et al. 1996, Tallal & Piercy 1973; for a review see Farmer & Klein 1995). However, even if some forms of language-based learning disabilities result from generalized sensory deficits, it is not yet clear whether those deficits are specific to timing or to more general features such as complex stimuli or rapidly changing stimuli.

MOTOR TIMING

Because movements involve changes in muscle length over time, motor control and timing are inextricably related. Most movements involve the coordinated activation of agonist muscles to initiate motion and antagonist muscles as a brake. These activations require accurate timing on the order of tens of ms. Indeed, pathologies that disrupt the timing between agonist and antagonist actions lead to dysmetric or inaccurate movements. Lesions of the cerebellum, for example, tend to delay the activation of antagonist muscles, which causes movements to be hypermetric or to overshoot (e.g., Hore et al. 1991). Cerebellar patients often display oscillating-like tremors during movements as they make a series of overshoots and corrections. A recent study shows that for saccade eye movements, which also involve agonist muscles to initiate and antagonist muscles to brake, the activity of populations of cerebellar Purkinje cells precisely encodes the onset and offset of a saccade (Thier et al. 2000). Motor control represents a clear example of an inherently timing-intensive computation in the range of tens to hundreds of ms.

Numerous studies focusing on timing have made use of repetitive movements as their readout. In particular, Keele, Ivry, and others have used such movements as rhythmic tapping of the finger to pursue the hypothesis that the cerebellum is a general-purpose timer in the tens-to-hundreds-of-ms range (e.g., Ivry & Keele 1989). In the prototypical experiment, subjects are first asked to tap their finger in time with a metronome (say at 400-ms intervals). After a brief training period, the subject continues tapping without the metronome. The main dependent measure is variability in the intertap intervals. This and similar paradigms have been used as screens to find brain regions for which damage disturbs the timing of the taps. These and related findings are discussed in more detail below in the section on the cerebellum.

Timed Conditioned Responses

One of the more experimentally tractable forms of motor timing is seen in the precise learned timing of classically conditioned eyelid responses. In a typical eyelid-conditioning experiment, training consists of repeated presentation of a tone paired with a reinforcing stimulus such as an air puff directed at the eye. Over the course of 100–200 of such trials the animals acquire conditioned eyelid responses: The eyelids close in response to the tone (Figure 3*a*). The time interval between the onsets of the tone and the puff influences the nature of this learning (Figure 3*b*). Conditioned responses are acquired only when the tone onset precedes the puff by at least 100 ms and by less than ~3 s. Within this range, the timing of the conditioned responses is also affected by the tone-puff time interval. Short intervals promote the learning of responses with short latencies to onset and fast rise times. As the interval increases, the learned responses have longer latencies to onset and slower rise times. The result is that, in general, the responses peak near the time at which the puff is presented.

Several studies have demonstrated that these responses are a genuine example of timing and exclude the previously generally accepted alternative that response timing derives from response strength. For example, Millenson et al. (1977) and Mauk & Ruiz (1992) trained animals by presenting the puff on alternate trials at two different times during the tone. The responses the animals learn have two peaks, each corresponding to one of the times at which the puff was presented.

PSYCHOPHYSICAL STUDIES

The predominate working hypothesis in the psychophysical literature has been a centralized internal clock model (Creelman 1962, Treisman 1963; for a review see Allan 1979), in which an oscillator beating at a fixed frequency generates tics that are detected by a counter. These models often assume that timing is centralized, that is, the brain uses the same circuitry to determine the duration of an auditory tone and for the duration of a visual flash. The alternate view is that timing is distributed, meaning that many brain areas are capable of temporal processing and that the area or areas involved depend on the task and modality being used. In addition to the question of centralized versus distributed mechanisms, there is the issue of timescale specificity. A universal clock (of which there could be a single instantiation or multiple instantiations) could be the sole timing mechanism for all intervals/durations, or there could be a set of dedicated circuits, each specific to given lengths of time (referred to as interval-based mechanisms; Ivry 1996).

Interval and Duration Discrimination

The best-studied temporal tasks in humans are interval and duration discrimination (Divenyi & Danner 1977, Getty 1975, Wright et al. 1997). In a typical interval discrimination task two brief tones separated by a standard interval (T, e.g., 100 ms) or longer interval (T + ΔT) are presented to the subject. The presentation order of the short and long intervals is randomized. The subject may be asked to make a judgment as to whether the longer interval was the first or second. ΔT can be varied adaptively to estimate the interval discrimination threshold. Duration discrimination tasks are similar, except each stimulus is a continuous tone (filled interval).

The relationship between the threshold and the standard interval constrains the underlying mechanisms. Figure 4 shows the relationship between threshold and the standard interval for a compilation of interval and duration discrimination studies in the range of tens of ms to one second. In untrained subjects the threshold for a 100-ms standard interval is ~20 ms (Weber fraction of 20%). Note that although in absolute terms the threshold increases with increasing intervals, the Weber fraction (threshold/standard interval) decreases for short intervals (50 to 200 ms). For intervals from 200 to 1000 ms, the Weber fraction is fairly constant, perhaps suggesting that different neural mechanisms are responsible for interval discrimination at these intervals.

INTERMODAL TIMING Psychophysical studies have attempted to address the issue of centralized versus distributed timing by comparing performance on intra- versus intermodal tasks. In the intermodal tasks a standard interval may be demarcated by a tone at 0 ms and a flash of light at 100 ms. Performance on the intermodal condition is then compared to pure auditory and visual discrimination. The first observation that comes from these studies is that interval discrimination

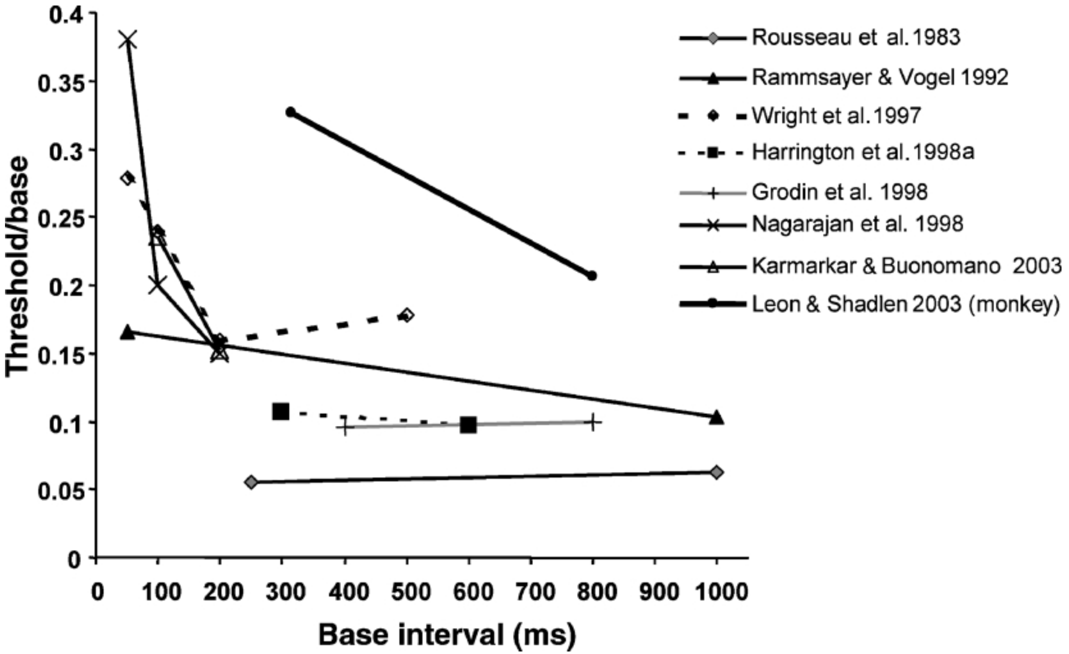

Figure 4 Cross-study interval discrimination thresholds. The standard or base interval is represented on the X axis, and thresholds are plotted in the Y axis as Weber fractions (threshold/standard interval). Thresholds are calculated differently in different studies, thus comparing absolute thresholds across studies is not appropriate. Lines join the thresholds from different intervals within studies. These data indicate that, at short intervals, temporal discrimination thresholds do not follow a Weber fraction. However, at longer intervals, above 200 ms, thresholds are fairly constant in relation to the standard interval.

in the auditory modality is better then that in the visual modality (Rousseau et al. 1983, Grondin & Rosseau 1991). Additionally, these studies show that interval discrimination between modalities is significantly worse than that within modalities (Rousseau et al. 1983, Grondin & Rousseau 1991, Westheimer 1999). Specifically for standard intervals in the range of 100–250 ms, the threshold for tone-light discrimination can be 50%–300% worse than for light-light discriminations. Interestingly, Rousseau et al. (1983) showed that intermodal discrimination was significantly more effected for a 250-ms interval as compared to a 1-s interval. Within a modality, changing stimulus features also decreases performance. If the first tone is played at 1 kHz and the second tone is played at 4 kHz, interval discrimination is significantly worse than if both tones were played at the same pitch (Divenyi & Danner 1977).

These data are consistent with the notion of distributed timers. Specifically, because the stimulus features that delimit the interval in a cross-modality task are arriving at different timers, performance is decreased. However, an alternative explanation is that timing is still centralized, but intermodal timing is simply a more difficult task because it requires a shift of attention from one modality to the other.

Psychopharmacology of Temporal Processing

On the timescale of seconds, dopamine antagonists produce temporal overshoot, and stimulants such as methamphetamine produce temporal undershoot (for a review see Meck 1996). On the timescale of a second and below, Rammsayer (1999) has shown in human psychophysical experiments that the dopaminergic antagonist, haloperidol, significantly impaired discrimination thresholds for 100-ms and 1-s intervals. Remoxipride, a dopamine antagonist more selective for D2 receptors, impaired processing on the scale of a second but not for a 50-ms interval (Rammsayer 1997). Experiments with benzodiazepines also support the dissociation between millisecond and second processing by showing that performance in a 50- or 100-ms task is unaffected, whereas performance in a 1-s task is significantly worse (Rammsayer 1992, 1999). Together these results show that two distinct drug classes (dopaminergic antagonists and benzodiazepines) can selectively interfere with second but not with millisecond processing. Future experiments will be necessary to determine whether the above results are due to direct action on a timing mechanism or to more nonspecific actions on arousal and/or cognition.

Interval Discrimination Learning

Can temporal resolution improve with practice? One of the first studies on this issue reported no perceptual learning (Rammsayer 1994). In this study, subjects were trained on 50-ms intervals for 10 min a day for 4 weeks. Subsequent studies revealed robust learning with training (Wright et al. 1997, Nagarajan et al. 1998, Karmarkar & Buonomano 2003). In these studies subjects were generally trained for an hour a day (400–800 trials) for 10 days.

GENERALIZATION OF INTERVAL DISCRIMINATION The perceptual learning studies, in addition to suggesting that the neural mechanisms underlying timing can be fine-tuned with experience, provide a means to examine the issue of central versus distributed timing. We can ask, after training on 100-ms intervals using 1-kHz tones, if performance improves for different intervals and frequencies.

Generalization studies reveal that interval discrimination learning is specific to the temporal domain, and generalization occurs in the spatial domain (Wright et al. 1997, Nagarajan et al. 1998, Westheimer 1999, Karmarkar & Buonomano 2003). Figure 5 shows the results from a study in which subjects were trained on a 100-ms–1-kHz interval discrimination task. Subjects were pre- and posttested on conditions that varied across the temporal and spatial domain: 100-ms–4-kHz, 200-ms–1-kHz, and a 100-ms–1-kHz continuous tone condition. Generalization to the 100-ms–4-kHz tone was virtually complete, and there was no generalization to the 200-ms interval. This eliminates the possibility that learning was due to a nonspecific improvement such as task familiarization.

Interval learning has also been reported to generalize across modalities. Nagarajan et al. (1998) show that training on a somatosensory task can produce

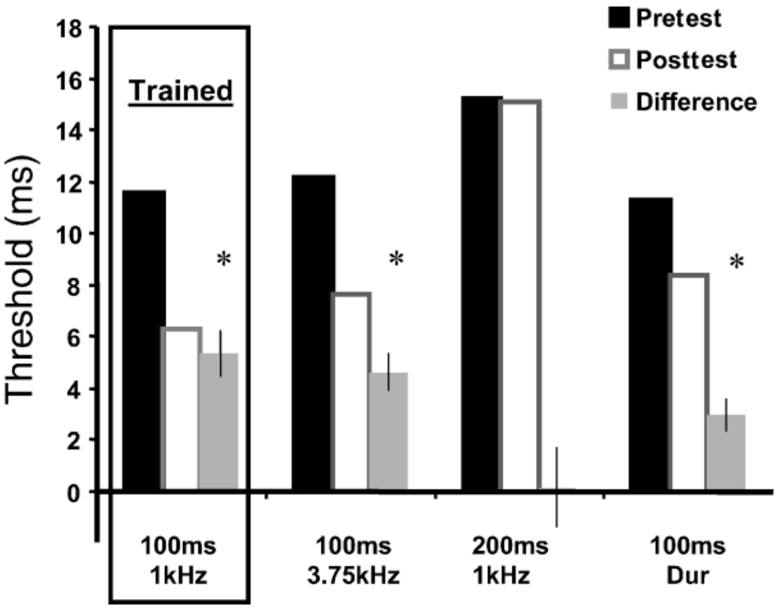

Figure 5 Generalization of interval discrimination learning. A group of 10 subjects underwent training on a 100-ms–1-kHz interval discrimination task. After 10 days of training (an hour a day), they exhibited significant learning (*left bars*). Pre- and posttests on 3 different conditions revealed generalization to the same interval played at a different frequency, as well as to the duration discrimination task (continuous tone) at the same absolute time (100 ms). However, no generalization to novel intervals was observed. Modified from Karmarkar & Buonomano 2003.

improvement on an auditory interval discrimination task similar to the interval used for somatosensory training. Even more surprising, training on an auditory task appears to result in an interval-specific improvement in a motor task requiring that the subjects tap their fingers to mark specific intervals (Meegan et al. 2000).

The simplest interpretation of these data is that centralized circuits exist for each interval, and with training, either the temporal accuracy or the downstream processing of these circuits undergoes plasticity. In this interpretation, timing is centralized but interval based. However, it is possible that in these tasks learning occurs as a result of interval-specific cognitive processes other than temporal processing per se. For example, because interval discrimination tasks require comparing the test interval and a standard interval, improvement could rely on better representation of the standard interval or improved storage or retrieval from working or short-term memory. Such alternative explanations would be consistent with the generalization across different stimulus markers and modalities, as well as the lack of generalization to novel intervals. Alternatively, it could be argued that, although many circuits are capable of temporal processing, the relatively simple nature of these temporal tasks allows the brain to use multimodal pathways and a single timing circuit.

TEMPORAL SELECTIVITY AND ANATOMICAL LOCALIZATION

A fundamental step in understanding the neural basis of temporal processing is finding neurons that are selective to the temporal features of sensory stimuli or responsible for the generation of timed motor responses. To date, interval, duration, or temporal-combination sensitive neurons have been described in a variety of different systems. These findings range from simple interval or duration-sensitive cells in bats and amphibians to more complex temporal-combination sensitive cells involved in song-selectivity in birds. Below we examine the electrophysiological and anatomical data that address the potential mechanisms and location of temporal processing. We believe that the range of tasks and behaviors that rely on temporal processing, and the number of areas putatively involved, suggest that temporal processing is distributed and a ubiquitous intrinsic property of neural circuits.

Brainstem: Frogs and Bats

To communicate, some anuran amphibians (frogs and toads) use vocalizations rich in temporal information. The temporal structure of some frog calls is used to discriminate between vocalizations (Klump & Gerhardt 1987, Rose & Brenowitz 2002). Specifically, calls can be distinguished based on the number and frequency of pulses. Alder & Rose (1998, 2000) show that neurons in the auditory midbrain can be tuned to both the frequency and the number of auditory pulses. Selectivity was not sensitive to intensity. Neurons exhibited a preferred pulse frequency (e.g., 80 Hz) at which they would produce their maximal number of spikes. Lower or higher frequencies elicited fewer or no spikes. These studies provide an elegant example of temporal tuning curves, a temporal analog to orientation tuning curves in V1 neurons. It is not yet known whether the temporal tuning arises primarily from synaptic/cellular or network properties.

Neurons in the bat auditory brainstem also respond selectively to specific temporal features such as the pulse-echo delay and sound duration (Covey & Cassidy 1999). Neurons in the inferior colliculus can be tuned to pulse-echo delays or to sounds of specific durations. Temporal tuning in these cells is known to rely on inhibition (Casseday et al. 1994, Saitoh & Suga 1995). One hypothesis is that stimulus onset produces inhibition, and the offset of inhibition causes rebound depolarization. If this rebound coincides with the second excitatory input (produced by sound offset), a duration-specific response can be generated. However, this mechanism may be a specialized brainstem process, and it is not clear if it will generalize to more complex patterns (see below).

Temporal Selectivity in Songbirds

One of the best-studied systems regarding temporal processing is in songbirds. Similar to human language the songs of birds are rich in temporal structure and composed of complex sequences of individual syllables. Each individual syllable and the interval between syllables is on the order of tens of ms to 200 ms. The areas involved in the generation and learning of song have been identified (Bottjer & Arnold 1997, Doupe & Kuhl 1999). Song selectivity is often established by comparing the response to the normal song against the same song in reverse or reversing the syllable order. Recordings in the HVc (Margoliash 1983, Margoliash & Fortune 1992, Mooney 2000) and in the anterior forebrain nuclei (Doupe & Konishi 1991, Doupe 1997) reveal neurons that are selective to playback of the birds own song, specifically syllable sequences played in the correct order. Additionally, song selectivity of neurons in cmHV can be modified by a behavioral task requiring song discrimination (Gentner & Margoliash 2003). Thus, experience can lead to selectivity of complex temporal-spatial stimuli in adult birds.

Figure 6 shows an example of an order-sensitive cell in the HVc (Lewicki & Arthur 1996). Two syllables (A and B) are presented in all combinations with a fixed interval between them. The cell is selective to the AB sequence, and it does not respond well to either syllable individually or to BA. The order selectivity in neurons from HVc has been well established. Interval and duration selectivity have been less studied. Although, in some cases the neurons are also sensitive to the interval between sounds (Margoliash 1983, Margoliash & Fortune 1992). The mechanisms underlying this selectivity are not understood. Unlike simple detection of the interval between two tones, these cells are selective to both the spatial-temporal structure within each syllable, as well as to the sequence in which these elements are put together. This selectivity emerges in stages because neurons in earlier auditory areas of the songbird respond selectively to syllables but not to the sequence (Lewicki & Arthur 1996).

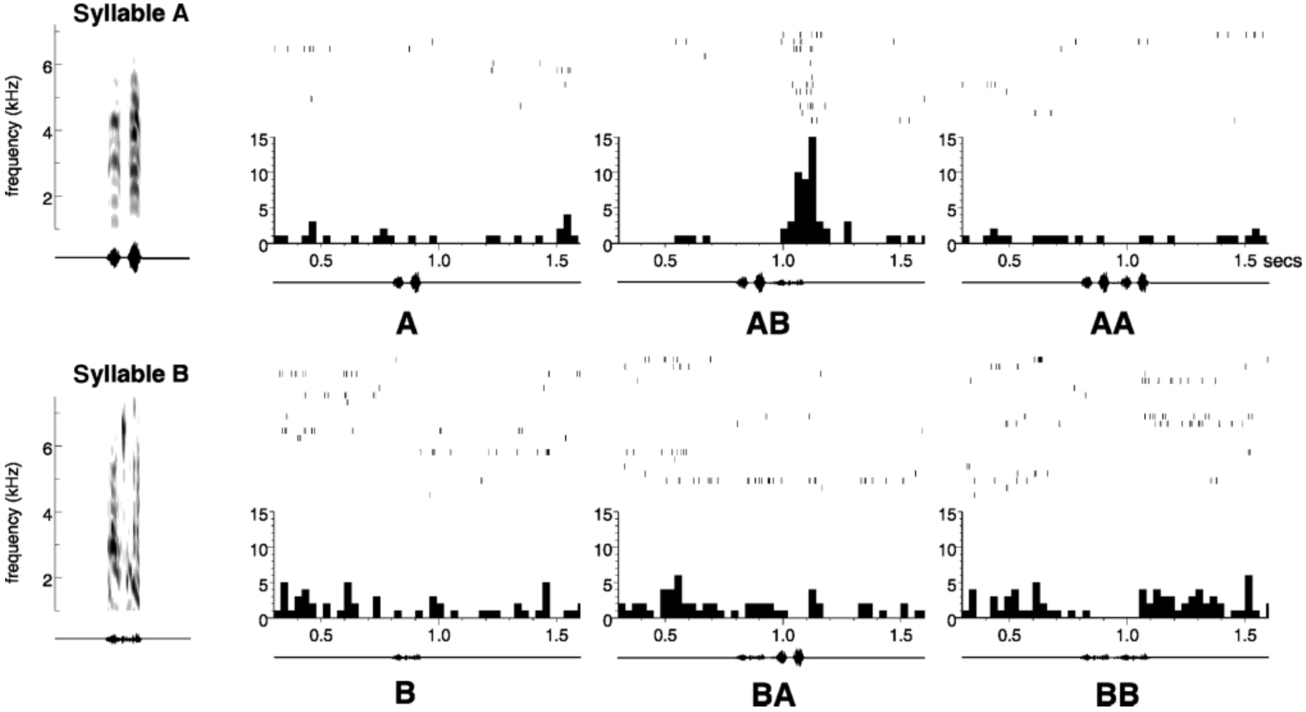

Figure 6 Example of a temporally combination-sensitive neuron of a songbird. Recordings from a neuron in HVc in response to two syllables from the bird's own song. Spectrograms of each syllable are shown to the left. Above each histogram is the response of the neuron to each presentation of the stimuli. This cell is selective to syllable B only if preceded by syllable A. Modified from Lewicki & Arthur 1996.

Because HVc neurons can respond selectively to the auditory presentation of songs (these studies are generally done under anesthesia), these neurons are clearly sensitive to temporal information in the sensory domain. However, these same cells are also active during singing and can be activated at precise times during song production. A subset of HVc neurons may be responsible for generating the timed responses that drive the sequence of syllable production (Hahnloser et al. 2002). Whether or not this is true, it is clear that the song circuity is capable of temporal processing because cross correlations with peaks in the tens-to-hundreds-of-ms range have been reported (Hahnloser et al. 2002, Kimpo et al. 2003).

Basal Ganglia

There are numerous studies suggesting the basal ganglia is involved in timing; however, most of the data focus on the timescale of seconds rather than in the range of tens to hundreds of ms. Much of these data relies on pharmacology studies. Specifically, drugs that act on the dopaminergic system interfere with timing. Because the basal ganglia is important in the dopaminergic system, the basal ganglia is likely involved in temporal processing (for a review, see Meck 1996). Studies of Parkinson patients, who in some cases have shown specific deficits in temporal tasks, support this claim (Artieda et al. 1992, Harrington et al. 1998a, Riesen & Schnider 2003).

Imaging studies have reported changes in BOLD signals in the basal ganglia. Rao et al. (2001) showed an increase in the BOLD signal in the basal ganglia during a duration discrimination task of 1.2 s. No significant basal ganglia activation was observed during a control frequency discrimination task using a similar stimulus protocol. Similarly, an fMRI study by Nenadic et al. (2003) revealed activation of the basal ganglia (putamen) during a 1-s duration discrimination task compared to a frequency discrimination task. This study also revealed activation of the ventrolateral prefrontal and insular cortex, but not the cerebellum, in the temporal condition.

Thus the basal ganglia likely plays a role in timing of sensory and motor events on the timescale of seconds. However, to date, there are few data that suggests involvement of the basal ganglia in temporal processing in the range of tens to hundreds of ms.

Cerebellum

Although the cerebellum is generally viewed as primarily a motor structure, it has also been proposed to be a general-purpose interval timer in the range of tens to hundreds of ms. "General purpose" in this sense encompasses both sensory and motor timing. One advantage of such a theory is that the synaptic organization and physiology of the cerebellum are known. Much is known about the relationships between the cerebellum and forms of motor learning such as eyelid conditioning and adaptation of the vestibulo-ocular reflex (Raymond et al. 1996; Boyden et al. 2004, in this volume).

Support for the role of the cerebellum in timing is based on both motor and sensory timing experiments. Ivry and others presented a variety of evidence demonstrating cerebellar involvement in timing tasks. The fundamental observation was made in experiments in which the task required human subjects to make rhythmic taps with their finger. Analysis was based on a hypothetical construct that divides errors (tapping at the wrong time) into those attributable to motor execution versus those attributable to a timer (Wing & Kristofferson 1973). Ivry et al. (1988) showed that patients with lesions of the medial cerebellum have increased motor errors, whereas lesions that were more lateral increased timer errors. Cerebellar patients also display deficits in interval discrimination (Ivry & Keele 1989) and are impaired at judging the speed of moving visual targets (Ivry & Diener 1991, Nawrot & Rizzo 1995). Ackermann and colleagues (1997) observed that patients with lateral cerebellar lesions are impaired in their ability to discriminate phonemes that differ only in the timing of consonants. Imaging studies also suggest a potential connection between timing and the lateral neo-cerebellum in humans. PET imaging was used to detect activation in lateral portions of the cerebellum during an interval discrimination (Jueptner et al. 1995).

The timing hypotheses of cerebellar function attempt to explain the various tasks for which the cerebellum is engaged or is necessary in terms of the need to gauge the explicit timing between events in the hundreds-of-ms range. Despite the intent that these theories build on a computational base, supporting data remain mostly task-based. Most data involve demonstrations that the cerebellum is activated during, or is required for, tasks that we view as examples of timing.

CEREBELLUM IN TIMING OF CONDITIONED RESPONSES Lesions and reversible inactivation studies have shown that learned response timing of conditioned eyelid responses is mediated by the cerebellar cortex. Perrett et al. (1993) used a within-subject design to demonstrate the effect of cerebellar cortex lesions on eyelid response timing. Animals were trained to make a fast response to one tone and a slower response to a second tone. Using this two-interval procedure, it was demonstrated that lesions of the cerebellar cortex in already trained animals spare conditioned responses but abolish response timing (Figure 3*c*). The results demonstrated that the lesions do not produce a fixed shift in timing. Rather, the postlesion timing defaults to a short, fixed latency independent of the prelesion timing. Subsequent studies have replicated this effect on response timing using reversible inactivation techniques. Garcia & Mauk (1998) showed that disconnection of the cerebellar cortex with infusion of a GABA antagonist into the cerebellar interpositus nucleus (the downstream target of the relevant region of cerebellar cortex) also cause response timing to default to very short latency (Figure 3*d*). Recent studies have demonstrated similar results with infusions of lidocaine in the cerebellar cortex (W.L. Nores, T. Ohyama & M.D. Mauk, manuscript in preparation).

The implications of conditioned eyelid response timing involve much more than the finding that the cortex of the cerebellum is necessary. Eyelid conditioning is an especially useful tool for studying the input/output computations of the cerebellum, owing to the relatively direct ways in which eyelid conditioning engages the cerebellum. Several decades of research, beginning with the studies of Thompson and his colleagues (e.g., Thompson 1986) have solidified three important findings in this regard (see Figure 7):

1. During eyelid conditioning the conditioned stimulus, often a tone, is conveyed to the cerebellum via activation of mossy fiber afferents from the pons.
2. Similarly, the reinforcing or unconditioned stimulus, usually a mild shock around the eye from a puff of air directed at the eye, is conveyed to the cerebellum via climbing fiber afferents from the inferior olive.
3. Output from the cerebellum, in the form of increased activity of particular neurons in the cerebellar interpositus nucleus, drives the efferent pathways responsible for the expression of the learned responses.

Because of these three findings, the extensively characterized behavioral properties of eyelid conditioning can be applied as a first approximation of what the cerebellum computes (Mauk & Donegan 1997, Medina et al. 2000, Medina & Mauk 2000, Ohyama et al. 2003).

The involvement of the cerebellum in both interval timing tasks and in the timing of learned responses raises the question: Is the computation performed by the cerebellum best understood as an interval timer or clock, or does cerebellar involvement in eyelid conditioning reveal a more learning-related computation? Based on recent evidence we support the latter. Specifically, cerebellar involvement in both tasks can be explained by the hypothesis that the computation performed by the cerebellum is a learned, feed-forward prediction. Additionally, the temporal portion of the computation would not rely on fixed timers or clocks but instead on network mechanisms that can perform both temporal and spatial computations. Several authors have argued that the cerebellum makes a feed-forward prediction, or generates forward models (e.g., Ito 1970, Kawato & Gomi 1992). Here we focus on the feed-forward computation itself and implications of its temporal specificity. Although it is easier to introduce the feed-forward prediction idea in the context of motor control, the computation is presumably applicable to nonmotor tasks influenced by the cerebellum as well (see Schmahmann 1997).

FEED-FORWARD PREDICTION AND THE CEREBELLUM To help make movements accurate, sensory input can be used in two general ways: feedback and feed-forward. Feedback is like a thermostat; outputs are produced by comparing sensory input with a target. When input from its thermometer indicates the room is too cold, a thermostat engages the heater. Although accuracy is easily achieved with feedback, it has the inherent disadvantage of being slow. Adjustments are only possible once errors have already occurred.

In contrast, feed-forward use of sensory input can operate quickly but at the cost of requiring experience through learning. To react to a command to change room temperature quickly, a hypothetical feed-forward thermostat would predict the heater blast required from current sensory input. This prediction would draw upon previous experience and require associative learning in which error signals were used to adjust decision parameters for errant outputs. If our hypothetical feed-forward thermostat undershoots the target temperature, then learning from the error signal should adjust the connections of recently activated inputs so that in subsequent similar situations the heater is activated a little longer. Thus, through associative, error-driven learning it is possible to acquire the experience necessary to make accurate feed-forward predictions.

Eyelid conditioning reveals that cerebellar learning displays precisely these properties (see Mauk & Donegan 1997, Ohyama et al. 2003). Learning associated with feed-forward prediction should be associative, and there should be a precise timing to the association. An error signal indicates that the prediction just made was incorrect. For example, an error signal activated by stubbing one's toe when walking indicates that in similar circumstances the leg should be lifted higher. Thus, error signals should modify feed-forward predictions for the inputs that occurred approximately 100 ms prior (Figure 8*a*). This means the results of the learning will be timed to occur just prior to the time error signals arrive. Eyelid conditioning displays these properties. The conditioned responses are timed to occur just before the time at which the error signal (puff to the eye) normally occurs (Figure 8*b*).

The timing displayed by conditioned eyelid responses reveals both temporal specificity and flexibility to this associative learning, both in ways that are useful for feed-forward prediction. Timing specificity is revealed in the way conditioned eyelid responses are time locked to occur just before the arrival of the puff. This is consistent with what feed-forward associative learning must accomplish. When a climbing fiber error signal arrives, learning should selectively alter the cerebellar output that contributed to the faulty movement. Thus, learning should produce changes in output that are time locked to occur around 100 ms prior to the climbing fiber input, as is seen in the timing of eyelid responses. The flexibility of the timing is revealed by the way in which eyelid conditioning can occur with a range of time intervals between the onsets of the tone and puff. Even though learning can occur for mossy fiber inputs that begin 100 to ~2500 ms prior to the climbing fiber input, the changes in output remain time locked to occur just before the climbing fiber input (Figure 8*b*). To accomplish this, the learning must have the capacity to delay the responses with respect to the onset of the mossy fiber input—again, as eyelid conditioning reveals. These examples show the utility for feed-forward control of learning that is time locked to occur just before error signals (when the decisions actually have to be made) but that can vary with respect to the timing of predictive sensory signals (see Ohyama et al. 2003).

TEMPORALLY SPECIFIC FEED-FORWARD PREDICTION AND TIMING Considering cerebellar function in terms of its feed-forward computation provides an example of the cerebellum's role in timing. Feed-forward prediction helps determine the force required for agonist muscles and the force and timing of activating

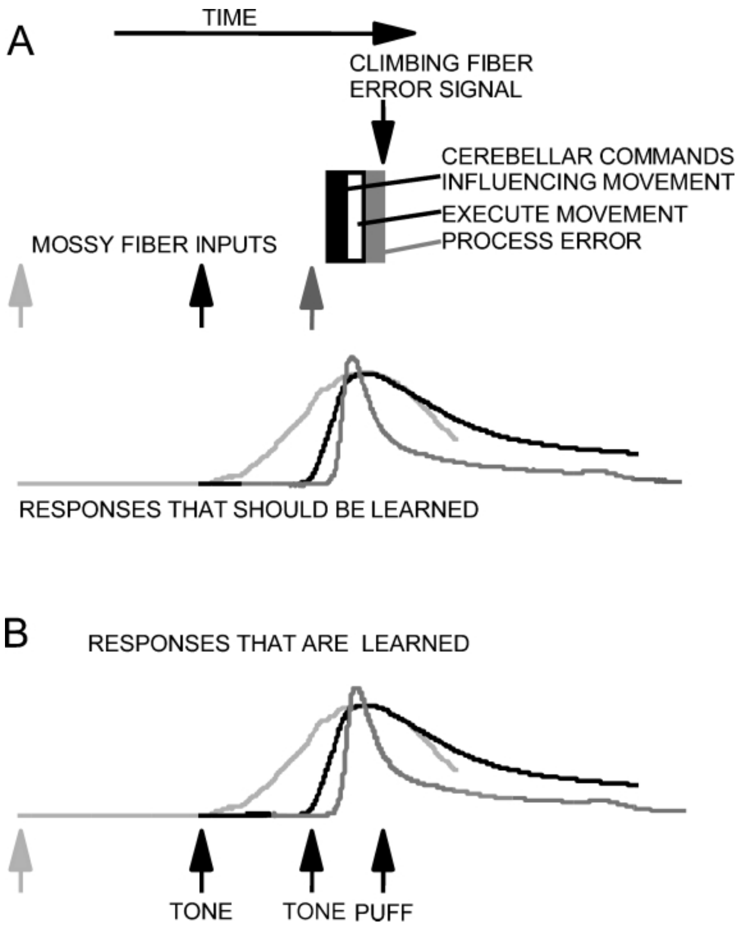

Figure 8 Feed-forward learning is enhanced by temporal specificity. (*A*) A schematic representation of the timing required for error-driven associative learning supporting feed-forward predictions. A climbing fiber input to the cerebellum (*gray*) signals movement error as detected by an inappropriate consequence (e.g., stubbing the toe while walking). The cerebellar output that contributed to this errant movement (*black*) occurred approximately 100 ms prior, owing to the time required to execute the movement (*white*) and the time required to detect the error and convey the signal to the cerebellum. To improve subsequent performance, learning must alter cerebellar output for the time indicated by the black region. Because mossy fiber inputs that predict this error may occur at varying intervals prior to the output commands (*light gray, black, and dark gray*), the cerebellar learning mechanism must be able to delay learned responses elicited by the mossy fiber input so that they can be time locked to occur just before arrival of the error signal (*corresponding light gray, black, and dark gray traces*). (*B*) The learned timing of eyelid responses indicates that cerebellar learning displays temporal specificity in its learning. Response timing is delayed with respect to the tone (mossy fiber) onset so that it can be time locked to peak when the puff (climbing fiber) occurs.

antagonist muscles. Deficits from the absence of this contribution would be especially notable for movements that involve stopping and starting, as in the timing experiments that require finger tapping. This is consistent with the deficits seen from medial cerebellar damage (vermal and intermediate cerebellum), whose outputs contribute relatively directly to movement execution through descending pathways.

This view is also consistent with recent findings that apparent timing deficits are specific to discontinuous timing tasks relative to continuous ones. Spencer et al. (2003) tested cerebellar patients on two similar timing tasks. Two groups of subjects were required to draw circles at regular intervals. The "discontinuous" group was required to keep a beat by pausing at the top of each circle. The "continuous" group was instructed to keep a beat by drawing circles using a steady continuous motion. Cerebellar damage affected discontinuous drawing and not continuous. The authors interpret these findings as evidence that the cerebellum is required for tasks where timing is explicitly represented, as in the discontinuous task. In this view, the cerebellum is not required by the continuous task because timing can be implicit—that is, timing can be produced by maintaining a constant angular velocity. Alternatively, such findings can be seen as examples of the contributions of feed-forward prediction in the starting and stopping of movements. Holmes (1939) made a similar observation (see also Dow & Moruzzi 1958). He asked a patient to first draw squares with the hand affected by the cerebellar lesion and then by the unaffected hand. Holmes found that the motor deficit of the affected hand was most notable at the corners of the square, where stopping and starting movements are required.

Although more speculative, the feed-forward computation of the cerebellum may provide a way to understand the activation of the cerebellum in many timing tasks and explain the timing deficits observed with lateral cerebellar damage. Feed-forward prediction in lateral cerebellum may be a mechanism for predicting when the next tap should occur in a timing experiment. The cerebellum therefore underlies some forms of motor timing. This timing relies on distributed network mechanisms as opposed to a dedicated clock or timer (see below).

CORTEX

The cortex has also been proposed to be the the primary site for temporal processing. If the cortex is involved in timing, whether virtually all cortical areas can processes time, or if specialized cortical areas devoted to temporal processing exist, is a fundamental issue.

Anatomy

Based on data from stroke patients Harrington et al. (1998b) suggested the right parietal cortex may be involved in temporal processing. Specifically, right hemisphere, but not left hemisphere, lesions produced a deficit for 300- and 600-ms interval discrimination. Imaging studies also reported changes in blood flow during temporal tasks in various cortical areas. In a PET study Belin et al. (2002) report activity in the right fronto-parietal network and prefrontal cortex during a 300-ms duration discrimination task. However, this study did not include a control task, and thus activation could be related to any form of processing. A second PET study in the visual modality reported activation in a number of cortical areas during a 700-ms duration discrimination task but no significant difference regarding an intensity discrimination task (Maquet et al. 1996). Onoe et al. (2001) showed activation of the dorsolateral prefrontal cortex in a monkey PET study. This study used a visual duration discrimination task in the range of 400 to 1500 ms. They report activation of the dorsolateral prefrontal cortex. Although there was no control task, they did report that bicuculline administration to the dorsolateral prefrontal cortex impaired duration discrimination more so than position discrimination.

Two fMRI studies revealed specific increases in BOLD signal, and both reported activation of the right parietal and dorsolateral prefrontal cortex (Rao et al. 2001, Nenadic et al. 2003). In both these studies the increases were in comparison to a pitch discrimination task using stimuli in the 1-s range. As mentioned above, both these studies also revealed increased signal attributed to temporal processing in the basal ganglia but not in the cerebellum.

Electrophysiology

In addition to imaging data a few studies attempted to find, in the mammalian cortex, neurons that respond selectivity to temporal features. Vocalization-sensitive neurons were reported in primary auditory cortex of marmoset monkeys (Wang et al. 1995). Neurons responded more robustly to conspecific vocalizations compared to the same vocalization played in reverse. Additionally, vocalization-sensitive neurons were also reported in early auditory areas of Rhesus monkeys (Rauschecker et al. 1995). Creutzfeldt et al. (1989) described speech-specific neural responses in the human lateral temporal lobe. However, to date, no areas have been described in which the neurons exhibit the same degree of selectivity to vocalizations as that observed in songbirds. Other investigators have looked for combination or interval-sensitive neurons using tone pairs or sequences. Selectivity has been observed in primary auditory areas in cat (McKenna et al. 1989, Brosch & Schreiner 1997) and monkey (Riquimaroux 1994). Kilgard & Merzenich (1998, 2002) characterized the temporal selectivity of auditory cortical neurons to sequences of tones. In one study three element sequences such as high tone (H), low tone (L), noise burst (N) were paired with basal forebrain stimulation in awake rats (Kilgard & Merzenich 2002). A significant increase was reported in the number of sites that exhibited facilitated responses to the target sequence, indicating experience-dependent plasticity. For example, after training in H-L-N sequence, an enhanced response to N preceded by H–L was reported, as compared to N alone. The enhanced responses often generalized to degraded stimuli such as L-H-N. The temporal feature selectivity of cortical neurons undergoes experience-dependent plasticity. However, future research is necessary to determine the degree of selectivity and whether these areas represent the primary locus for features such as interval, duration, and order.

To date, one study has looked for neurons that may code for time in awake-behaving monkeys. Leon & Shadlen (2003) recorded in the lateral intraparietal cortex in two monkeys trained on a duration discrimination task in the visual modality. Two standard durations were examined: 316 and 800 ms. The individual neurons contained information about time from stimulus onset. Time from stimulus onset was encoded in the instantaneous firing rate, which changed predictably with time. The encoding was very dynamic; specifically, the same neuron would show an upward or downward ramping of its firing rate depending on the location of the short or long target used for the response. Additionally the rate of change was slower for long durations than for short durations. Thus timing might be achieved by complex network mechanisms capable of dynamically changing firing rates in a context-specific manner. Whether the same neurons would contain temporal information if the task was auditory, or whether neurons in other areas contained the same information, has not been determined.

In Vitro Studies

It has been proposed that cortical neural networks are intrinsically capable of processing temporal information (Buonomano & Merzenich 1995). If this is the case it may be possible to observe timed responses in vitro. In vitro studies cannot address whether the observed timing is behaviorally relevant. They can, however, establish whether neurons and neural circuits are capable of processing temporal information or whether specialized mechanisms are present. Long-latency timed action potentials in response to continuous synaptic stimulation (Beggs et al. 2000), or in response to single stimuli (Buonomano 2003), have been observed. In organotypic cortical slices, neurons can respond reliably at latencies of up to 300 ms after a single stimulus (Buonomano 2003). Thus cortical circuits are intrinsically capable of generating timed responses on timescales well above monosynaptic transmission delays. Mechanistically, timing relied on network dynamics, specifically, activity propagated throughout functionally defined polysynaptic pathways. The propagation path was a complex function of the functional connectivity within the network and was not simply a result of spatial wave-like propagation.

To date, relatively few studies have revealed cortical neurons strongly tuned to the interval or duration of tones or to complex sounds on the scale of hundreds of ms. These data contrast sharply with the tuning of cortical neurons to spatial stimuli such as orientation, ocular dominance, tonotopy, and somatotopy. It is more difficult to study temporal selectivity because temporally tuned neurons may not be topographically organized. In the visual cortex, if we record from a cell selective to vertical bars, the neighboring cells may also be tuned to vertical bars. Given the vast number of possible spatio-temporal stimuli, and the potential absence of chronotopy, it may prove difficult to localize temporal selective neurons with conventional extracellular techniques.

NEURAL MECHANISMS AND MODELS OF TIMING

Analyses of the neural basis of timing have generally focused on three general computational strategies: mechanisms based on neural clocks, mechanisms based on arrays of elements that differ in terms of some temporal parameter, or mechanisms that emerge from the dynamics of neural networks. In general, these models must accomplish some variant of the same computational task. They must recode the temporal information present in an input into a spatial code. That is, in some way different cells must respond selectively to temporal features of the stimulus. For example, to discriminate differences in the duration of two stimuli, there must be differential neuronal responses to each duration.

Clock Models

When considering the mechanisms of timing it is perhaps most intuitive to think in terms of clocks or interval timers. The basic computational unit of clock theories involves an oscillator and a counter (Creelman 1962, Treisman 1962). Conceptually, the oscillator beats at some constant frequency, and each beat would then be counted by some sort of neural integrator. These ideas have not yet been expressed concretely in terms of the synaptic organization of a specific brain region. Indeed, in its simplest form, if such a clock were used for the discrimination of 100-ms intervals (and allowed the discrimination of a 100- and 105-ms interval) the period of the oscillator would have to be at least 200 Hz. At the neurophysiological level, oscillating at this frequency, as well as accurately counting each beat, seems unlikely. However, as proposed by Meck and colleagues, clock-like mechanisms could be involved in timing on the scale of seconds and minutes (Meck 1996, Matell & Meck 2000).

OSCILLATOR-PHASE MODELS In addition to the oscillator/counter models mentioned above, more sophisticated models based on oscillators have been proposed (Ahissar et al. 1997, Ahissar 1998, Hooper 1998). These include the use of oscillators placed in phase-locked loop circuits. Specifically, Ahissar and colleagues have proposed (Ahissar et al. 1997, Ahissar 1998) that the thalamo → cortical → thalamo loop may use dynamic oscillators (oscillators that can change their period in an adaptive manner) to decode temporal information from the vibrissa during whisking in rodents.

Spectral Models

Many of the proposed models share the characteristic of decoding time using arrays of neural elements that differ in terms of some temporal property. The most generic of these is the spectral timing model of Grossberg and colleagues (Grossberg & Schmajuk 1989), which has been expressed in varying forms. The original model assumed a population of cells that react to a stimulus with an array of differently timed responses. Two variants of this motif have also appeared. One is a variant of clock models: Stimuli activate arrays of cells that oscillate at different frequencies and phases. By doing so, points in time following the onset of a stimulus can be encoded by activity in a subset of neurons that differs, at least somewhat, from the subsets of cells active at other times (Miall 1989, Gluck et al. 1990). In another model generally referred to as tapped delay lines, simple assumptions about connectivity lead to a sequential activation of different neurons at different times following a stimulus (Desmond & Moore 1988, Moore 1992, Moore & Choi 1997).

A number of studies propose biologically plausible implementations of spectral models. In these models all elements share a common implementation, but at least one of the variables is set to a different value, which allows each unit to respond selectively to different intervals. A wide range of biological variables have been proposed, including the kinetic constants of the metabotropic receptor pathway (Fiala et al. 1996), the time constant of slow membrane conductances (Hooper et al. 2002; see also Beggs et al. 2000), the decay time of inhibitory postsynaptic potentials (IPSPs) (Sullivan 1982, Saitoh & Suga 1995), short-term synaptic plasticity (Buonomano 2000, Fortune & Rose 2001), or even cell thresholds (Antón et al. 1991).

Spectral models have the advantage of encoding the time since the arrival of a stimulus by having different subsets of cells active at different times. Combined with simple learning rules where a teaching or error signal modifies connections for only active cells, spectral models can learn outputs that are properly timed and can even show the Weber effect of increased variance with increased delay. However, to date, neither arrays of elements with different time constants, arrays of elements that oscillate at different phases and frequencies, nor connectivity that supports tapped delay lines are supported by identified properties of neurons or networks. Additionally, these models focused on simple forms of temporal discrimination and may not generalize well to more complex forms of temporal processing without additional network layers (see below).

Network or State-Dependent Models

The above models represent top-down approaches where timing is addressed by inferring a computation and then implementing the computation with neurons. An alternative bottom-up approach is to start with biologically realistic assumptions and then to ask the extent to which temporal processing can be found as an emergent property. These models have no built-in temporal processing or selectivity with ad hoc assumptions. That is, they do not rely on explicitly setting oscillators, synaptic or current-time constants, or some other variable that, in effect, functions as a delay line.

CORTICAL MODEL It has been proposed that cortical networks are inherently able to process temporal information because information about the recent input history is inherently captured by time-dependent changes in the state of the network (Buonomano & Merzenich 1995, Buonomano 2000, Maass et al. 2002). One set of studies has examined how interval selectivity can be encoded in a population of cortical neurons (Buonomano & Merzenich 1995, Buonomano 2000). In an interval discrimination task, when the first of a pair of tones arrives in a cortical network, it will stimulate hundreds of excitatory and inhibitory neurons, a subset of which will fire. In addition to producing action potentials in some neurons, a series of time-dependent processes will also be engaged. In this model the time-dependent properties were short-term synaptic plasticity (Deisz & Prince 1989, Stratford et al. 1996, Reyes et al. 1998, Zucker 1989) and slow IPSPs (Newberry & Nicoll 1984, Buonomano & Merzenich 1998b), but it could include many other time-dependent properties. In this model all synapses exhibit the same short-term plasticity temporal profile, as opposed to spectral models. Because of these time-dependent properties, the network will be in different states at 50, 100, and 200 ms. Thus, at the arrival of a second event at 100 ms, the same stimulus that arrived at 0 ms will arrive in a different network state. That is, some synapses will be facilitated/depressed, and some neurons may be hyperpolarized by slow IPSPs. As a result, the same input can activate different subpopulations of neurons dependent on the recent stimulus history of the network. The differences in the population activity produced by the second and first pulse can be used to code for the 100-ms interval. Given the high dimensionality and abundance of time-dependent properties of cortical networks, this type of model could provide a realistic means to decode complex temporal and spatial-temporal patterns of sensory information (see below).

CEREBELLAR MODEL The evidence from the cerebellum illustrates how timing and performance on experimental tasks designed to study timing are mediated by computations that include temporal processing. For example, cerebellar-mediated, feed-forward prediction may be the computational basis for the temporal processing responsible for timing tasks in the millisecond range.

Buonomano & Mauk (1994) used the correspondence between eyelid conditioning and the cerebellum to test the timing capabilities of a network model of the cerebellar cortex. Although this model failed in many of its key properties, it showed how the connectivity of the cerebellar cortex could represent the time since the onset of a stimulus with subsets of different granule cells that become active at different times (Figure 9*A*). This time-varying stimulus representation was similar in many respects to the activity assumed in certain of the spectral timing models described above. The key mechanistic difference was that this activity was the natural consequence of the sparse, distributed, and recurrent connectivity of the cerebellar cortex.

By incorporating a more complete representation of the connectivity of the olivo-cerebellar circuitry, and by including recent findings regarding the specific synaptic conductances found in cerebellar neurons, a second-generation model now accounts for all key temporal properties of eyelid conditioning (Medina & Mauk 2000). As shown in Figure 9*B*, the timing of conditioned eyelid responses was partly derived from a competitive learning mechanism that increases the temporal specificity of the cerebellar learning was one of the key findings from these simulations (Medina et al. 2000). The key process involves the bidirectional learning in the cerebellum that eyelid conditioning and other forms of learning reveal (Raymond et al. 1996).

Thus, computer simulations and related eyelid conditioning experiments suggest that timing mechanisms in the cerebellar cortex involve three interacting processes (Figure 9). First, sparse recurrent interactions between cerebellar Golgi and granule cells lead to the activation of different granule cells at different times during a stimulus. The activity in granule cells therefore not only codes stimuli, as suggested in seminal theories of cerebellum (Marr 1969), but also codes time elapsed during stimuli. With this temporal code it is then possible for a coincidence-based form of plasticity, such as cerebellar LTD (see Hansel et al. 2001), to mediate learned responses that can be specific for certain times during a stimulus. Finally, competition between excitatory and inhibitory learning sharpens the temporal resolution of the timed responses.

In these network or state-dependent models, timing does not arise from clocks or even from brain systems specifically dedicated to temporal processing. Rather, the evidence from the cerebellum, for example, illustrates how timing and performance on experimental tasks designed to study timing may be mediated by computations that include temporal processing but that are not accurately characterized as interval timers or clocks.

FUTURE CHALLENGES: COMPLEX STIMULI

Most of the experimental and theoretical studies discussed above have focused on relatively simple stimuli. In particular, much of the work has been on the discrimination of the interval or duration of stimuli or on the generation of a single, timed motor response. The mechanisms underlying speech and music recognition, as well as the ability to process Morse code, require sophisticated mechanisms that can process multiple temporal cues in parallel and sequences composed of a continuous stream of elements with no a priori first and last element. Thus, a fundamental issue, particularly in relation to the computational models, is whether these models are sufficiently robust to account for more complex data. Indeed, if a model is limited to the discrimination of simple first-order stimuli (interval and duration), then this model is unlikely to represent the biological mechanisms underlying temporal processing in the range of tens to hundreds of ms.

Higher-Order Stimuli

Consider the stimuli shown in Figure 10, in which a subject must discriminate between 2 sequences composed of 2 intervals (3 tones): 50–150 and 150–50. In reality, in this task one would include 50–50- and 150–150-ms stimulus conditions to prevent the use of simple strategies. In clock or spectral models, neurons would have to respond selectively to the 50- and 150-ms intervals. Additionally, because both stimuli would activate the 50- and 150-ms interval detectors, another circuit would have to keep track of the order of activation, to discriminate between (50–150 and 150–50). Thus as sequences become more complicated, additional circuitry is generally required to keep track of the higher-order features.

Reset Problem

The processing of sequences, as opposed to a single interval or duration, also imposes another constraint on the potential mechanisms underlying temporal processing. Let us consider how a spectral model will perform in response to the sequences shown in Figure 10. In a model based on a slow conductance such as an IPSP, the first tone will activate an IPSP of a different duration in each cell. If the second pulse arrives at 50 ms, the 50-ms detector will fire (owing to the interaction between IPSP offset and arrival of the second stimulus). However, the second pulse is also the first pulse of the second interval, and thus to detect the subsequent 150-ms interval, the second pulse would essentially have to reset the inhibitory conductance. We refer to this as the reset problem. When stimulus elements arrive on the same timescale as the intervals being processed, discrimination requires that the event that marks the end of one interval engage the initiation of the timing of the next interval. Resetting of synaptic conductances, in particular, is unlikely. In spectral models, a potential solution for this problem is to look at the above task as detecting two intervals 50–200 (50 + 150) versus 150–200 (150 + 50). In this manner the second pulse would not have to reset the timer because all timing would be relative to the first pulse. Nevertheless, the second pulse could not interfere with the ongoing computation of the 200-ms interval. This could perhaps be achieved by assuming that the first pulse saturated or depleted the mechanisms responsible for inhibition. However, we believe it is unlikely that spectral models are robust enough to generalize to complex temporal processing involved in speech and music recognition and complex motor patterns.

In contrast, models based on network dynamics may better generalize to the processing of more complex temporal patterns. In state-dependent network models (see above; Buonomano & Merzenich 1995, Buonomano 2000, Maass et al. 2002), the current state of the network is always dependent on the recent history of activity. Thus, in the above example, if the third input arrives at 200 ms, the network will be in a different state depending on whether the second pulse arrived at 50 or 150 ms. In these models, time-dependent properties, such as short-term synaptic plasticity, slow PSPs (e.g., $GABA_B$ or NMDA-dependent currents), or, potentially, slow conductance, function as state-dependent memory traces of the recent stimulus history. In contrast to single-cell models, these time-dependent properties are not tuned for any particular interval; rather these states are expressed as changes in the probability of different neurons becoming activated.

Figure 10 shows results from a state-dependent network model capable of discriminating intervals as well as simple sequences (Buonomano 2000). The network was composed of 400 excitatory and 100 inhibitory units; all synapses exhibited short-term synaptic plasticity, and a slow IPSP was also present. As a result of the time-dependent properties, the network is in a different state at 50 and 150 ms; thus different neurons will respond to the second pulse depending on its arrival time. Because different neurons responded to the second pulse, state-dependent change will be cumulative and alter the response to the third pulse in a different manner depending on the stimulus history. There are two potential shortcomings of state-dependent networks. First, the network must be in a specific regime that allows that expression of the state-dependent changes, which can be nontrivial because a balance between excitation and inhibition is required. Specifically, inhibition must enable excitatory neurons to fire while preventing run-away excitation. Second, because these networks encode time as relative to previous stimuli, they would be least effective at identifying specific intervals embedded in sequences, for example, comparing a 100-ms interval defined by two tones with a 100-ms stimulus embedded within a sequence of tones.

CONCLUSIONS

The study of the neural basis of temporal processing is in its infancy. Few agree on whether temporal processing is centralized or distributed and which structures are involved. Indeed, if all neural circuits can intrinsically process temporal information, then virtually any circuit could be involved, and the location of temporal processing would depend on the nature and modality of the task at hand. Despite the fact that these important questions remain unanswered, the studies, to date, allow several insights into the nature of timing. First, although researchers do not agree on which areas are involved in sensory timing, it seems clear that the cerebellum is responsible for some forms of motor timing. Whether it is the sole source of motor timing and whether it is involved in sensory processing remain open to debate. Second, much evidence indicates that distinct neural mechanisms underlie millisecond and second timing.

Many models of timing have focused on specialized synaptic and cellular mechanisms aimed specifically at processing temporal information, and investigators assumed that spatial and temporal information are essentially processed separately. Given the inherent temporal nature of our sensory environment, and the continuous, real-time motor interaction with our environment, we favor the view that temporal and spatial information are generally processed together by the same circuits, and that there is no centralized clock for temporal processing on the scale of tens to hundreds of ms. Additionally, we propose that temporal processing does not rely on specialized mechanisms, such as oscillators or arrays of elements, as with a spectrum of different time constants. Rather, we believe that neural circuits are inherently capable of processing temporal information as a result of state-dependent changes in network dynamics.

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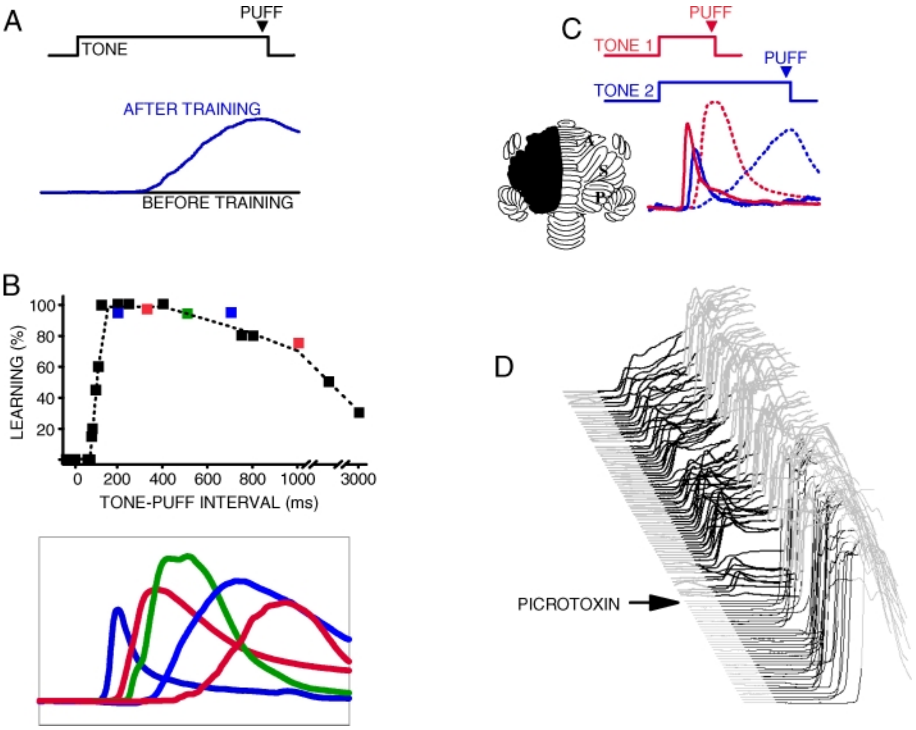

Figure 3 Temporal properties of learned eyelid responses. Classical or Pavlovian eyelid conditioning displays learned timing. (*A*) In a typical experiment, training involves presentation of a neutral stimulus, such as a tone, paired with a reinforcing stimulus, such as a puff of air directed at the eye. (*Lower traces*) Repeated presentation of such trials leads to the acquisition of learned eyelid responses. Before training the tone does not elicit an eyelid response, whereas after training the upward deflection of the trace indicates that the tone elicits learned eyelid closure. In this case the tone-puff interval is 500 ms. (*B*) The time delay between the onsets of the tone and puff influences learning in two ways. First, learning only occurs for delays between approximately 100 and 3000 ms. Best learning is produced by delays ranging from 200 to 1000 ms. The tone-puff delay also determines the timing of the learned responses. These are sample learned responses for animals trained with the delays coded by the color of the points in the graph. (*C*) Lesions of the cerebellar cortex disrupt learned response timing. Animals trained using two tones and two tone-puff delays were then subjected to lesions of the cerebellar cortex (*example shown in inset*). The lesions produced a short and relatively fixed latency-to-onset interval independent of prelesion timing. Modified from Perret et al. 1993. (*D*) Reversible lesions or disconnection of the cerebellar cortex produce the same effect on timing. These are example responses from a training session in which the cerebellar cortex was functionally disconnected via infusion of the GABA antagonist picrotoxin into the cerebellar interpositus nucleus. The darker portion of each trace indicates the tone; responses are chronologically organized front to back. Modified from Medina et al. 2000.

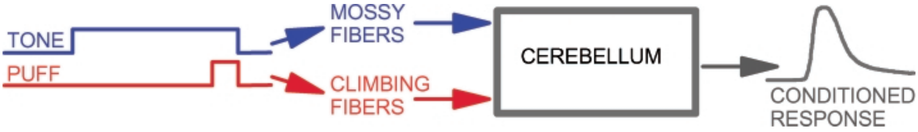

Figure 7 Eyelid conditioning engages the cerebellum relatively directly. This is a schematic representation of the relationship between eyelid conditioning and the cerebellum. Output of the cerebellum via its anterior interpositus nucleus drives the expression of conditioned responses. Stimuli such as tones are conveyed to the cerebellum via activation of mossy fiber inputs. Reinforcing stimuli such as the puff of air directed at the eye are conveyed to the cerebellum via activation of climbing fibers.

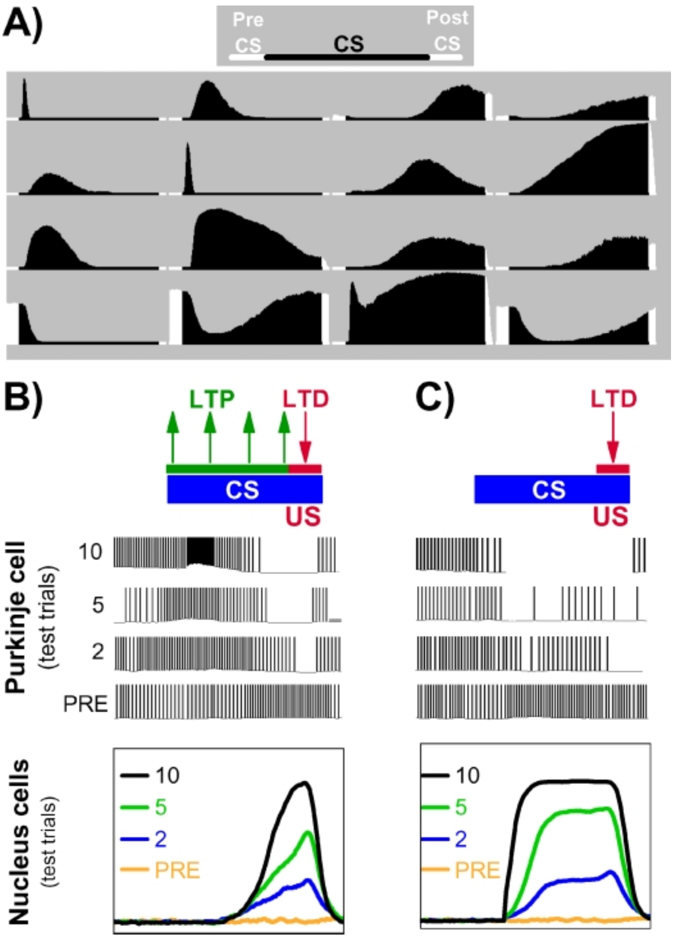

Figure 9 Mechanisms of timing-specific learning in the cerebellum. Computer simulations of the cerebellum in the context of eyelid conditioning suggest mechanisms for learned response timing. (*A*) Peri-stimulus histograms of simulated granule cells for the presentation of a tone-like mossy fiber input to the cerebellum. This sample shows how different granule cells respond at different times during this stimulus. These simulated granule cells have identical temporal properties; these differently timed responses arise from network interactions with mossy fiber inputs and with cerebellar Golgi cells. (*B*, *C*) The simulations suggest that learned timing is enhanced by competitive learning within each trial. Proper timing requires mechanisms both for learning (LTD) responses, when a climbing fiber is present, and unlearning (LTP) responses, when it is absent. (*B*) Through these two mechanisms, the simulated cerebellar Purkinje cells can learn well-timed modulation of their activity during learning. (*C*) In simulations with unlearning disabled, timing of Purkinje cell response and of the learned responses of the simulation is impaired. Modified from Medina & Mauk 2001.

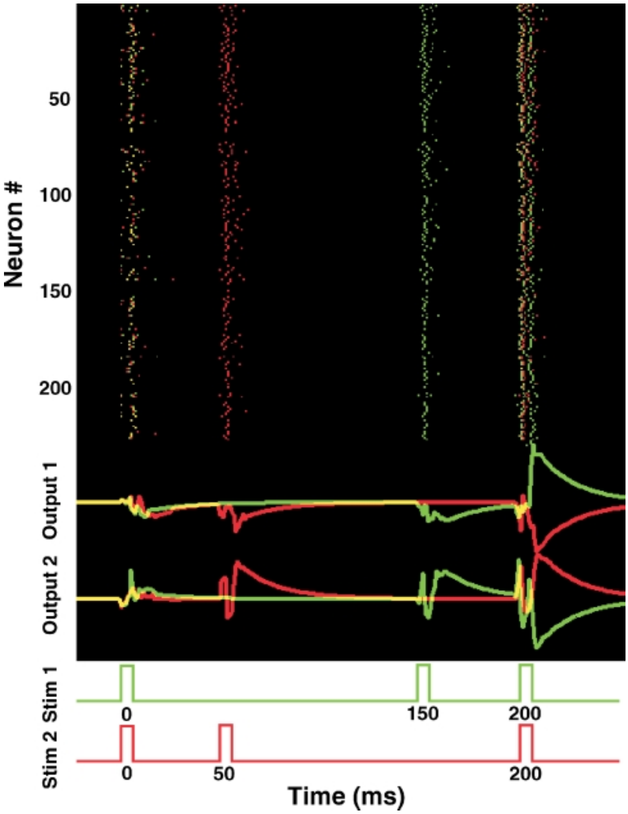

Figure 10 State-dependent model of sequence recognition. The model is composed of excitatory and inhibitory neurons. The connectivity and synaptic weights are randomly assigned, the synapses exhibit short-term synaptic plasticity, and a slow-IPSP is present. The time constant of the short-term plasticity and slow IPSP is the same for all synapses in the network. The raster plot shows which excitatory neurons fired to the long-short stimulus (*green*) and to the short-long stimulus (*red*). If the neuron responded at the same time to both stimuli the spike is plotted in yellow. Note that there is more yellow in response to the first pulse than to the last (all points in response to the first pulse are not yellow because of intrinsic noise). Each pulse of a stimulus will activate a population of neurons and trigger short-term plasticity; thus at the arrival of the second pulse the network will be in a different state, depending on whether the second pulse arrived at 150 (*green*) or 50 ms (*red*). For both stimuli (long-short or short-long) the third pulse arrives at 200 ms; however, the network will be in a different state depending on the stimulus, allowing the network to respond differently to the same pulse. The two lower traces represent the voltage of two output neurons that receive input from all the excitatory neurons above. The weights on the output neurons were set by training (using a nontemporal learning rule) on different stimulus set presentations. Outputs 1 and 2 respond selectively to the long-short and short-long stimuli, respectively.

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Remembering the time: a continuous clock

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The neural mechanisms for time measurement are currently a subject of much debate. This article argues that our brains can measure time using the same dorsolateral prefrontal cells that are known to be involved in working memory. Evidence for this is: (1) the dorsolateral prefrontal cortex is integral to both cognitive timing and working memory; (2) both behavioural processes are modulated by dopamine and disrupted by manipulation of dopaminergic projections to the dorsolateral prefrontal cortex; (3) the neurons in question ramp their activity in a temporally predictable way during both types of processing; and (4) this ramping activity is modulated by dopamine. The dual involvement of these prefrontal neurons in working memory and cognitive timing supports a view of the prefrontal cortex as a multipurpose processor recruited by a wide variety of tasks.

Introduction

Awareness of the passage of time is inextricably intermingled with memory. This is not only true for the remembrance of things past. Sometimes we must remember the beginning of an event to judge its duration but often we must also remember the time as it passes, and if distracted we can 'lose track of time' and burn the muffins or miss the train. In this article, we propose that the same neurons which are used for working memory can also be used to index the passage of time.

Most models of how the brain measures time acknowledge the link between time and memory. In scalar expectancy theory [1], a framework which has dominated the field for almost 30 years, working memory takes the form of an accumulator process which collects quantized ticks from a hypothetical neural pacemaker. A more recent model [2], the multiple time scales (MTS) framework, dispenses with the pacemaker entirely and proposes that time can be measured using the decaying strength of memory traces. In this article, we expand upon this idea by suggesting that continuous, temporally predictable changes in firing rate could be used to measure time, and observe that some of the prefrontal 'delay' cells which are known for their role in working memory actually behave in this manner during timed intervals.

We propose that this temporally predictable ramping activity might serve as the timekeeping process during cognitively controlled time perception. Our hypothesis is supported by four crucial points. First, the dorsolateral prefrontal cortex, where these cells are located, is necessary for cognitively controlled time measurement tasks. Second, both working memory and cognitively controlled timing are modulated by dopamine and disrupted by manipulation of the mesolimbocortical dopamine pathway, which projects to the dorsolateral prefrontal cortex. Third, prefrontal neurons have been shown to ramp their activity in a temporally predictable way during timed intervals, and fourth, this ramping activity appears to be modulated by dopamine. We begin with an explicit definition of the form of time perception under discussion.

What is cognitively controlled timing?

Some timing processes help us to synchronize with our environment, including circadian and ultradian rhythms, for which the mechanisms are relatively well understood [3]. Other forms of time measurement, such as that needed for the coordination of complex movements, estimation of how long it takes to perform specific tasks, or prediction of when the train is about to depart, remain more mysterious. Because these tasks vary widely, it would be surprising if they all drew upon the same brain system.

Many researchers have suggested that distinct mechanisms exist for the measurement of different temporal durations [4–8], for motor versus nonmotor timing [9] and, more recently, for the timing of continuous cyclical versus discrete broken movements [8,10]. Several authors [8,11,12] have also suggested the existence of distinct mechanisms for automatic and cognitive forms of timing.

In a recent article [13], we built upon these findings by proposing that it is not any single characteristic, but rather a constellation of several characteristics which determines which timing system is recruited in any particular task. We tested this proposal using a meta-analysis of the neuroimaging literature on time measurement. Although other task characteristics might also be important, our analysis was constrained to consider just three: the duration measured, whether or not the timed intervals were defined by movement and, whether timing was continuous (e.g. an unbroken series of predictable intervals) or intermittent (e.g. broken into discrete measurements by the presence of unpredictable irregular intervals). Our findings indicated that tasks involving continuous measurement of a series of predictable subsecond intervals defined by movement (e.g. rapid paced finger tapping) tend to recruit primary

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sensorimotor and premotor areas, whereas tasks with the opposing characteristics tend to recruit right hemispheric prefrontal and parietal cortices (Figure 1). These results suggest that tasks recruiting only the sensorimotor system can be performed relatively automatically, whereas tasks which draw upon multipurpose prefrontal and parietal modules known for their involvement in working memory and attention might require more cognitive involvement.

Importantly, our analysis showed that having any two out of the three characteristics associated with a task type (cognitive or automatic) dramatically increased the probability that the areas associated with that timing system would be recruited. Accordingly, we can think of any task having two or more cognitive attributes (e.g. measuring more than a second, discontinuously, and without relying upon movement) as a 'cognitively controlled timing task', and any task with two or more of the opposing characteristics as an 'automatic timing task'. These definitions can be applied *post hoc* to any study of time measurement, a strategy which is useful in determining whether or not the existing literature supports the cognitive–automatic framework.

Cognitively controlled timing, right dorsolateral prefrontal cortex, and memory

Cognitively controlled timing activates the right hemispheric dorsolateral prefrontal cortex (DLPFC) more frequently than any other brain area [13]. The remainder of this article will focus specifically upon this region and its role in tracking the passage of time.

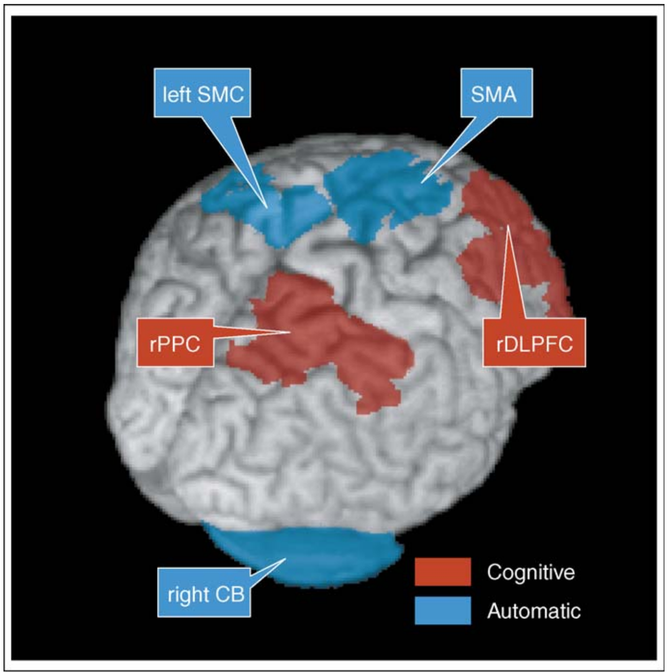

Figure 1. 3D depiction of the human brain regions associated with cognitively controlled (red) and automatic (blue) timing systems. These areas, identified in a meta-analysis of imaging studies [13], were defined for illustration using voxel-labelled templates in the automatic anatomical labelling atlas [50] and the mri3dX Brodmann atlas, rendered onto the SPM canonical brain (http://www.fil.ion.ucl.ac.uk/spm). Abbreviations: CB, cerebellum; SMA, supplementary motor area; SMC, sensorymotor cortex; rPPC, right posterior parietal cortex; rDLPFC, right dorsolateral prefrontal cortex.

The right DLPFC corresponds to the middle portion of middle and superior frontal gyri (e.g. Brodmann areas 9, 9/46 and 46) in humans, and to the region adjacent to the superior frontal sulcus in macaques [14]. That this part of the prefrontal cortex is strongly associated with working memory is evident from numerous studies using targeted lesions and single unit recording in monkeys, as well as from patient work and a vast collection of neuroimaging data [15]. Given the consensus that some form of working memory is important for timing, it is unsurprising that the DLPFC is essential to some timing tasks and that cells in this area exhibit a variety of time-sensitive behaviours [16]. Support for the right hemispheric lateralization of the involvement of this region in timing comes from neuropsychological work [17,18], examination of parkinsonian patients with unilateral deficits influencing the prefrontal cortex [19], and neuroimaging studies showing activity here during timing tasks (see Macar *et al*. [20] and Rubia and Smith [21] for reviews).

Importantly, right dorsolateral prefrontal activity is much more common in cognitively controlled timing tasks than in those classified as automatic [13]. Lesions to this area have been shown to disrupt cognitive timing [17], and the differential involvement of the right DLPFC in cognitive and automatic timing has been supported by a recent transcranial magnetic stimulation study showing impaired reproduction of suprasecond (more cognitive) but not subsecond (more automatic) intervals [22]. A parallel study showed that repetitive transcranial magnetic stimulation to the right but not left DLPFC disrupts the timing of suprasecond durations [23].

Overall, these data suggest that the region of the DLPFC that is known to be important for working memory is also essential for cognitively controlled time measurement but with an apparent bias to the right hemisphere. This area does not appear to be important for more automatic forms of timing.

Working memory and cognitive time measurement draw upon the same mental resources

Behavioural evidence that working memory and time measurement draw upon the same cognitive resources stems from dual-task studies showing interference between these two types of processing. Both visuospatial and phonological working memory tasks disrupt timing, and the extent of such disruption has been shown to correlate with the extent of working memory load (e.g. number of items to be remembered, number of syllables to be rehearsed or degrees of mental rotation) [24]. It is important to note that these experiments used timing tasks that would be classified as cognitively controlled.

Turning to pharmacology, manipulations targeting working memory can also disrupt cognitive timing. For example, benzodiazepines that influence working memory impair the processing of suprasecond intervals [6,8,11,25], whereas timing at the range of milliseconds appears to be unaffected by these drugs [26]. Similar dissociations have been shown for drugs thought to influence attentional processing such as the selective noradrenaline reuptake inhibitor reboxetene [25]. Rammsayer and co-workers [8,11,25] have interpreted this as evidence for two distinct timing mechanisms: an automatic mechanism for the measurement of durations in the millisecond range and a cognitive mechanism, mediated by attention and drawing upon working memory, for the measurement of intervals in the range of seconds. This proposal differs from our cognitive–automatic framework [13] only in that these authors regard the timed duration as the prime discriminant between systems, whereas we propose that a combination of characteristics determines which system is recruited. Also, Rammsayer and co-workers investigated extremely brief intervals (~50 ms) and placed the cut-off between timing systems at around 500 ms, whereas we suggest that the critical value is closer to 1 s. Irrespective of these minor differences, both frameworks agree that separate systems exist for different types of time measurement and that at least one of these systems draws upon cognitive processors in the prefrontal cortex, with those regions known to be involved in working memory as prime candidates.

Dopamine, DLPFC, time, and memory

Additional evidence linking time perception to working memory stems from the observation that both are modulated by dopamine, a neurotransmitter which regulates activity throughout much of the brain, including the prefrontal cortex. The influence of prefrontal dopaminergic projections upon working memory is well documented [27]. Both increases in prefrontal dopamine and application of dopamine antagonists have been shown to disrupt this process [28], suggesting that deviation from an optimal level is detrimental to performance. Additionally, prefrontal dopamine levels increase during working memory tasks [29] and recording studies have demonstrated dopaminergic modulation of the layer III pyramidal cells associated with maintenance of information in working memory [30] (e.g. ‘delay’ neurons [28]). The importance of dopamine for temporal processing is also well established. A comprehensive review of work in nonhumans [31] argues that increasing levels of dopamine leads to a speeding up of subjective time. By contrast, decreasing dopamine leads to a slowing of subjective time [18]. In humans, both control subjects [8] and parkinsonian patients [4,19] have demonstrated a strong dopaminergic influence upon temporal processing, although it has been difficult to replicate the precise effects seen in the animal data [32].

Because the basal ganglia are heavily innervated by dopamine, and because their function is severely disrupted in Parkinson’s disease, the influence of dopamine on subjective time measurement has typically been interpreted as support for the central role of these structures in timing. However, in addition to the mesostriatal dopaminergic pathway projecting from the substantia nigra to the striatum, the dopaminergic system includes a mesocortical pathway with projections from the ventral tegmental area to the prefrontal cortex. This provides a direct route by which dopaminergic inputs might act upon the prefrontal cortex to influence time perception [8,11,33,34]. The suggestion that mesocortical dopamine might influence cognitive time perception is informed not only by the anatomical overlap between the prefrontal regions innervated by this pathway and those known to be involved in time measurement, but also by the observation that parkinsonian patients experience more severe deficits in temporal processing in the late stages of the disease, when cells in the ventral tegmental area have been destroyed [35,36]. The recent demonstration of temporal deficits in several other dopaminergic disorders involving the prefrontal cortex, such as Huntington’s disease [37], schizophrenia [38], and attention deficit hyperactivity disorder [39], are also in line with this view.

Pharmacological studies provide further evidence for the involvement of mesolimbic dopamine in cognitive timing. In a series of targeted investigations, Rammsayer and co-workers capitalized upon the differential influences of various dopamine antagonists upon mesostriatal and mesocortical pathways to determine the relative importance of each for different forms of time perception. They found that remoxipride, an atypical neuroleptic agent which blocks dopamine D2 receptors in the mesocortical system but not in the mesostriatal system, disrupts comparison of durations in the seconds range, without affecting comparisons of durations in the range of milliseconds, or movement timing [11]. The same study showed that haloperidol, which blocks D2 receptors in both systems, impairs the timing of both short and long duration processing and also interferes with movement timing. In conjunction with the results from studies with benzodiazepines and noradrenergic blockers discussed above [6,8,11,25], these data support the role of mesocortical dopamine in a cognitive timing system which draws upon working memory and attention, and of mesostriatal dopamine in both this cognitive system and a more automatic timing process [8,11,25]. Recent work with deep brain stimulation in the subthalamus has also supported a role for the mesostriatal dopaminergic system in cognitively controlled timing [40], with the suggestion that the observed effects might be mediated by striatocortical projections. This raises the possibility that the mesostriatal dopaminergic pathway influences cognitive timing via striatocortical projections, whereas mesostriatal influences on automatic timing are mediated in some other fashion – a proposal which could reconcile the broad literature on dopaminergic influences on timing with the evidence that prefrontal involvement is specific to cognitive timing. This possibility is also in good keeping with our suggestion that dopaminergic influences on cognitively controlled timing stem from the influence of this transmitter on pyramidal cells of the DLPFC because this region receives numerous striatocortical projections (Figure 2).

Overall, the data on dopamine suggest a selective influence of prefrontal dopamine on more cognitive timing tasks, thus implying that this form of timing might be mediated via the same dopamine-sensitive processors as working memory.

Time measurement and memory decay traces

The proposal of time measurement as a continuous process suggests that, rather than using a discrete ticking clock, we use something akin to a continuously fading memory trace of neuronal activity to track the passage of time. This idea was initially suggested at a theoretical level in the form of the MTS model [2]. This model proposes that forgetting

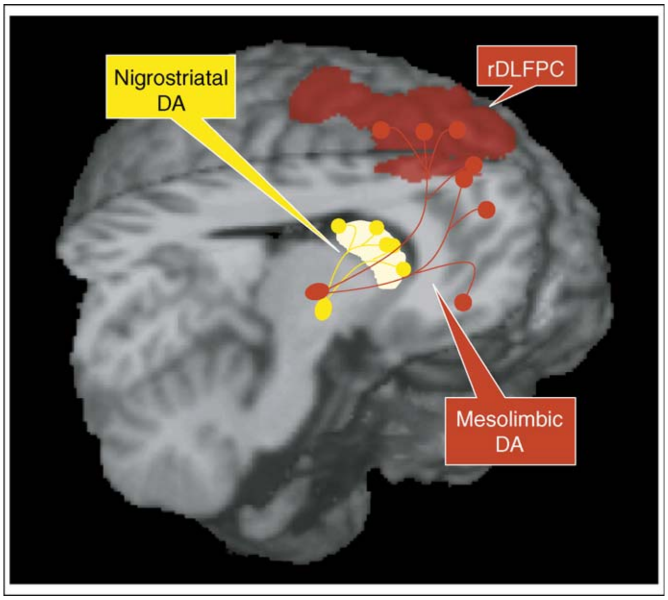

Figure 2. 3D depiction of a human brain which has been sliced to reveal the midbrain. The mesostriatal dopaminergic pathway, which projects from the substantia niagra pars compacta to the striatum, is depicted in bright yellow, with the caudate (one of the basal ganglia) shown in paler yellow. The mesocortical dopaminergic pathway, which projects from the ventral tegmental area to the cortex (particularly the frontal lobes), is represented in bright red, with the rDLPFC shown in darker red. These areas were defined using voxel-labelled templates derived from the mri3dX Brodmann atlas and rendered onto the SPM canonical brain. Abbreviations: DA, dopaminergic pathway; rDLPFC, right dorsolateral prefrontal cortex.

occurs along a predictable time course, which can be described as a sum of exponential curves [41] (Figure 3a), so the strength of a memory could be used to determine how much time has passed since it was formed. The MTS model involves several mathematical constraints that are not easily matched by individual prefrontal neurons, such as the requirement for logarithmic decay, and precise details of how the level of starting activity is stored and compared with the level of activity later in an interval. Nevertheless, a looser interpretation of the memory decay idea, in which the memory is held within a population of cells (Figure 3c), provides a compellingly parsimonious framework that can predict the fundamental psychophysical properties of interval timing (e.g. scalar timing and bisection at the geometric mean) [2,42].

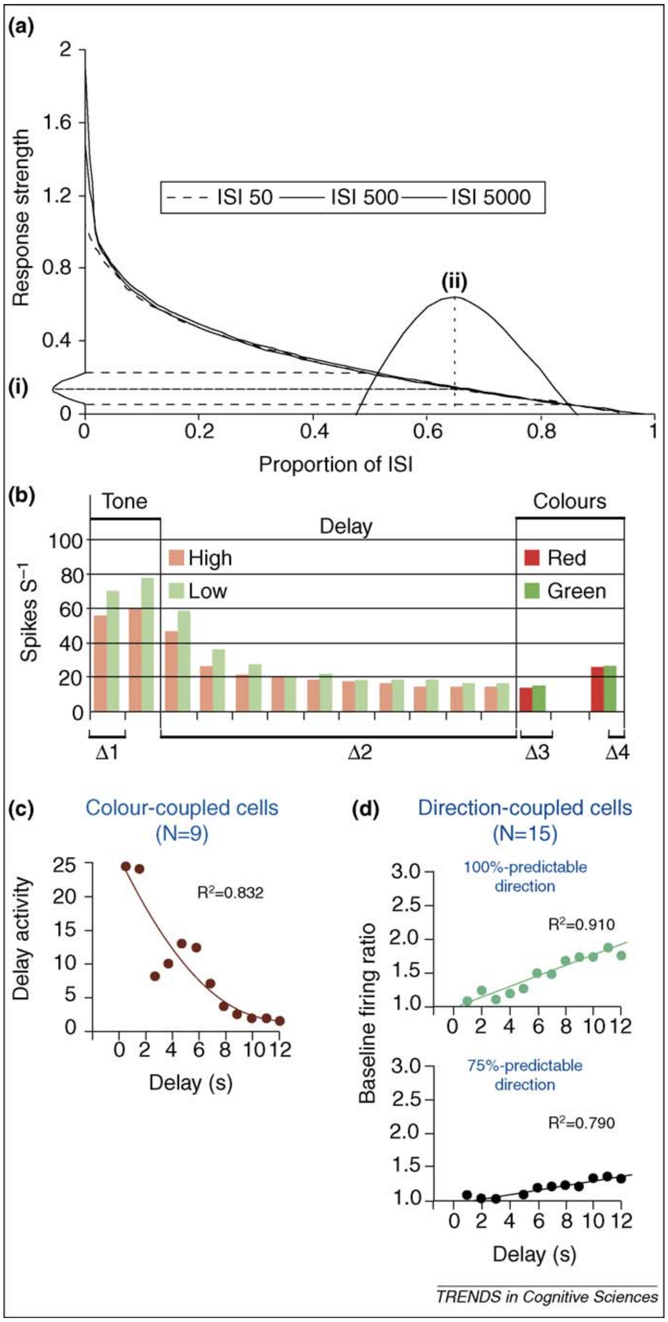

Figure 3. Memory for time. **(a)** Illustration of how 'forgetting curves' could be used to measure time under the MTS model. Three overlapping memory traces are shown for three intervals, all decaying along a predictable trajectory, such that measurements of strength at any given point can be used to determine how much time has passed. A threshold (horizontal line) with associated noise is assumed to trigger output from the system. The scalar property of timing arises naturally from this construct because a fixed uncertainty window in the memory strength (I) leads to variance in estimated duration (II), and the three curves have equal proportional variance. Modified, with permission, from Ref. [51]. **(b)** The activity of a monkey prefrontal neurone during the delay interval (Δ2) between presentation of tones and colours. The activity decays smoothly. Modified, with permission, from Ref. [46]. **(c,d)** Population data for similar prefrontal cells [46] showing decay (c) or ramping activity (d) across the 12-s delay interval.

The physiological feasibility of time measurement using a continuously decaying (or increasing) signal has become apparent as specific populations of cells behaving in this way during timing have been identified [34,43,44]. For instance, cells in the macaque prefrontal cortex have been shown to 'ramp' their activities in a predictable way during temporal comparison [45], and similar activities have been observed in rats during temporal production [43]. These firing patterns are highly reminiscent of the increases of firing rates ('delay activity') which occur when information is held online [46], and which are thought to serve as a basis for working memory (Figure 3b,c). Neuroimaging work in humans also supports this hypothesis; a recent study showed that functional magnetic resonance imaging signal in the DLPFC varies with the duration being measured [47]. Interestingly, some subregions of the DLPFC increased their average activity as the presented interval increased, whereas other subregions decreased their activity, supporting the idea that both increasing and decaying activity could serve as a measure of time. Surprisingly, these correlations were observed in the left rather than the right hemisphere and were found in different locations during encoding and retrieval.

Concluding remarks: can time be measured using the same neural machinery as working memory?

We have outlined a substantial body of evidence suggesting that both cognitive time measurement and working memory rely upon the right hemispheric DLPFC. Dual-task interference suggests that both forms of computation place demands upon the same cognitive processing units. Both processes are influenced by dopamine, a neuromodulator known to effect function in this region, and we have argued that both types of processing might even draw upon the same cell population in this region – the dopamine-sensitive layer III pyramidal delay neurons.

The importance of memory for time perception is widely acknowledged. However, a traditional perspective has been to suppose that working memory is used in time perception – for instance, in the manner of an accumulator process keeping track of the ticks from a neural oscillator as proposed by the scalar expectancy theory model. In this article, we have drawn upon concepts from the newer MTS model to suggest that, instead of merely keeping track of the progress of a separate time keeper, these working memory processes might actually constitute the time-dependent process itself. This formulation can be taken one step further by proposing that the prefrontal time keeper function does not rely upon working memory *per se* but instead simply draws upon the same neural processors as working memory. Thus, the same regions – and potentially even the same cells – that are involved in working memory can be thought of as serving a distinct function when they are used for time measurement.

Our suggestion that the prefrontal processing units used in working memory can also be used to measure time is in keeping with the adaptive coding hypothesis [48], which proposes the prefrontal cortex as a multipurpose processor recruited for a wide variety of functions. This hypothesis explains why the same prefrontal regions are involved in so many cognitive tasks, including working memory, word generation, divided visual attention, problem solving, response suppression and cognitive time perception. A conceptually similar framework suggests that the parietal cortex might provide multipurpose calculations of magnitude [49], thus explaining its involvement in diverse tasks, including perception of size, number, and intensity, distance, as well as time. Taken together, the proposals of adaptive coding in the prefrontal cortex, and of generalized magnitude calculation in the parietal cortex, represent a move away from functional modularity and towards a more flexible and integrative view of the brain.

Although this article focuses on the right DLPFC, several other regions have consistently been shown to be important for cognitively controlled time measurement. Although the right DLPFC might serve as the time-dependent process within cognitively controlled timing tasks, this does not preclude the involvement of areas such as insula–operculum, basal ganglia, supplementary motor area and cerebellum in this and other forms of timing. These regions might work in conjunction with the right DLPFC or form alternate timing systems recruited in parallel with it. Because ramping neural activity is fairly common throughout the prefrontal cortex, it is also possible that timing activities in other parts of the prefrontal lobe might rely upon a similar mechanism. More research is needed both to test this proposed mechanism and to explore the roles of these other regions in timing (Box 1).

Box 1. Questions for further research

- Does concurrent performance of a working memory task disrupt automatic timing? How does this differ from the influence of identical tasks upon cognitively controlled timing?
- Do drugs like haloperidol and remoxipride (which antagonize the dopaminergic system), benzodiazepines (which influence working memory) and reboxetine (which influences attentional procession) show differential effects upon cognitive and automatic timing tasks?
- What is the relative importance of specific task characteristics (e.g. duration timed, continuousness of timing and involvement of movement in timing) for dissociation between cognitive and automatic timing via dual tasks and drugs (see above)?
- Are other task characteristics important for dissociating between cognitive and automatic timing?
- How does dopamine influence the pattern of ramping activity in dorsolateral layer III pyramidal cells during timing tasks? Is there a clear relationship between such influence and the observed behavioural effects?
- Can perturbation of the ramping activity in the right DLPFC (perhaps by microstimulation) influence the perceived duration of a stimulus?
- Might ramping activity in other areas [e.g. supplementary motor area (SMA) or pre-SMA and premotor cortex] underpin automatic timing?

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Temporal order in memory and interval timing: An interference analysis

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Abstract

The effect of varying load in memory tasks performed during a time interval production was examined. In a first experiment, increasing load in memory search for temporal order affected concurrent time production more strongly than varying load in a spatial memory task of equivalent difficulty. This result suggests that timing uses some specific resources also required in processing temporal order in memory, resources that would not be used in the spatial memory task. A second experiment showed that the interference between time production and memory search involving temporal order was stronger when, during the timing task, a decision was made on the temporal position of a memory item, than when information on temporal order was retained throughout the interval to be produced. These results underscore the importance of considering the specific resources and processes involved when the interference between timing and concurrent nontemporal tasks is analyzed.

PsycINFO Classification: 2340 Cognitive processes

Keywords: Timing; Memory; Attention; Interference

1. Introduction

The interference effect is one of the most consistent findings in research on time perception (Brown, 1997). This effect generally refers to a disruption in perceived time when some

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nontemporal task is executed simultaneously, and more precisely to a shortening of perceived time relative to conditions in which timing is performed alone. Increasing difficulty of the nontemporal task typically leads to an increase of the interference effect. These results are classically observed in prospective timing tasks, when participants know in advance that temporal judgments are required. A shortening of perceived time with increasing difficulty of concurrent processing was obtained with a wide range of tasks involving perceptual (Brown, 1985; Casini & Macar, 1997; Coull, Vidal, Nazarian, & Macar, 2004; Field & Groeger, 2004; Macar, 2002; Zakay, 1993), memory (e.g., Fortin & Couture, 2002; Fortin & Massé, 1999; Hicks & Brundige, 1974; Rammsayer & Ulrich, 2005), and verbal (McClain, 1983; Miller, Hicks, & Willette, 1978; Zakay, 1989) processing.

A common interpretation of these results is that temporal processing, defined as accumulating temporal cues in a timer mechanism, requires attention (Brown, 1985; Meck, 1984; Thomas & Weaver, 1975; Zakay, 1989). When attention must be shared with some concurrent task also requiring attention, the accumulation process is disrupted. Over a certain period of time, missing cues will lead to a general decrease in the number of accumulated temporal cues, hence shorter perceived duration. This attentional allocation model accounts for numerous results in time estimation research, where underestimation is directly related to the level of difficulty of concurrent nontemporal tasks (Fortin & Massé, 1999; Sawyer, Meyers, & Huser, 1994; Zakay, Nitzan, & Glickson, 1983) or to the proportion of attention deliberately allocated to nontemporal features of a stimulus (Casini & Macar, 1997; Coull et al., 2004).

This attentional framework widely used to interpret behavioral data in timing research has been supported recently by a review of brain imaging data showing that patterns of activation observed in a variety of timing tasks include areas such as the dorsolateral prefrontal, the anterior cingulate cortex and/or the right parietal cortex, all areas involved in attentional systems and working memory (Macar et al., 2002). The involvement of these areas would derive from relationships postulated in most current timing models between attention and the temporal accumulator. The accumulator is assumed to be located in striatal structures, a hypothesis based on brain lesions and pharmacological manipulations in animal studies (see Gibbon, Malapani, Dale, & Gallistel, 1997; Meck, 1996 for reviews) which have revealed the role of the striato-frontal dopaminergic system in time processing. Such findings are in accordance with neuropsychological data showing that lesions in the basal ganglia (Harrington & Haaland, 1999; Rammsayer & Classen, 1997) may lead to deficits in time discrimination, as do lesions in the cerebellum (Ivry & Keele, 1989; Malapani, Khati, Dubois, & Gibbon, 1997). Support for the involvement of the striato-frontal dopaminergic system in timing is finally found in brain imaging studies showing clear activation of the supplementary motor area (SMA), which is part of the striato-frontal pathway (Jürgens, 1984), during timing tasks (e.g., Coull et al., 2004).

However, despite the numerous studies supporting the idea of a strong relationship between attention and timing, some behavioral data from the timing literature can obviously not be explained by a simple attentional allocation model. For example, in a systematic analysis of bidirectional interference between temporal and nontemporal tasks, Brown (1997) noted that when three nontemporal tasks, pursuit rotor tracking, visual search and mental arithmetic, were performed with 2- or 5-s interval production, temporal production was disrupted by the three tasks whereas only mental arithmetic was disrupted by timing. According to Brown, a more sophisticated framework than a general attention allocation model, such as the multiple resource model (Wickens, 1984, 1991, 1992) or the working

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memory model (Baddeley, 1986, 2000; Baddeley & Hitch, 1974) is needed to account for this pattern of results.

This proposition was supported by data obtained in a recent study, in which cognitive tasks were carried out with time discrimination of short (100 ms) and long (1000 ms) intervals in a dual-task paradigm (Rammsayer & Ulrich, 2005). In one experiment, mental arithmetic (addition of digits) was performed concurrently with time discrimination (Experiment 1). In two other experiments participants had to recognize letters (Experiment 2) or a visual pattern (Experiment 3) after the time discrimination task was completed so that letter and visuospatial patterns had to be retained in memory while the temporal task was executed. Whereas adding digits during time discrimination disturbed timing performance, letter or visual pattern recognition did not. As the authors concluded, the absence of interference from retention tasks in Experiments 2 and 3 may be explained by the fact that these tasks involved passive storage of information essentially, by which timing appeared undisturbed in previous studies (Fortin & Massé, 1999; see also Field & Groeger, 2004); the relatively low level of task difficulty in those experiments may also have been a factor. There was a slight effect of concurrent timing on recognition errors in the spatial memory task, but disruption of recognition in the visuospatial task was clearly weaker than the corresponding effect of arithmetic on timing. In addition to supporting attentional models of time estimation, Rammsayer and Ulrich's study suggests that time discrimination is especially affected by active processing in working memory when functions associated with the central executive are involved. This conclusion, which applies to discrimination of both short and long intervals, is in agreement with the data from Brown's study and with their interpretation.

This interpretation promotes a conception of attention in terms of specialized resources or subsystems. For example, in the multiple resource model, attentional resources are assumed to be distributed in multiple pools defined in terms of processing stages (perceptual/central resources vs. response resources) and processing codes (spatial vs. verbal resources) (Wickens, 1991). In Brown's (1997) analysis, assuming that mental arithmetic and timing are both associated with perceptual/central resources (and possibly verbal resources if the timing task permits subvocal counting) leads to the prediction of clear bidirectional interference between the two tasks. Visual search would involve primarily perceptual/central and spatial resources, which would explain why only unidirectional interference with timing is reported with this type of task. Although pursuit rotor tracking would require spatial and response-based resources essentially, central resources used to coordinate concurrent execution of this task with time production could account for the effects observed on timing.

Similarly, a working memory model composed of a central executive, a phonological loop and a visuospatial sketchpad (Baddeley, 1986; Baddeley & Hitch, 1974) would explain the interference between mental arithmetic and timing by some contribution of the central executive in both tasks (possibly by an executive timing subsystem), and perhaps of the phonological loop also. Visual search and pursuit rotor tracking would rely mainly on the visuospatial sketchpad, reducing competition for central timing resources. This interpretation assumes that timing is controlled mainly by the central executive, which is also responsible for coordinating and scheduling processes in dual-task situations (Brown, 1997). In this view, timing would rely to a much lesser extent on the phonological and visuospatial subsystems, their involvement being mainly limited to the use of strategies such as counting.

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A previous experiment showed that interference with concurrent timing was increased if – in addition to deciding whether a memory item was present or not – the difficulty of item recognition was increased by asking participants to verify the temporal position of the probe (Fortin & Massé, 1999; Experiment 1). This result could be explained by the increased difficulty of the memory task when temporal order must be processed which would lead to increased demands on general undifferentiated resources. Alternatively, this result could be explained by specific resources being required simultaneously in processing temporal order in memory and timing. This issue was examined in the first experiment of the present study by comparing the effects of either temporal or spatial memory-based processing on concurrent time production. Two memory tasks of comparable levels of difficulty should interact similarly with concurrent timing if the need for general resources was the main factor explaining the effect of processing temporal information in Fortin and Massé's study. In contrast, if their result was due to specific common resources required by temporal memory processing and time production, the effect of increasing load in a temporal order memory task should be stronger than the effect of increasing load in a spatial memory task. This might be expected given that, as summarized in Brown's (1997) analysis, sequential order information is considered as one of the main attributes of psychological time (e.g., Fraisse, 1984); to the extent that temporal order is related to perceived duration, it may be assumed that they both involve similar processing resources.

Whereas processing temporal information interfered with temporal production in Fortin and Massé's (1999) study, produced intervals were not affected by increasing the number of items to be maintained in memory in their temporal order of presentation. This dissociation between the effects of processing and maintenance of information on concurrent time production was investigated thoroughly in a subsequent study; results showed that increasing the number of colors or tone timbres to retain during a time production task had no effect (Field & Groeger, 2004; Experiments 2 and 3) whereas retention of pitch information or tone durations showed load-related effects (Field & Groeger, 2004; Experiments 1 and 4). The interference from pitch maintenance was considered as a particular case, but interference from retention of tones durations was attributed to the common requirement of retaining temporal information in the memory task and in the time production task. In the second experiment of the present study, the number of items to be maintained in their correct temporal order was varied during a time interval production task and this condition was compared directly with a similar load manipulation involving the retrieval of information on temporal order. Although previous results (Field & Groeger, 2004; Fortin & Massé, 1999; Rammsayer & Ulrich, 2005) suggest that a dissociation should be obtained such that produced intervals would lengthen with increasing load in the processing task but not in the retention task, increasing load in the passive retention condition might also affect time production because the memory and timing tasks both require the maintenance of temporal information.

In Experiment 1, we examined whether increasing load in a temporal memory task and in a spatial memory task would affect concurrent time production similarly. In Experiment 2, we compared the relative effects of increasing load either in processing or in maintaining temporal order information on time production. In the two experiments, letters were memorized. A probe was then presented and a decision was made on its temporal (Experiments 1 and 2) or spatial (Experiment 1) position in the memory set. This decision was made either during a time interval production (Experiments 1 and 2) or immediately after its termination (Experiment 2). In both experiments, the main question of interest was

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whether increasing load, defined as the number of letters in the memory set, would have different effects in the experimental conditions that were compared (spatial vs. temporal in Experiment 1, and processing vs. maintenance in Experiment 2).

2. Experiment 1

A memory task in which participants verified the temporal position of a stimulus in a memorized sequence of letters was contrasted with a task in which the spatial position of a stimulus in a memorized matrix of letters was verified. In both tasks, the number of memory items (set size) was varied (two or four). The relative difficulty of the tasks was first evaluated in a reaction time (RT) condition by testing whether increasing set size had a comparable effect with the two tasks. Then, in a concurrent processing (CP) condition, each task was performed concurrently with time production and the effect of increasing set size on produced intervals was examined.

2.1. Method

2.1.1. Participants

Twenty-five participants, 15 women and 10 men, aged between 18 and 63 (mean age = 25.5; SD = 9.17) took part in the experiment. The participants, students or workers at Université Laval, received $10 for their participation in the RT condition or 20 in the CP condition. They were all naive regarding the experimental hypotheses.

2.1.2. Apparatus and stimuli

Stimulus and feedback presentations as well as data collection were controlled by a PC-compatible computer using the MEL (Micro Experimental Laboratory) software system. The visual stimuli were displayed on an IBM VGA color monitor with a 20 × 27 cm screen. Responses were provided by pressing one of three keys on the numerical keyboard of the computer. Reponses times were recorded to the nearest millisecond. The participants were tested individually in a sound-attenuated test chamber, where they were seated at an approximate distance of one meter from the screen.

The set of items used in the experiment was composed of seven consonants (D, Q, G, R, S, P, F) and three vowels (A, E, U). Memory-set size (n = two or four different letters) randomly varied from trial to trial with the constraint that each set size appeared equally often across the experiment. The letters constituting the memory set, and the probe letter ($n = 1$) were selected randomly and varied from trial to trial. A letter was never repeated in a memory set. The letters were presented in white on a black background and subtended a visual angle of 0.2° in height and 0.4° in width.

2.1.3. Procedure

Fifteen participants were randomly assigned to the RT condition. Each of these 15 participants was tested both with the spatial and temporal memory tasks in four experimental sessions, that is, two successive sessions with the spatial task and two successive sessions with the temporal task. Participants were tested with the spatial and the temporal tasks in counterbalanced order.

Ten other participants were tested in the CP condition, which included two sessions in which participants practiced producing a 2.7-s target interval. Practice sessions were

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followed by four experimental sessions divided in two successive experimental sessions with the spatial task and two successive sessions with the temporal task. Participants were tested with the spatial and temporal tasks in counterbalanced order.

2.1.3.1. RT condition. Each of the four sessions included five blocks of 36 trials, one block of practice trials and four blocks of experimental trials. There were 30-s rests between blocks. Sessions lasted between 20 and 30 min. An experimental trial began with the presentation of the word "Ready" in the middle of the screen. The word "Ready" remained present until participants initiated the trial by pressing the "2" key on the numerical keyboard. This key press triggered the letter presentation as described below.

Schematic illustrations of experimental trials in the spatial and temporal tasks are presented in Fig. 1a and b, respectively. As illustrated in Fig. 1a, the letters of the memory set appeared simultaneously in the spatial task. When four items were presented, they were placed on two rows in the four corners of an imaginary square. When the memory set comprised two letters, they appeared on a single row in a middle position between the top and bottom of the square. The letters remained present for one second per item, that is, for two and four seconds when two and four items were presented, respectively. After the memory set presentation, an asterisk (*) appeared, serving as a fixation stimulus until the participant pressed the "2" key anew. A probe letter was presented 500 ms later at one of the spatial positions where letters had been memorized. The other locations were filled with a neutral stimulus, a number sign (#). The probe remained present until the response was provided. The instructions were to press the "1" key as quickly as possible when the spatial position of the probe was correct or the "3" key when the position was incorrect.

In the temporal task, each item of the memory set was presented successively for 1 s at the same location on the screen, with no delay between items (see Fig. 1b). After the memory set presentation, a fixation stimulus (*) appeared and remained present until the participant pressed the "2" key anew. This key press triggered the simultaneous presentation of a probe letter and of a digit, the digit being placed just below the probe. The two stimuli, probe and digit, remained present until the participant responded to the temporal order task. The instructions for responding maintained the same mappings as the spatial task. Participants were to respond by pressing the "1" key if the digit corresponded to the temporal position of the item and they were to press the "3" key if the digit did not correspond to the temporal position of the item. As in the spatial condition, the probe item was always taken from the current-trial memory set.

In both memory tasks, a visual feedback (correct or error) was presented for 1 s immediately after the response. The feedback was followed by the word "Ready", which informed participants that they could initiate the next trial when ready. In both memory task conditions, participants were asked to fixate the center of the screen from the time they started the trial by pressing the "2" key until the end of feedback presentation. The probe was always present in the memory set and the position of the probe was selected randomly on each trial. The number of trials at each set size and the number of positive and negative response trials were balanced within blocks of trials. Response times and response accuracy were recorded.

2.1.3.2. CP condition. Participants completed six sessions in the CP condition, two practice sessions of temporal production followed by four experimental sessions in which the

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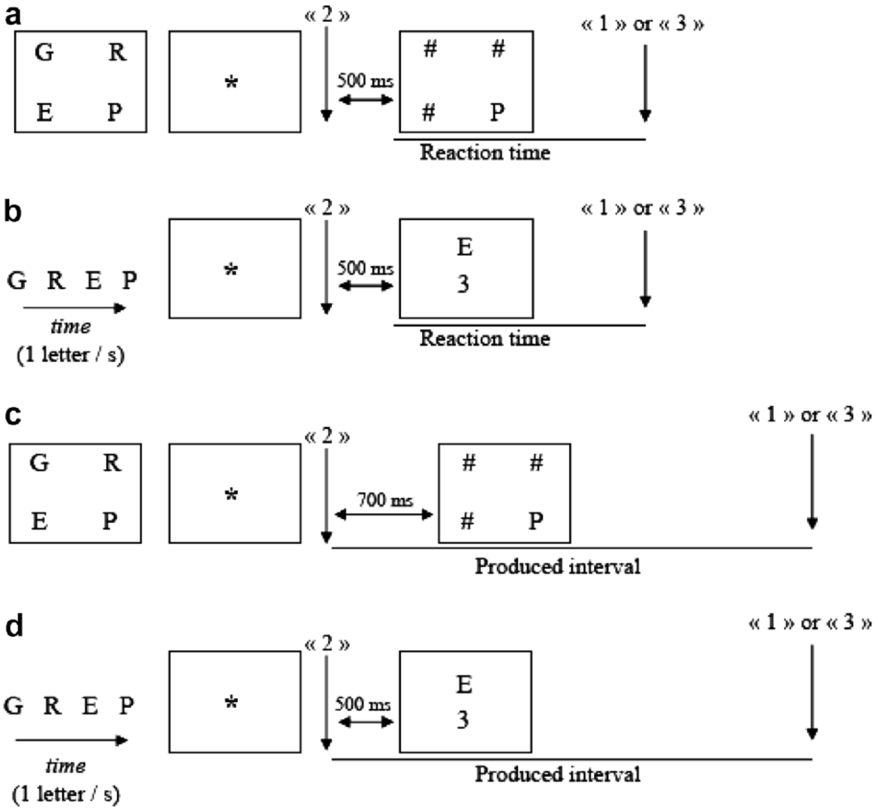

Fig. 1. Experiment 1. Experimental trials in the RT condition with the spatial memory task (a), and the temporal memory task (b). Experimental trials in the Concurrent Processing (CP) condition when the spatial memory task (c) and the temporal memory task (d) were interpolated in a time interval production. Trials started either with simultaneous (a and c) or sequential (b and d) presentation of letters to be memorized. A fixation stimulus then appeared and remained on the screen until the participant pressed the "2" key, which triggered the presentation of the probe in the RT condition (a and b), and which began the interval production in the CP condition (c and d). The instructions were to press the "1" or the "3" key to indicate whether the probe's spatial (a and c) or temporal (b and d) position represented correctly or not its position in the memory set. Participants were asked to respond to the probe as quickly as possible in the RT condition (a and b), and to respond when they judged that the target interval to be produced had elapsed in the CP condition (c and d).

temporal or spatial memory task were executed concurrently with time production. Sessions lasted between 30 and 40 min. There was a 30-s break between blocks of trials within a session.

Practice sessions enabled participants to stabilize their time interval production performance. These sessions included four 48-trial blocks with feedback on produced intervals, and one 48-trial block without feedback. At the beginning of the experiment, participants were provided examples of the target interval to be produced with a 2.7-s tone. Participants were not informed of the interval duration in formal units of time. A trial started with a fixation stimulus ($*$) presentation. The task was to produce the target interval as precisely as possible by pressing the "2" key twice on the numerical keyboard. In the first four blocks, a visual feedback was provided, informing the participant that the temporal

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production was too short, correct, or too long, relative to a 10% window centered on the 2.7-s interval standard. In the fifth block, no feedback was provided in order to practice participants producing without feedback.

The four experimental sessions included six blocks of trials. These sessions started with a 48-trial block of temporal productions alone with feedback as in practice sessions to reset the target duration. This first block was followed by a block of 12 practice trials introducing the CP condition, in which temporal production was performed with the memory task. Four 36-trial experimental blocks were then completed. In these blocks, a trial began with a fixation stimulus (∗). When ready to begin the trial, the participant pressed the “2” key on the numerical keyboard. The following events varied according to the memory task to be performed as described hereafter.

The letters of the memory set were displayed simultaneously in the spatial task (see Fig. 1c). Immediately after the memory set presentation, a fixation stimulus (∗) appeared and remained present until the participant pressed the “2” key to begin the temporal interval production. Seven hundred milliseconds later, a probe letter appeared at one of the possible spatial positions of the memory set items, with the remaining locations filled with a neutral stimulus (#). The probe was present until the participant ended the temporal production when she/he judged that the target interval had elapsed, by pressing the “1” or the “3” key depending on the correct or incorrect spatial position of the probe.

Each item of the memory set was presented successively for 1 s in the temporal memory task (see Fig. 1d). A fixation stimulus (∗) then appeared and lasted until the participant pressed the “2” key. Five hundred milliseconds after this key press, the probe and digit were presented. They remained present until the target interval was terminated by pressing the “1” or the “3” key depending on the digit corresponding or not to the temporal position of the probe. A visual feedback on the response to the memory task was then presented for 1 s. No feedback was provided on time production in experimental trials. The feedback was followed by the word “Ready”, which indicated that the next trial could be started.

Note that in the CP condition, the probe was presented 700 ms after the beginning of the temporal production when the interpolated task was the spatial memory task, whereas it was presented after 500 ms with the temporal memory task. It was decided to present the probe 200 ms later with the spatial task because, as described in the result section below, RTs in the spatial task were shorter than in the temporal memory task by about 200 ms on average. The probe was therefore presented 200 ms later with the spatial task so that participants would not have more time to process the probe in the spatial than in the temporal task during the interval production, which might have favored a stronger interference effect with the temporal memory task.

2.2. Results and discussion

Data from the first experimental block (36 trials) had to be eliminated for one participant because he did not understand the task well. Trials in which an incorrect response was provided in the memory task were removed from the data set. These errors represented respectively 5.99% and 6.02% of the data in the spatial and temporal tasks in the RT condition, and 1.97% and 2.81% in the spatial and temporal tasks in the CP condition. Outliers (±3 SDs from the mean and SD of each participant) were then eliminated, which

Table 1
Experiment 1: RT condition

Memory task	Memory-set size			
	2		4	
	RT	Error	RT	Error
Spatial	668	5.05	834	6.95
Temporal	895	5.05	1041	6.99

Standard errors of the means (SEM) for RTs = 29.95, SEM for percent errors = 0.82 (computed with a pooled mean square error (MSE), see Loftus and Masson, 1994).
Mean RTs (ms) and mean percent errors at each value of memory-set size in the spatial and temporal memory tasks.

represented 1.45% and 1.38% of the data in the spatial and temporal tasks in the RT condition, 1.11% and 1.39% in the spatial and temporal tasks in the CP condition. For each participant, a mean RT or a mean temporal production was computed at the two values of set size in the spatial and temporal memory tasks. In the RT and CP experimental conditions, two repeated measures ANOVAs were carried out with memory set size (two, four) and memory task (temporal, spatial) as factors, one on response times (RTs in the RT condition and temporal productions in the CP condition), and one on mean error rates.

2.2.1. RT condition

2.2.1.1. RTs. Table 1 shows mean RTs for the memory tasks. RTs significantly increased with set size, $F(1,14) = 35.91$, $p < .001$ and were significantly longer in the temporal than in the spatial task, $F(1,14) = 29.52$, $p < .001$. The interaction between set size and memory task was not significant, $F < 1$. The absence of interaction reveals that the slopes of RT functions were comparable in the two memory conditions, 73 and 83 ms per item in the temporal and spatial tasks respectively, which means that increasing load had a similar effect on RTs in the two tasks.

2.2.1.2. Error rates. There was a slight increase in error rates with set size (see Table 1), an effect which happened to be marginally significant, $F(1,14) = 4.40$, $p < 0.055$. Neither the memory task nor the interaction between set size and memory task had significant effects on error rates, $F_s < 1$.

The absence of interaction between set size and memory task shows that the rate of processing was equivalent in the spatial and temporal memory tasks, confirming that they were of equivalent levels of difficulty. Results in the RT condition also show that RTs were, on average, about 200 ms longer in the temporal than in the spatial task. This additional processing time may reflect the time necessary to encode the digit representing the temporal position in the temporal memory task and to translate the digit in information on temporal order. There was no such encoding and translation needed in the spatial memory task because there was a direct representation of the probe's position in the stimulus matrix. For this reason, in the CP condition, the probe stimulus was presented 200 ms later when the spatial task was interpolated in the temporal production than when the temporal memory task was interpolated (see Fig. 1c and d).

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Table 2
Experiment 1: CP condition

Memory task	Memory-set size			
	2		4	
	PI	Error	PI	Error
Spatial	2767	2.21	2818	1.73
Temporal	2689	2.22	2784	3.40

SEM for PIs = 42.30, SEM for percent errors = 0.58 (Computed with a pooled MSE, see Loftus and Masson, 1994).
Mean produced intervals (PI) (ms) and mean percent errors, at each value of memory-set size in the spatial and temporal memory tasks.

2.2.2. CP condition

2.2.2.1. Temporal productions. Mean intervals produced with the spatial and temporal memory tasks are presented at the two values of memory-set size in Table 2. Produced intervals did not differ with the two tasks $F(1,9) = 1.08$, $p = .33$. The absence of a significant difference in mean produced intervals with the spatial and temporal tasks shows that by presenting the probe 200 ms later in the spatial task than in the temporal task, we succeeded in our attempt to make concurrent processing time equivalent with the two tasks. The general effect of set size did not reach significance, $F(1,9) = 2.86$, $p = .13$. The critical result however is that the interaction between set size and order condition was significant $F(1,9) = 6.09$, $p = .04$. Tests of simple main effects showed that increasing set size lengthened produced intervals significantly with the temporal memory task, $F(1,9) = 5.58$, $p = .04$, but not with the spatial task, $F(1,9) = 1.16$, $p = .31$.

2.2.2.2. Error rates. Mean percent error rates in the memory tasks are presented in Table 2. Neither the effect of set size, $F(1,9) = 1.29$, $p = .29$, nor the effect of memory task, $F(1,9) = 1.48$, $p = .25$, nor the interaction between these two factors, $F(1,9) = 2.04$, $p = .19$, were significant. These results show that accuracy in detecting the position of the probe was equivalent in both tasks. This confirms that the effect of set size when the temporal memory task was interpolated in produced intervals cannot be explained by some differential speed-accuracy trade-off favoring precision at the expense of speed of processing with the temporal task.

The main finding in Experiment 1 is that although the rate of processing was comparable in the spatial and temporal memory tasks as revealed by the results in the RT condition, the lengthening of produced intervals with increasing number of items was more important when the concurrent memory task involved searching for temporal order than searching for spatial position. This dissociation suggests that the need to process temporal information simultaneously in the temporal memory task and in the time production task contributes specifically to the interference effect in the CP condition. Searching for spatial order would use spatial resources not used in interval timing, which might reduce the competition for central timing resources.

This interpretation supports an analysis of interference between temporal and nontemporal tasks in terms of multiple attentional resources (Brown, 1997). Indeed, these data could not be accounted for within a simple attentional allocation model because according to this model, two tasks of comparable difficulty should have the same effect on concurrent time estimation. A better account is provided by a theoretical framework integrating specialized resources such as the working memory model (Baddeley & Hitch, 1974) or the multiple resource model (Wickens, 1984). As suggested by an analysis referring to specialized resources or subsystems, the interference between searching for temporal order and time production would be explained by the common use of the central executive and possibly of the phonological loop in working memory or, in a multiple resource model, by the concurrent use of central and possibly verbal resources. The nonsignificant effect of increasing load in the spatial memory task on timing would be explained by spatial resources or the visual sketchpad contributing to performance in the memory task, but not in the time production task.

3. Experiment 2

Memory processing often perturbs concurrent timing but there is usually no such effect with maintenance of information in memory (Field & Groeger, 2004; Fortin & Breton, 1995; Fortin & Massé, 1999; Rammsayer & Ulrich, 2005). However, produced intervals were lengthened by increasing the number of tone durations to remember during an interval production, which was considered to be caused by both tasks requiring remembering temporal information (Field and Groeger, Experiment 4). In Experiment 2, we tested whether this reasoning might be extended to maintenance of temporal order with an experimental task very similar to that used in Experiment 1. In one condition, the memory probe was presented during the temporal interval production ("Probe-In" condition). This condition was compared to a condition in which the probe was presented after the temporal production was terminated ("Probe-After" condition). The memory set had therefore to be searched for temporal position during the interval in the Probe-In condition, whereas it had to be maintained in correct temporal order throughout the interval in the "Probe-After" condition.

3.1. Method

The method used in Experiment 2 was similar to that used in Experiment 1 in most respects. In the Probe-In condition, the task was almost identical to that in the temporal order condition of Experiment 1. The target interval to be produced was shorter, 2.0 s (vs. 2.7 s in Experiment 1), to enhance generality of results. The apparatus and testing conditions were the same as in Experiment 1, with the exceptions described below.

3.1.1. Participants

Twenty participants, 8 men and 12 women, aged between 20 and 43 years old (mean age = 23.2; SD = 5.47) took part in the experiment. They received $20 for their participation.

3.1.2. Stimuli

The 20 consonants of the alphabet were used as stimuli. Memory-set size (n = two, four, or six different letters), memory items, and the probe letter (n = 1) were selected randomly and varied from trial to trial.

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3.1.3. Procedure

Each participant was tested in two separate sessions completed in counterbalanced order in the two experimental conditions, Probe-In and Probe-After. Experimental sessions were preceded by three practice sessions, which included four 48-trial blocks with feedback on produced intervals followed by one 48-trial block without feedback. Trials were identical to practice trials in Experiment 1, except that the target interval was 2.0 s. The two experimental sessions included five blocks of trials: a 48-trial block of temporal productions alone with feedback to reset the target duration, followed by four 36-trial blocks in which time production was executed either with processing or maintenance of temporal order in the concurrent memory task.

In the Probe-In condition, the probe and digit were presented 500 ms after the beginning of the temporal production as in Experiment 1. The temporal production was executed by pressing first the "2" key on the numerical keyboard, and then by pressing the "1" or "3" keys depending on the digit corresponding or not to the correct temporal position of the probe in the memory set. In the Probe-After condition, the beginning and the end of the temporal production were executed by pressing the "2" key. The key press ending the interval production triggered the probe and digit presentation, and participants were instructed to press one of two keys, "1" or "3", depending on the probe presenting a correct or incorrect position in the memory set. Trials were identical to those in the temporal order condition of Experiment 1 in all other respects.

3.2. Results and discussion

Trials with errors in the memory task were eliminated from the data set, which represented respectively 12.2% and 9.2% of the data in the Probe-In and Probe-After conditions, respectively. Outliers (±3 SDs from the mean and SD of each participant) were then eliminated, representing 1.45% and 0.3% of the data in the Probe-In and Probe-After conditions. Mean productions were computed at each set size for each participant, and repeated measures ANOVAs were carried out on mean produced intervals and on mean percent error rates in the memory tasks.

3.2.1. Temporal productions

Mean produced intervals in the Probe-In and the Probe-After conditions are presented at each value of set size in Table 3. The effects of memory set size, $F(2,38) = 11.34$, $p < .001$, and of probe condition, $F(1,19) = 12.82$, $p = .002$, were statistically significant but the

Table 3
Experiment 2: Mean produced intervals (PI) (ms) and mean percent errors in the Probe-In and the Probe-After Conditions, at each value of memory-set size

Condition	Memory-set size					
	2		4		6	
	PI	Error	PI	Error	PI	Error
Probe-In	2424	4.90	2538	8.34	2640	23.43
Probe-After	2267	4.69	2315	5.21	2333	17.60

SEM for PIs = 45.82, SEM for percent errors = 1.25 (computed with a pooled MSE, see Loftus and Masson, 1994).

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interaction between these two factors was not significant, $F(2,38)=2.18$, $p=.13$. This result shows that there was an effect of memory load, whether temporal information was processed or maintained in memory.

To investigate further the relationship between temporal performance and memory load in these conditions, we conducted a trend analysis on these data. For the set size factor, this analysis showed a significant linear trend, $F(1,19)=13.78$, $p=.001$, and a nonsignificant quadratic trend, $F<1$. There was also a significant interaction between condition and set size for the linear trend, $F(1,19)=6.92$, $p=.016$, and no interaction for the quadratic trend, $F<1$. The interaction for the linear trend is an indication that the slopes in the Probe-In ($M=53.93$) and the Probe-After ($M=16.44$) conditions are different. Separate tests for trends in the Probe-In and the Probe-After conditions showed that the linear trend was significant in the Probe-In, $F(1,19)=16.44$, $p=.001$, but not in the Probe-After condition, $F(1,19)=2.59$, $p=.12$.

3.2.2. Error rates

Error rates increased significantly with set size $F(2,38)=63.91$, $p<.001$, and were higher in the Probe-In than in the Probe-After condition $F(1,19)$ $p=12.54$, $p=.002$. The interaction between set size and probe condition was also significant $F(2,38)=3.68$, $p=.04$; the increase in error rates was stronger in the Probe-In than in the Probe-After condition (see Table 3). These results show that memory performance was generally more disturbed by timing in the Probe-In than in the Probe-After condition, and that this disruption was greater as the memory load increased. The effect of set size was significant in both conditions as revealed by tests of simple main effects, $F(2,38)=68.28$, $p<.001$ (Probe-In) and $F(2,38)$ $p=27.42$, $p<.001$ (Probe-After).

To summarize, increasing memory load lengthened produced intervals whether temporal information had to be searched for or only to be maintained in memory because there was a general effect of increasing set size on produced intervals. A trend analysis revealed that the form of the relationship relating time productions to memory load was linear. The linear trend differed in the two memory tasks however, being significant only when there was active processing of temporal order during the interval production. Moreover, when temporal order was processed, participants made more errors in the memory task, and increasing load had a stronger effect on errors than when order was maintained. It is thus possible to conclude that processing temporal order in memory interferes more with timing than passive retention of temporal order. There is, nonetheless, some effect of increasing load when items only have to be retained as revealed by the general effect of set size on mean produced intervals.

4. General discussion

Varying load had comparable effects on reaction times with a temporal memory task and a spatial memory task in Experiment 1 of the present study. In contrast, increasing load in the same temporal memory task had a much stronger effect on time intervals produced concurrently than increasing load in the spatial memory task. These results support an interpretation of the interference between timing and concurrent tasks in terms of specialized resources (Wickens, 1984, 1992) or memory subsystems (Baddeley, 1986, 2000; Baddeley & Hitch, 1974) as proposed by Brown (1997). Assuming that the temporal memory task uses resources from the central-executive mainly and that the spatial memory task

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relies mostly on a visuospatial subsystem, a stronger effect from processing temporal order on concurrent timing may be explained if timing uses resources associated with executive-control functions of working memory but not spatial resources associated with a visuospatial memory subsystem. This conclusion is supported by Brown's data showing that visual search and spatial pursuit were not affected by concurrent temporal production. It is also be interesting to note that in previous experiments, increasing the load in a visual search task did not lengthen simultaneous time productions whereas a lengthening was observed with corresponding manipulations in equally difficult item recognition tasks (Fortin, Rousseau, Bourque, & Kirouac, 1993). Taken together with the results of Experiment 1, these findings suggest that time production does not rely heavily on the use of visuospatial resources.

Another conclusion from the present study concerns the dissociation between the effects of processing and maintenance of information in memory on concurrent timing. The interference between searching for temporal order in memory and time estimation was clearly stronger than the interference caused by maintenance of temporal order information, even though information must be maintained throughout the interval to be estimated. This is in line with previous results showing that passive retention had no effect on concurrent time production (Field & Groeger, 2004; Experiments 2 and 3; Fortin and Breton, Experiment 1; Fortin & Massé, 1999; Experiment 2) and on time discrimination (Rammsayer & Ulrich, 2005). In only two experiments was retention found to have an effect in similar tasks, one in which information on pitch (Field and Groeger, Experiment 1), and another in which durations of tones (Field and Groeger, Experiment 4) had to be remembered. Pitch information was presented in the form of one to four pure tones of varying pitch, presented sequentially. One possibility mentioned to explain the effect of pitch retention on time production is that retaining pitch would involve more active processing than retention of other memoranda. This would be related to the potential of pitches to form a meaningful group of stimuli or a melody, which is less likely with other types of information. The effect of retaining duration of tone might be due to the fact that in this case, the information retained is identical to that processed in the timing task, that is, durations or time intervals. In the present study, the results from Experiment 2 partly support this interpretation because there was an effect of increasing load on produced intervals with maintenance of temporal order, an effect that may be explained by the similarity of information involved the memory and time production tasks. Finally, it must be noted that in one experiment, maintenance of visuospatial patterns was slightly disrupted by concurrent time discrimination (Rammsayer & Ulrich, 2005; Experiment 3) although discrimination performance was not affected by the retention of visuospatial material. Taken together, these data suggest that timing is relatively undisturbed by concurrent maintenance of information in memory, except perhaps when this information has a clear temporal or sequential – as for pitch in Field and Groeger's first experiment – component.

To conclude, the results of the present study suggest that timing is especially dependent on resources also used in processing temporal order in memory. Given that processing temporal order involves processes generally associated with central executive functions (e.g., scheduling processes in dual-task situations), this is in agreement with previous studies relating timing to these functions (Brown, 1997; Rammsayer & Ulrich, 2005). It must be noted however that the duration values tested in the two experiments were restricted to 2.7 (Experiment 1) and 2.0 s (Experiment 2). Although the relationship between memory functions might be restricted to intervals around these values, recent experiments showed

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similar effects from cognitive tasks on concurrent timing with intervals in the range of milliseconds (100 ms) and of longer duration (1000 ms) (Rammsayer & Ulrich, 2005). This suggests that results similar to those obtained in the present study could be obtained with shorter durations.

Detailed analyses of disruptions in timing from interfering tasks such as those used in the present and other studies (e.g., Brown, 1997; Macar, 2002; Rammsayer & Ulrich, 2005) contribute to pinpoint the type of attentional resources involved when timing tasks are performed, a fundamental issue considering the central role of attention in most current influential models of timing (Gibbon, Church, & Meck, 1984; Zakay & Block, 1996). Finally, from a practical perspective, given the use of timing tasks in measuring mental workload (e.g., Liu & Wickens, 1994), a more detailed definition of the processes involved in timing might also contribute to providing a better index of the workload imposed by a variety of tasks (O'Donnell & Eggemeier, 1986).

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Individual differences in working memory capacity and divided attention in dichotic listening

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The controlled attention theory of working memory suggests that individuals with greater working memory capacity (WMC) are better able to control or focus their attention than individuals with lesser WMC. This relationship has been observed in a number of selective attention paradigms including a dichotic listening task (Conway, Cowan, & Bunting, 2001) in which participants were required to shadow words presented to one ear and ignore words presented to the other ear. Conway et al. found that when the participant's name was presented to the ignored ear, 65% of participants with low WMC reported hearing their name, compared to only 20% of participants with high WMC, suggesting greater selective attention on the part of high WMC participants. In the present study, individual differences in divided attention were examined in a dichotic listening task, in which participants shadowed one message and listened for their own name in the other message. Here we find that 66.7% of high WMC and 34.5% of low WMC participants detected their name. These results suggest that as WMC capacity increases, so does the ability to control the focus of attention, with high WMC participants being able to flexibly "zoom in" or "zoom out" depending on task demands.

Since Baddeley and Hitch (1974) first published their seminal chapter on working memory (WM), many theories regarding the construct have been proposed. One of the more widely supported theories, particularly when applied to individual differences in WM, is the controlled attention theory of WM (Engle & Kane, 2004; Kane, Bleckley, Conway, & Engle, 2001; Kane & Engle, 2002), according to which there is a domain-general component of WM responsible for guiding attention as well as domain-specific components responsible for maintenance of task-relevant information. Individuals who score high on tests of working memory capacity (WMC) therefore may do so because of greater controlled attention and/or because of better use of domain-specific skills and strategies to aid maintenance. Engle and colleagues have argued that the domain-general controlled attention ability is related to both higher-level cognition, such as fluid intelligence, reading comprehension, and problem solving, and lower level cognition, such as performance of simple visual and auditory attention tasks that require cognitive control (for a review, see Engle & Kane, 2004).

To date, all of the experiments that have demonstrated a relationship between WMC and lower level cognition have come from *selective* attention paradigms. For example, Kane et al. (2001) demonstrated the relationship using a visual orienting paradigm (i.e., pro- and antisaccade tasks). They found no difference between high and low WMC participants in the prosaccade task but high WMC participants performed significantly better than low WMC participants on the antisaccade task (see also Unsworth, Schrock, & Engle, 2004). The relationship between WMC and controlled attention was also observed in the Stroop task (Kane & Engle, 2003). In conditions that demanded less attention to maintain the task goal (i.e., when the ink color and the color word matched on either 0% or 100% of the trials) there was no difference in performance between high and low WMC participants; however, when the task demanded more attention to maintain the task goal (i.e., when the ink color and the color word matched on 75% of the trials) high WMC participants performed significantly better than low WMC participants.

Most relevant to the present project, the relationship between WMC and controlled attention has also been observed in the dichotic listening paradigm (Conway, Cowan, & Bunting, 2001). In a dichotic listening task, two messages are presented simultaneously, one to each ear. Conway et al. instructed participants to shadow the words presented to one ear while ignoring the words presented to the other ear, hence participants were required to use selective attention. Each participant's own name was presented to the ignored message, and Conway et al. found that 65% of participants with low WMC reported

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hearing their name, while only 20% of participants with high WMC reported hearing their name. Participants with greater WMC were better able to control their attention and focus on the relevant message, thus hearing their name less often.

Even though the above cited evidence supports the controlled attention view of WM, one limitation of previous research is that all the experiments tested *selective attention* only. It is therefore an open question as to whether WMC will be related to performance in a divided attention paradigm. Cowan (2005) suggests that the spotlight (or focus) of attention is flexible, and that individuals differ in their ability to adapt the focus of attention according to task goals. If the task requires selective attention, then the spotlight of attention should be zoomed in and only the information relevant to the task should be processed. If the task requires attention to be divided, then the spotlight of attention should be zoomed out accordingly so that all information relevant to the task may be processed. However, the nature of individual differences in the flexibility of the spotlight of attention is unknown. It may be that higher WMC leads only to being able to focus (i.e., remain zoomed in). In contrast, it may be that higher WMC is related to the ability to flexibly adjust attention (i.e., zoom in or out depending on task demands). The nature of the selective attention tasks used in previous individual differences experiments does not allow us to examine flexibility because participants were expected to continuously focus their attention; therefore, divided attention tasks will allow us to explore flexibility because participants need to "zoom out" to perform the task appropriately.

The motivation for the present experiment was to explore whether WMC is related to performance in a divided attention paradigm. To explore this, participants performed a dichotic listening task similar to that used by Conway et al. (2001) except participants had to divided their attention between the two messages. The results of previous studies (Kane et al., 2001; Kane & Engle, 2003) suggest that the level of attentional demand that a task has may influence the relationship that WMC plays in the completion of the task. Therefore, in the present experiment we manipulated attentional demand in two ways. First, we required subjects to perform two versions of the dichotic listening task, once while shadowing (i.e., high attentional demand) and once while not shadowing (i.e., low attentional demand). Second, we manipulated the signal-to-noise ratio (SNR) between the two messages that were presented, such that the more relevant message was either quieter than, the same volume as, or louder than the message with the name (i.e., more attentionally demanding to less attentionally demanding, respectively). If WMC is related to the ability to control attention, then a relationship should be observed between WMC and performance on the divided attention task, such that as WMC increases, performance on the attention task should increase. However, similar to the results obtained in the aforementioned selective attention experiments, this difference should only be observed in situations where the task is more attentionally demanding. Therefore, even though dividing attention while not shadowing does require attention, it has a low attentional demand and is not likely to require the control of attention to complete the task and it is predicted that WMC will not impact the outcome, whereas dividing attention while shadowing has a high attentional demand and is expected to require a greater control of attention to complete the task and it is predicted that WMC will have a significant effect on the outcome.

METHOD

Participants

The sample comprised 118 (71 male, 47 female) undergraduate students from the University of Illinois at Chicago subject pool who received course credit for participating. The participants were native English speakers, with normal hearing, and monosyllabic first names. All participants were screened for WMC prior to performing the dichotic listening task.

Working Memory Screening

The procedures used to measure WMC were adapted from versions of the operation span task and reading span task used by Kane, Hambrick, Tuholski, Wilhelm, Payne, and Engle (2004). We followed the administration and scoring guidelines recommended by Conway et al. (2005). To be consistent with the Conway et al. terminology, each task consists of "items" that vary in difficulty, which is manipulated by varying the number of "elements" per item. This terminology is consistent with psychometric lingo where a test (or task) consists of items that vary in difficulty. Each task, operation span and reading span, consisted of 12 items. The number of elements per item varied from 2 to 5, with three items at each level of difficulty.

In the operation span task, each element consisted of a mathematical operation and a word (e.g., IS [7∗3] + 4 = 21 ? SNOW). The participant's task was to read the math problem aloud, say "yes" or "no" to indicate whether the given answer was correct or incorrect and then say the word. After all the elements in an item were presented the participant was required to write the words in correct serial order. The difficulty of the items was randomized such that the number of elements was unpredictable at the outset of an item.

In the reading span task, each element consisted of a sentence, followed by a letter (e.g., Andy was stopped by the policeman because he crossed the yellow heaven. ? R). The participant's task was to say the sentence aloud, respond "yes" or "no" to indicate whether the sentence made sense and then say the letter. As with operation span, after all the elements in an item were presented the participant was required to write the letters in correct serial order and the difficulty of the items was randomized such that the number of elements was unpredictable at the outset of an item.

Proportion scores were computed for each item by dividing the number of correctly recalled stimuli by the total number of stimuli in that item (e.g., if the participant correctly recalled two of four words, then the score for that item would be .5). The total proportion score was simply the average of the item proportion scores multiplied by 100 to yield a scale of 0–100. Finally, an overall proportion score for WMC was computed by averaging the total proportion scores for operation span and reading span.

Divided Attention Procedure

Each participant performed two tasks: divided attention-shadow and divided attention-no shadow. The order of the tasks was counterbalanced. Participants completed the tasks at one of three SNRs: −8, 0, and +8 (i.e., the more relevant message was presented either −8, 0, or +8 decibels compared to the less relevant message). Participants completed the two tasks at only 1 SNR and SNR was randomly assigned. In the divided attention-shadow condition, participants were instructed to listen to the more relevant message (presented to the right ear) and to repeat (shadow) each word as soon

Table 1
Descriptive Statistics of WMC, Shadowing Errors, and Name Detection

Measure	*M*	*SD*	*N*
WMC	66.14	12.23	118
Shadowing Errors			
SNR −8	54.36	28.57	39
SNR 0	50.15	27.82	40
SNR +8	35.97	26.66	39
Total	46.86	28.56	118
Name Detection			
Shadow	50.00	50.21	118
No shadow	85.60	35.27	118

Note—WMC, working memory capacity; SNR, signal-to-noise ratio.

as it was heard, making as few errors as possible. Participants were told that their name would be presented in the unshadowed message and upon hearing their name they should press the space bar on the computer keyboard. Participants were asked to continue shadowing until all sound on the more relevant message had stopped. While participants were shadowing, the experimenter was seated at a separate table in the room and recorded shadowing errors. Prior to the divided attention-no shadow condition participants were told that their name would be presented somewhere within the two messages they would listen to, and upon hearing their name, they should press the space bar. The name was always presented to the left ear. Unlike selective attention dichotic listening experiments, participants were not asked at the end of the experiment whether they heard their name. This was not necessary as pressing the space bar allowed for assessment of the participants hearing their name.

Divided Attention Stimuli

The auditory stimuli were digitized onto a computer at a sampling rate of 22 kHz and dynamic range of 16 bits. There were three sets of auditory stimuli, each of which comprised a more relevant and a less relevant message. They were presented through stereo headphones, with each set being presented at one of three SNRs. The stimulus lists for the divided attention-no shadow task were the same as in the shadowed task; however, participants were presented with a list that they had not shadowed, thus each separate list appeared unique to the participant. The more relevant message consisted of 180 unrelated monosyllabic words (i.e., did not form a coherent text) recorded in a monotone female voice at a rate of 60 words per min and lasted 3 min. The less relevant message contained 150 unrelated monosyllabic words recorded in a monotone male voice at a rate of 60 words per min and lasted 2.5 min. The onset of the more relevant message began 30 words prior to the presentation of the less relevant stimuli, allowing participants to become acquainted with the more relevant message without distraction. The onsets of the words in the two channels were synchronized. The order of the words in each SNR group (−8, 0, +8) was identical across participants except for the names. Participants' first names were randomly inserted into the less relevant message in place of a word, either early, at 1 min 30 sec, or late, at 2 min 30 sec.

RESULTS

Descriptive Statistics

Descriptive statistics for all measures are reported in Table 1. The distribution of scores for the span tasks are similar to those obtained in others labs (see Conway et al., 2005; Kane et al., 2004). As expected, the percentage of participants who reported hearing their name was greater in the no-shadowing condition ($M = 85.6\%$) than in the shadowing condition ($M = 50\%$) [McNemar test ($1, N = 118$) $= 31.5, p < .05$]. Not surprisingly, these percentages are higher than the 33% that is typically observed in selective attention versions of this task (Conway et al., 2001; Moray, 1959; Wood & Cowan, 1995).

Name Detection

Two separate (shadow, no shadow) hierarchical binary logistic regression analyses were conducted to assess the role that WMC and SNR play on the likelihood of a participant hearing their name. For all analyses, WMC and SNR were entered in the first step of the regression analysis and the WMC × SNR interaction was entered in the second step. WMC was centered. SNR was treated as a continuous variable, coded in order of decreasing attentional demand (i.e., −8, 0, and +8, coded as 0, 1, and 2, respectively).

The results of the shadow analysis indicated that there was a significant main effect due to WMC (Wald $= 3.85$, $p < .05$; OR $= 1.03$). Therefore, for each 1 unit increase in WMC, participants were 3% more likely to hear their name. More concretely, a one standard deviation increase in WMC (12 points) means that a participant was 36% more likely to detect their name. Both SNR and the interaction were not significant (Walds = .15 and .24, respectively).

The same results are presented by WMC category (see Figure 1), to better compare the present results with those in the parallel selective attention version of this task reported by Conway et al. (2001). Conway et al. compared only two categories of subjects: high span and low span. High spans had WMC scores that fell in the upper quartile of a large distribution of WMC scores ($M = 24.85$; range of 17–44) and low spans had WMC scores that fell in the lower quartile ($M = 8.22$; range of 6–12). In the present project we collected dichotic listening data from the entire range of WMC; therefore, to compare our results with those from Conway et al., we constructed two WMC categories: high WMC (upper quartile) ($M = 82.16$; range of 75–91.04) and low WMC (lower quartile) ($M = 50.81$; range of 31.53–57.99).[1] With these boundaries, 66.7% of high WMC participants and 34.5% of low WMC participants heard their name. This pattern of results is particularly striking when compared to the results of Conway et al. (2001), who observed the opposite pattern in a selective attention task; 65% of the low WMC participants reported hearing their name and only 20% of the high WMC participants reported hearing their name.

The results of the no shadow analysis indicated that neither WMC, SNR, nor the interaction were significant (Walds = .10, 1.70, and .30, respectively). The results broken down by WMC category are presented in Figure 1. As predicted, WMC did not have an effect on hearing the name in the no shadow task.

Shadowing Errors

A hierarchical linear regression was conducted to examine the relationship between WMC, SNR, and shadowing errors. The results of the initial model accounted for a significant proportion of variance [adjusted $R^2 = .08$; $F(2,115) = 6.35, p < .05$]. SNR was a significant predictor of the number of shadowing errors ($\beta = -.24$, $t = -2.64, p < .05$), whereas WMC was only marginally sig-

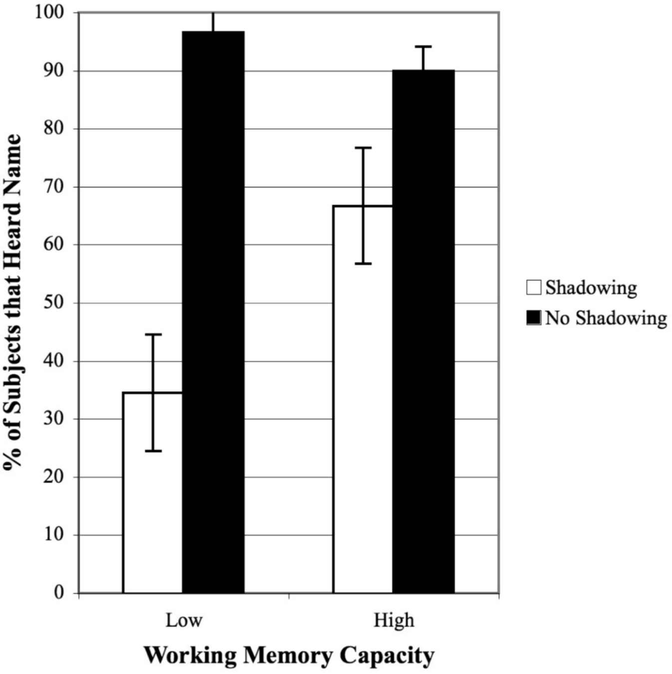

Figure 1. The percentage of high WMC and low WMC participants that heard their name. Error bars represent standard errors.

nificant ($\beta = -.18$, $t = -1.97$, $p = .051$). There was not a significant change in the amount of variance predicted with the addition of interaction term (R^2 change $= .00$, F change $= .33$, $p > .05$). These results suggest that participants with greater WMC made fewer errors than participants with lesser WMC. Therefore, it is unlikely that the larger proportion of participants with greater WMC hearing their name is due to higher WMC participants neglecting the shadowing task.

DISCUSSION

The results of this experiment provide additional yet unique support for the controlled attention theory of WM. Previously, the relationship between WMC and the ability to control attention was only supported by research on selective attention. Here we demonstrate that individuals with greater WMC are also better able to divide attention than are individuals with lesser WMC. Not surprisingly, when the divided attention task was less demanding (i.e., no shadowing), there was not a significant effect of WMC on task performance; however, when the task was demanding (i.e., shadowing), there was a significant effect of WMC, such that as WMC increased, so did performance on the attention task, as indexed by likelihood of name detection and shadowing errors. Unfortunately, the SNR manipulation did not impact the likelihood of name detection. As a result, it is not surprising that SNR did not interact with WMC to predict name detection.

The results of the no-shadowing divided attention task likely represent a ceiling effect, which makes it difficult to determine the role of WMC. However, the prediction of this effect was theoretically motivated. As discussed earlier, WMC is not related to performance in all situations that require attention, but seems to be selectively related to performance in attention tasks that place greater demands on executive attention. While the ceiling effect in the no shadowing condition does temper our conclusion about the attentional demand manipulations, it is reassuring to observe that low span participants were able to detect their names in this condition because it rules out the uninteresting interpretation that low span participants are simply unable to follow directions.

Comparing the results of the present study to the results obtained by Conway et al. (2001) presents a bit of a paradox, particularly when considering the performance of low span participants.[2] Conway et al. found that in the selective attention dichotic listening task 65% of low spans and only 20% of high spans reported hearing their name. The results of the present experiment revealed an opposite pattern, such that in the divided attention, shadowing task, 66.7% of high spans and 34.5% of low spans heard their name. The interpretation of the high span data is straightforward, i.e., these participants are better able to adjust the focus of attention according to task goals. They focus attention in the selective attention task, thus hearing their name less often, and they split their attention in the divided attention task, thus hearing their name more often.

But what does one make of the performance of low span participants? They were actually *less* likely to hear their name when they were told to listen for it than when they had no idea that it was coming! How do we reconcile these results? A critical difference between Conway et al.'s selective attention task and the present divided attention task is the way in which one's name was detected. In the selective attention paradigm subjects were asked, *after shadowing*, if they thought they heard their name in the ignored message. In the divided attention task, participants were required to press the space bar immediately after detecting their name. Thus, in the selective attention task low spans are more susceptible to attentional capture by a salient distractor and in the divided attention task they are less able to coordinate the demands of shadowing, listening for their name, and signaling name detection.

These results are consistent with Cowan's (2005) adjustable-attention theory of individual differences in WMC and fluid intelligence. Cowan argues that greater WMC, as well as greater fluid intelligence, is associated with the ability to adjust attention according to task goals. Individuals with greater WMC and greater fluid intelligence are better able to configure attention to meet task goals. Previous research on selective attention supports the notion that individuals with greater WMC are better able to focus attention and avoid distraction and the present results support the notion that individuals with greater WMC are better able to "zoom out" and divide attention. There is also evidence to support the notion that individuals with greater WMC are better able to configure visual attention, discontiguously rather than contiguously, depending on which configuration optimizes task performance (Bleckley, Durso, Crutchfield, Engle, & Khanna, 2003). However, what remains a question for future research is whether greater WMC is also related to the ability to *dynamically* adapt attention to meet task demands, rather than simply the ability to set the focus of attention according to given task goals. In other words, might high spans be able to dynamically adapt their focus of attention as task demands change or might they be more resistant to change their focus once it is set? This question awaits future research.

AUTHOR NOTE

This research was submitted to the University of Illinois at Chicago in partial fulfillment of the requirements of the Master of Arts degree by G.J.H.C. We thank Jennifer Wiley and James W. Pellegrino for their helpful comments during the preparation of the manuscript. Correspondence concerning this article should be addressed to G. J. H. Colflesh, University of Illinois Chicago, Department of Psychology (M/C 285), 1007 West Harrison Street, Chicago, IL 60607 (e-mail: colflesh@uic.edu).

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NOTES

1. The method of scoring WMC measures used by Conway et al. (2001) was different from that in the present experiment. Rescoring the WMC measures from the current experiment using the scoring procedure of Conway et al. yielded similar means and ranges for both the high ($M = 21.93$; range of 16–30) and low spans ($M = 8.05$; range of 1–13).

2. The dichotic listening procedure of the present experiment was based on that used by Conway et al. (2001). In both experiments, the gender, the nature and the rate of presentation of the messages were the same. However, there were differences between the two studies, but the authors feel that they do not detract from interpretation of the results. There were three differences between Conway et al. and the present study: (1) the length of the messages (5.5 vs. 3 min, respectively); (2) the time of the presentation of the name (at 4 or 5 min vs. 1.5 or 2.5 min, respectively); and (3) SNR (0 SNR vs. −8, 0, and +8 SNR, respectively).

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Decision making, impulsivity and time perception

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Time is an important dimension when individuals make decisions. Specifically, the time until a beneficial outcome can be received is viewed as a cost and is weighed against the benefits of the outcome. We propose that impulsive individuals experience time differently, that is with a higher cost. Impulsive subjects, therefore, overestimate the duration of time intervals and, as a consequence, discount the value of delayed rewards more strongly than do self-controlled individuals. The literature on time perception and impulsivity, however, is not clear cut and needs a better theoretical foundation. Here, we develop the theoretical background on concepts of time perception, which could lead to an empirically based notion of the association between an altered sense of time and impulsivity.

Introduction

The perception of time is a crucial factor when individuals have to make decisions and consider the outcomes associated with their choices. Rewards that are received sooner are often preferred over future rewards, that is the subjective value of an outcome is discounted as a function of the delay [1,2]. It is well known that impulsive subjects devalue temporally delayed rewards more strongly than do comparison subjects, and this behavior might be due to their altered sense of time. According to this hypothesis, impulsive individuals will opt for smaller and immediate rewards more often than for delayed but higher rewards because they estimate duration as being subjectively longer than do more self-controlled individuals. The perception of time as lasting too long is associated with too high of a cost, which leads to the selection of alternatives with more immediate outcomes (see Figure 1).

Several empirical studies pointing to a possible association among impulsivity, decision making and time perception have been conducted over the last few decades [3–8]. However, only recently has this notion been addressed in a more systematic way. Here, we develop a conceptual framework that can guide current and future research and might allow researchers to build a consistent theory framing impulsivity, decision making and the experience of time. We will point to some methodological factors that have to be controlled for to reach valid conclusions and to explain impulsive decision making in inter-temporal choices. First, findings will be reviewed on impulsive behavior in inter-temporal choices, particularly in delay-discounting tasks, which examine the influence of time on decision making. Second, cognitive models of time perception will be related to study results showing that impulsive subjects display an altered sense of subjective time. It will be argued that the association between time perception and mood states plays a fundamental role in interpreting these empirical results.

Decision making and impulsivity

Every day we have to decide between options that have immediate or delayed consequences. For instance, we might restrict our eating habits to reduce our body weight, thereby opting for a momentary loss of pleasure associated with food to gain the future benefits of better physical health and appearance. Similarly, a student might have to decide whether to go to a party tonight or to stay at home and study for an exam that is scheduled tomorrow (the possible later higher reward is here, of course, to pass the exam). The process of deciding whether to opt for an immediate or earlier reward or for a delayed but higher reward is strongly related to scholarly and professional success in life [9]. To function effectively, one voluntarily has to postpone impulsive urges for immediate gratification and rather persist in goal-directed behavior to achieve positive outcomes in future [10].

Results from decision-making experiments show that people avoid risk when they have to choose between options associated with probable versus sure outcomes. Specifically, individuals choose a sure thing over rewards with a probabilistic outcome – even when the probabilistic alternatives have equal or even higher expected value [11]. The duration between the choice and the reception of the reward is another important factor that biases our decisions. A delayed outcome of a choice reduces the subjective value of the reward, a phenomenon called delay discounting [12,13]. Generally speaking, one prefers to receive rewards sooner rather than later. Future rewards are discounted such that they are worth subjectively less as a result of the delay. One way to measure temporal discounting behavior in human participants experimentally is by presenting individuals with a hypothetical or a real choice between two options, for example ’would you prefer $10 right now or $20 in a week?’ In delay discounting procedures, participants make choices between rewards that are smaller but sooner versus rewards that are larger

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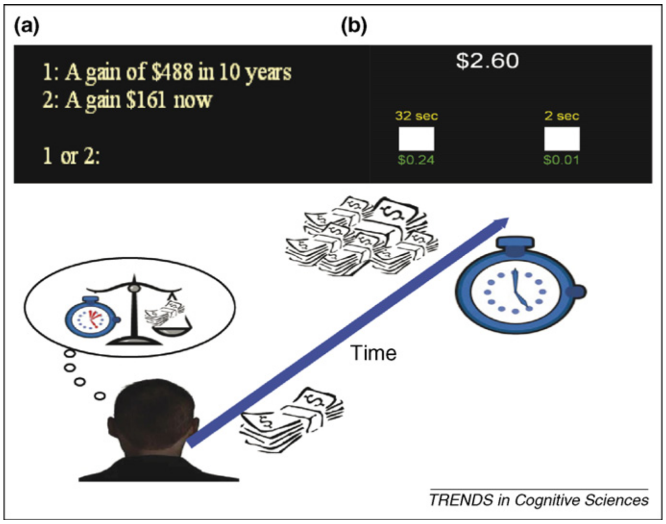

Figure 1. This figure shows two typical inter-temporal decision tasks. **(a)** In a hypothetical task, subjects are asked to decide between a smaller gain now and a higher reward in the future. Time scales for the delayed reward typically are varied from a few days up to decades [51]. **(b)** In a real task, subjects have to decide between a reward received within 2 s and larger rewards with delays of many seconds [14]. The actual money subjects can earn, based on their consecutive decisions, accumulates and is presented on the upper part of the screen. The lower illustration shows the degree to which an individual processes time as a cost in decision making. The internal representation of duration as the cost in time and the reward value are weighed against each other when choosing the immediate but smaller reward over the delayed but larger reward in the future.

but delayed (Figure 1). As the duration of the delay to the second option increases, preference for this option usually decreases. The temporal discounting pattern has repeatedly been described as following a hyperbolic function, meaning that after an initial steep decline of the subjective reward with increasing delays, even very remote outcomes retain some (albeit minute) value for the decision maker [1,14,15].

Individuals differ in how strongly they retain subjective value as a function of time. Moreover, the degree to which people are able to delay gratification is generally associated with the notion of willpower [16], whereas those who choose immediate gratification at the expense of important long-term interest are judged to be impulsive [1,17]. However, impulsivity is determined by a complex set of processes and consists of multiple components [18], and this contention is consistent with the finding that the correlations across different methods of assessing impulsivity are modest [19]. Nevertheless, impulsivity can be conceptualized as a pattern of behavior for which the potential of negative consequences has limited influence on the planning of actions. The external validity of using delay-discounting paradigms to quantify dysfunctions of impulse control is based on findings that children with attention deficit hyperactivity disorder (ADHD) [4], individuals with neuropsychiatric disorders [20], smokers [21], alcoholics [22] and substance-dependent individuals [23] show increased discounting of delayed rewards.

Despite the well-established finding that impulsive individuals discount delayed rewards more strongly than do more self-controlled individuals, the underlying cognitive and affective processes that account for this phenomenon are poorly understood. The decision-making processes associated with delayed discounting depend on neural substrates that are important for regulating emotions and feelings [16,24]. Functional imaging studies using delay discounting tasks are beginning to examine which brain areas are associated with impulsivity and self control (see Box 1). Findings from a different set of studies point towards the possibility that impulsive individuals have an altered sense of time [4–8,25], which might explain why they have difficulties in delaying gratification.

Cognitive models linking time perception and impulsivity

Experimental tasks that probe time-interval production and estimation

Although it is not yet clear how time keeping is implemented in the brain [26–29], several brain areas provide fundamental building blocks of an interval-timing system (a neural clock) for durations in the seconds range (see Box 2). Cognitive models, which assume that an internal clock with a pacemaker produces subjective time units [30], have been fairly successful in interpreting human time perception and animal timing behavior (see Figure 2). The subjective duration of time is defined by the number of temporal units accumulated over a certain time span. When individuals are asked to judge intervals of, for example, 30 s during a time-estimation task, an overestimation would correspond to an increased accumulation of temporal units over that period. In comparison, because of an increased accumulation of units over time, an individual would perform with a shorter production of the

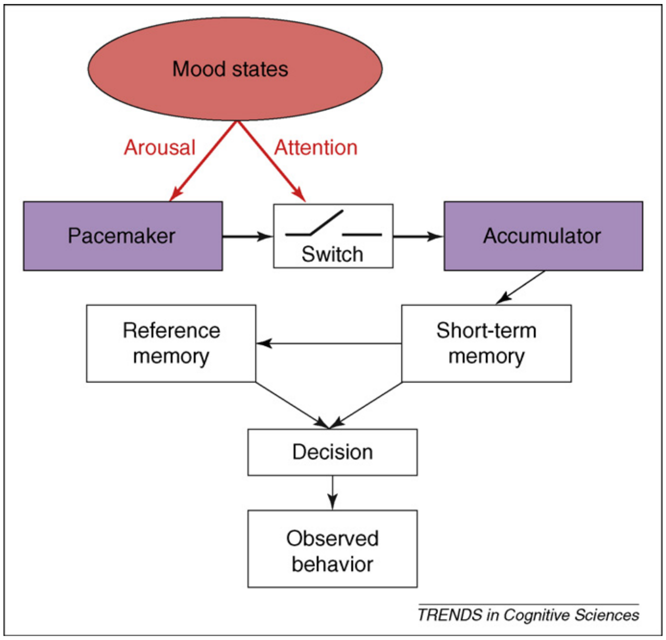

Figure 2. In cognitive models of time perception, a pacemaker produces a series of pulses that are fed into an accumulator. The number of pulses that has been recorded for a given time span represents experienced duration. The pulse number is compared with stored representations of time periods that can be verbalized (as seconds or minutes). Attentional gate models [30] assume that only when attention is directed to time pulses are accumulated. A switch is closed which then opens a gate to the accumulator. Two possible ways can be assumed for how mood states can influence the subjective experience of duration. Firstly, increased arousal leads to higher pacemaker rate and, thus, to a greater accumulation of pulses during a given time period. Secondly, increased attention to time leads to an increased inflow of pulses and, thus, also to their greater accumulation. The models of time perception contain multiple processing steps comprising a memory and a decision stage too [31].

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Box 1. fMRI studies on delay discounting

Functional magnetic resonance imaging (fMRI) studies have explicitly addressed impulse control using delay-discounting tasks and real rewards. Strong evidence of limbic and paralimbic cortical activation was found when subjects were presented with choices between a smaller earlier reward and a greater but delayed reward [54–56]. Lateral prefrontal and parietal cortices associated with executive control were activated when subjects delayed gratification, that is when they chose the delayed reward [54–56]. In addition, a study by Tanaka and colleagues [55] suggests that the striatum and the insula are implicated in the evaluation of reward outcomes as a function of delay. Specifically, the ventroanterior regions of these two brain structures were more activated when choices were presented in which subjects learned to select immediate rewards; conversely, the dorsoposterior regions were more activated when subjects learned to select future rewards. Tanaka and colleagues postulate that the ventroanterior parts of the insula and striatum might be involved in short-term reward prediction, whereas more dorsoposterior regions might be involved in long-term reward prediction. According to this model, the different pathways of the cortico-basal ganglia circuit might be specialized for reward prediction and action selection on different time scales [55,57]. This is indeed what we found in a recent fMRI study using a hypothetical delay-discounting task in which participants had to choose between immediate rewards and rewards with delays in the range of days to multiple years. Activity of the left-sided striatum co-varied positively with the perceived delay of the reward that will be received within one year's time versus one that will be received after one year's time. Thus, the amount of activation in this region coded for the delay of reception of the reward (See Figure I) [51].

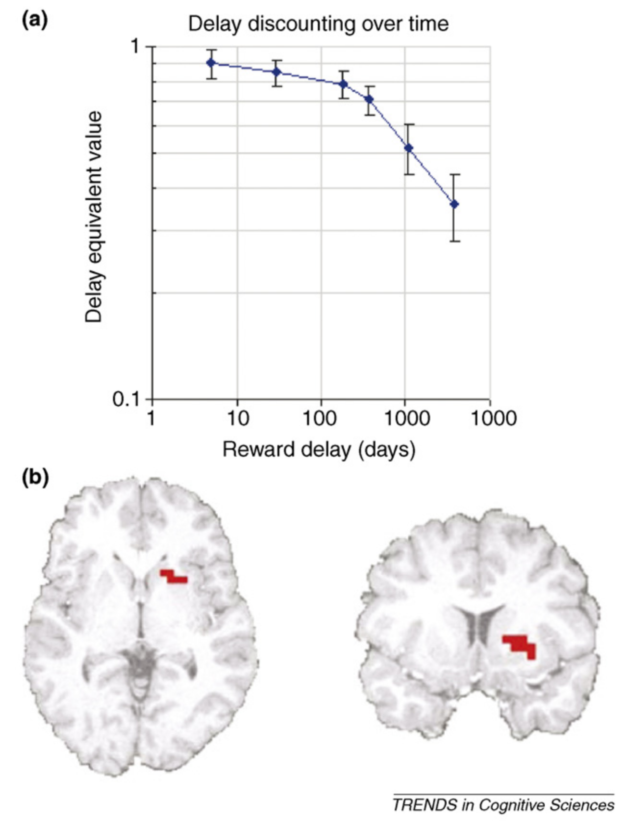

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Figure I. **(a)** Two different discounting slopes plotted for delays <1 year and ≥1 year (on double-logarithmic scales). In a hypothetical delay-discounting task, subjects had to choose between a smaller reward now and a greater reward with a delay. Delays varied between 5, 30, 180 days (<1 year) and 365, 1095, 3650 days (≥1 year). **(b)** On the axial and coronal brain slices left-sided activation of the caudate nucleus and putamen is shown for the contrast of presentations of choices between a reward now and <1 year and presentations of choices between a reward now and ≥1 year. These findings can be interpreted in the way that the activated brain regions code for the delay of reward. Adapted, with permission, from Springer-Verlag [51].

same duration during a time-production task. Cognitive models of time perception propose two mechanisms that could increase the number of pulses in an assumed accumulator [31] (see Figure 2): (i) increased attention to, as opposed to distraction from, time leads to an accumulation of more pulses over a time span, (ii) an arousal-related increased rate of pulses emitted by the pacemaker (a faster clock rate) leads to a faster accumulation of temporal units over time.

The hypothesis that impulsive choices could be due to an overestimation of time is supported by several studies showing that impulsive subjects overestimate and/or under-produce time intervals. First, when individuals were sleep deprived relative to being well rested, they were more

Box 2. Neural models of time perception

Multiple brain regions are usually activated in imaging studies on time perception suggesting that different processing components, such as attending to time, encoding an interval and keeping the representation of duration in working memory, as well as decision processes are involved [58,59]. Investigations using neuropsychological and pharmacological approaches to study time perception in animals and humans, however, have yielded the specific hypothesis that fronto-striatal circuits, which are modulated by the dopamine system, are crucial for temporal processing in the seconds range [50,60]. Individuals with structural damage to the frontal lobes [61] or traumatic brain injury predominantly affecting frontal areas [31] show impaired estimation of temporal intervals of several seconds. Neuroimaging studies with healthy volunteers show that temporal processing is predominantly associated with activation in the right prefrontal and striatal regions [50,62]. Thus, areas activated during the processing of duration are similar to those that are activated in delay-discounting tasks (see Box 1). Other brain regions, such as the cerebellum, also seem to play a decisive role in the processing of duration; however, the involvement of these regions is probably restricted to the time range of milliseconds to a few seconds [26]. Moreover, recent studies indicate that several areas of the brain can contribute to the processing of duration in the milliseconds range. Specifically, neural populations within each region could encode duration as a result of specific time-dependent neural changes, such as short-term synaptic plasticity [63]. Only future research that addresses both time perception and delay discounting in a combined study will reveal whether the same specific brain areas are involved in the processing of the two domains.

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impulsive, discounted delayed rewards more strongly and under-produced time intervals in the multiple-seconds range [5]. Second, impulsive borderline personality disorder patients under-produced time intervals between 10 and 90 s [32]. Third, patients with orbitofrontal cortex lesions, who were more impulsive during behavioral tests, considerably overestimated and under-produced time intervals [33]. Fourth, cocaine- or methamphetamine-dependent individuals participating in an inpatient alcohol and drug treatment program overestimated the duration of a 53 s interval, this judgment being associated with higher self-reported impulsivity [34]. Fifth, children with disruptive behavior disorders who exhibit increased impulsiveness and aggressiveness under-produced a one-minute interval more strongly than did control children [35]. Thus, findings from clinical populations clearly demonstrate that the subjective experience of time is associated with a higher level of both self-rated and behaviorally tested impulsivity.

Affective and cognitive factors altering time perception

Different mood states influence the degree to which someone attends to time or is distracted from time. Accordingly, boredom-prone individuals [36], patients with depression [37] or cancer patients with high levels of anxiety [38] perceive a slowing of the pace of time and overestimate durations in time-estimation tasks. In these cases, the acute stress might divert attentional resources away from ongoing thoughts and actions to the passage of time, which leads to an overestimation of duration [39]. In comparison, an impulsive subject who might experience distress because habitual impulsive acts often cannot be instantiated (e.g. in waiting situations) allocates more attentional resources to the passage of time, which in turn leads to an overestimation of perceived duration [34].

Alternatively, some findings support the hypothesis that impulsive individuals exhibit an increased cognitive processing speed, that is a faster pacemaker, which is consistent with increased activity level in these subjects [7]. Altered physiological conditions, for example an increase in body temperature, are associated with an overestimation of duration, an effect that has been explained by an increase in the rate of a cognitive pacemaker [40]. In animal studies, shortened production intervals have been reported after administration of stimulants, which are thought to increase the pacemaker rate [41]. Some investigators have proposed that subjects overestimate the duration of presented emotional faces relative to neutral faces because emotion leads to an increased arousal state and can alter the pacemaker rate [42].

The attention-related or activation-induced mechanisms that are proposed to alter the sense of time in impulsive individuals are not necessarily exclusive but could contribute to the phenomenon of altered time perception in an additive way [43]. For example, smokers who have cigarette cravings and feel a strong urge to smoke experienced that time passed more slowly [44]. This effect could to some extent be explained by an increased arousal due to the emotion-inducing craving symptoms. However, smokers might also attend more strongly to time as they wait for their chance to smoke.

Other experimental results are more equivocal about the relationship between impulsiveness and time estimation. For example, children and adults with ADHDs show impaired temporal processing within durations of milliseconds to multiple seconds on a variety of sensorimotor timing tasks [4,45,46]. Although these subjects showed a stronger discounting of delayed rewards, their verbal time estimates of intervals within the multiple-seconds range did not differ from estimates made by control subjects [11,43] (see also Box 3). One study even reported considerable overproductions of time intervals in children with ADHDs [47], and this finding would be consistent with the hypothesis that hyperactive children relative to comparison subjects pay less attention to the timing task. Thus, distractibility, which is a prominent feature in individuals with ADHD, might be associated

Box 3. Two essential features of studies on time perception

(1) There are basically four different methods for measuring subjects' accuracy in time estimation/perception [30]. (i) In the method of verbal estimation of duration, an interval is presented and the individual has to judge how many seconds/minutes have elapsed. (ii) In duration production tasks, a subject has to indicate when he/she thinks a certain time span has elapsed, for example by pressing a key. (iii) In duration reproduction tasks, a standard interval with a certain duration is presented. Subsequently, subjects have to reproduce the length of this interval by indicating when they believe that the duration is now identical to the standard interval. (iv) In duration comparison tasks, two intervals are presented and subjects have to decide which one is longer. In variants of this task, a subject is repeatedly exposed to a standard interval (the learning phase) and then later (the actual test phase) has to judge whether presented stimuli have equal duration compared with the standard interval.

In duration estimation and duration production tasks individuals have to translate between the experience of duration and conventional units of time (seconds, minutes). These two tasks can be used to explain individual differences in terms of attention mechanisms or the speed of a pacemaker. By contrast, the experience of time is indicated behaviorally in duration-reproduction and duration-discrimination tasks. However, because of the relative nature of the reproduction and the discrimination task (two intervals are compared with each other), any internal influence (attention, arousal) will affect the processing of both intervals – the standard and the comparison. Individual differences, that is allocation of more or less attention to time, will not reveal differences in outward performance. A disadvantage of the production as well the reproduction task is that a desire to end a trial prematurely will lead to the (re-)production of shorter intervals, a confounder especially relevant when testing impulsive individuals.

(2) It is crucial to control for the subject's ability to use counting as a strategy to keep track of time during time-estimation tasks. Chronometric counting, a language-based strategy using internal speech supports substantially more precise estimates than does the interval-timing system and is also guided by different brain structures [64]. Very often just the verbal instruction not to count is given to prevent participants from counting [5,34,48]. However, volunteers repeatedly report that the tendency to count or use other strategies for subdividing the presented time interval is rather strong. This tendency might have contributed to the lack of group differences in time estimation studies on impulsive subjects [4,65]. A reliable way to prevent participants from counting is to present them with a concurrent task during the time interval to be estimated. The concurrent task could be as simple as reading aloud numbers presented sequentially with randomized intervals, but it prevents subjects from counting internally [32,66].

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with slower accumulation of time pulses, which leads to longer interval productions. Finally, there was no relationship between impulsivity and time estimation in a comparably large group of young healthy college students [48]. It is possible that relatively normal variation of impulsivity levels might not be strong enough to alter the subjective experience of time. At this stage, methodological approaches and subject characteristics vary from study to study, which makes it difficult to compare some of these results directly. For future studies to overcome these shortcomings, two important factors have to be controlled for (Box 3).

Conclusions

There is a considerable body of knowledge about the cognitive-processing mechanisms that guide the experience of duration [30,49,50]. This knowledge can be brought to bear on understanding the mechanisms underlying impulsivity and self control in inter-temporal decisions [51]. Because the perception of time is strongly linked to our subjective well-being, the passage of time varies considerably depending on our emotional states. The feeling that time passes slowly seems to be a fair indicator of psychological distress resulting from an inability to focus on meaningful thoughts and to start interesting activities. Drive states, moods and emotions, visceral factors that operate in the here and now, often influence our decisions in a way so that we prefer immediate satisfaction, although in the long run we might have to face negative consequences [24]. Visceral factors might also have an impact on the sense of time, leading to a stronger focus on the present and an overestimation of time. Recently, a framework has been formulated for an anatomical and structural model for integrating interoception and the processing of emotional moments with the perception of time [52].

In summary, increased allocation of attentional resources to time and/or increased arousal states, possibly driven by emotional distress, could be the main factor that alters the way in which impulsive individuals take time into account when making decisions. According to cognitive models of time perception, the overestimation of a given temporal duration is a consequence of a stronger focus on time and of heightened arousal. We want to emphasize here that on many occasions impulsive individuals, particularly when they are distracted, do not overestimate time, which argues against a fundamental dysfunction of the 'inner clock'. Instead, these individuals are more likely to experience a slowing down of time during situations in which they are not able to act on their impulsive urges, for example when one has to wait for a delayed reward and is confronted with the passage of time. However, more research is needed to determine the causal relationships among decision making, emotional distress and time perception (Box 4). Studies with different subject populations provide clues that the sense of time is an important factor for the understanding of altered decision making. We highlighted some methodological issues that need to be taken into account when interpreting results from time processing studies.

Understanding why individuals with clinically relevant impulsive disorders strongly neglect future consequences is the first step in developing specific interventions to alter this behavior that has negative consequences for everyday life. For example, treatment programs could use intervention strategies that manipulate the temporal delay of rewards or that cognitively restructure the perception of inter-temporal choices [17,34,53]. In addition, intervention might eventually be able to alter directly the timing system, which in turn would profoundly affect the way individuals process delayed rewards and structure behavior towards health-promoting actions.

Box 4. Questions for future research

- Is an altered sense of time in the seconds-to-minute range associated only with inter-temporal choices in a similar time range or can the association also be detected with decision tasks using longer delays?
- With respect to cognitive models of time estimation, is the subjective lengthening of duration in impulsive individuals linked to a stronger focus on time or to an increase in arousal when attending to time?
- Which temporal intervals are crucial in time perception studies? Different interval lengths will to a varying degree, depending on the subject group studied and the timing task used, be sensitive for the effects under investigation.

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Processing of Temporal and Nontemporal Information as Predictors of Psychometric Intelligence: A Structural-Equation-Modeling Approach

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ABSTRACT Recent research suggests a functional link between temporal acuity and general intelligence. To better understand this relation, the present study took advantage of a large sample ($N = 260$) and structural equation modelling to examine relations among temporal acuity, measured by various tasks, speed of information processing as measured by the Hick reaction time task, and psychometric intelligence. Temporal acuity and the Hick task showed common variance in predicting psychometric intelligence. Furthermore, timing performance was a better predictor of psychometric intelligence and mediated the relation between Hick task performance and psychometric intelligence. These findings are consistent with the idea that temporal acuity reflects a basic property of neural functioning that is relevant to intelligence-related aspects of mental activity including speed of information processing.

INTRODUCTION

There is a large literature demonstrating a relation between higher mental ability and faster speed and efficiency of information processing on simple sensory, memory, and decision tasks (e.g., Deary, 2000a, 2000b; Jensen, 2004; Vernon, 1987). The most frequently used

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elementary cognitive tasks (ECTs) in this field include inspection time (Vickers, Nettelbeck, & Willson, 1972), simple and choice reaction time following the rationale of Hick (1952), Sternberg's short-term memory scanning (Sternberg, 1969), and Posner's letter-matching task (Posner & Mitchell, 1967). Current explanations for the observed relationship between psychometric intelligence and measures obtained from ECTs usually refer to the concept of "neural efficiency" as being responsible for faster and less error-prone information processing in individuals with high mental abilities (cf. Bates, Stough, Mangan, & Pellett, 1995; Neubauer, 2000; Sternberg & Kaufman, 1998; Vernon, 1993). In the absence of direct and uncontaminated measures of neural mechanisms, ECTs are often used as surrogates for direct neural measurement (McCrory & Cooper, 2005; Nettelbeck & Wilson, 2005). This procedure is based on the idea that these microlevel tasks are so basic as to eliminate the influence of strategy and educational contaminants, with the result that individual differences in performance can primarily be ascribed to differences in underlying neural processes (McCrory & Cooper, 2005).

The Temporal Resolution Power Hypothesis

In recent work, Rammsayer and Brandler (2002) extended this research by showing that higher mental ability was also related to greater accuracy on several measures of timing performance, specifically the discrimination of tones in the range of seconds and milliseconds, temporal-order judgment, and auditory flutter fusion. In a subsequent study (Rammsayer & Brandler, 2007), this effect was replicated in analyses that involved an expanded battery of timing and mental ability tasks as well as the Hick paradigm, a traditional ECT that measures speed of information processing. Notably, a timing factor predicted a greater proportion of variance in general intelligence (31%) than did a Hick factor (12%). The timing and Hick factors also shared variance, and the common variance predicted about 11% of the variance in general intelligence. This observation led to the question of whether timing ability reflects a process that is fundamental to performance on both general intelligence and speed-related tasks. We pursued this question here.

Rammsayer and Brandler's research (2002, 2007) was based on the idea that temporal accuracy as assessed by psychophysical timing tasks—in analogy to performances on ECTs—might reflect basic processes related to neural efficiency. A theoretical context for this notion is afforded by the master clock hypothesis outlined by Surwillo (1968), who proposed that the oscillation rate of a hypothetical general clock mechanism in the human central nervous system (CNS) is responsible for the coordination of a wide range of mental activities. According to this view, a high temporal resolution power or a high oscillation rate of a general timing mechanism should influence information processing by leading to shorter task completion times and less interference from distracting sources of information (cf. Lindenberger, Mayr, & Kliegl, 1993; Rammsayer & Brandler, 2002; Salthouse, 1991). According to this temporal resolution power hypothesis, then, temporal resolution would be associated with better abilities in both speeded and unspeeded mental ability tests, and might, in turn, be a fundamental contributor to psychometric intelligence.

The Present Study

The present study had two concerns: (1) to provide further evidence for the predictive power of timing performance as a new correlate of psychometric intelligence and (2) to get a better understanding of the relationships among temporal acuity, speed of information processing, and psychometric intelligence. For each of these three domains, several measures of performance have been employed in order to obtain adequate estimates of the general factors for each set of tasks (cf. Brody, 1992). The relations between these general factors, termed temporal *g*, psychometric *g*, and Hick *g*, were subject to structural-equation-modelling (SEM). Several models (see Figure 1) were tested. First, the question was whether temporal *g* and Hick *g* were systematically correlated (Model 2) or whether they were unrelated predictors (Model 1). If temporal *g* and Hick *g* are related, potential mediating effects will be analyzed in two further models. Model 3 is based on the idea that temporal *g* partly mediates the relation between psychometric *g* and Hick *g*. In Model 4, the question will be whether Hick *g* also mediates the relation between temporal *g* and psychometric *g*. In general, the goal is to determine whether temporal *g* or Hick *g* is a more powerful and proximate contributor to psychometric intelligence.

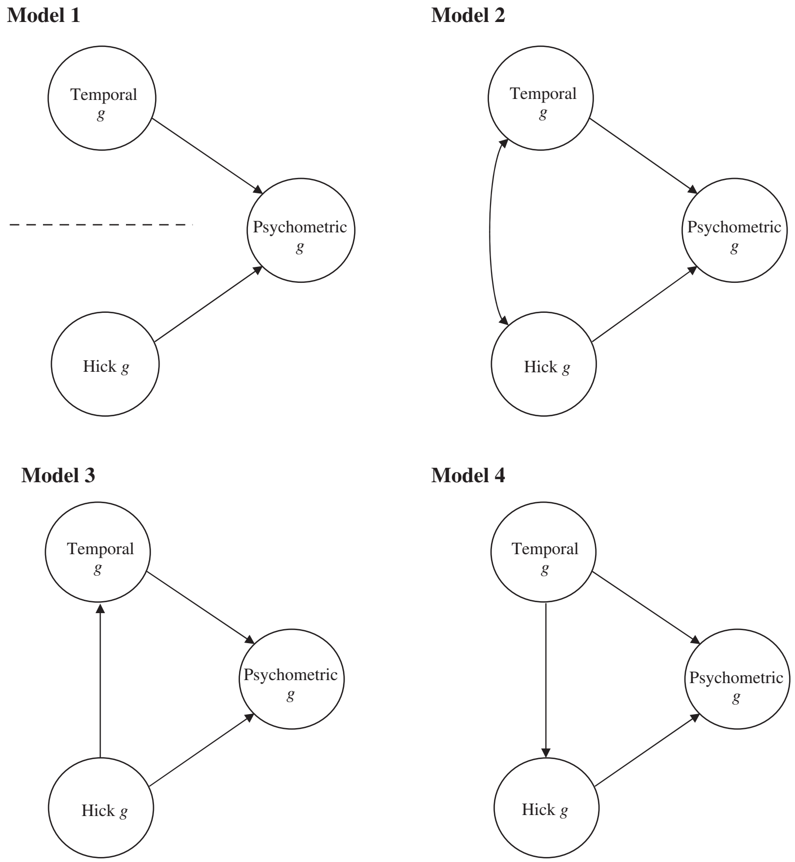

Figure 1
Model 1: Unrelated-predictor model; Model 2: Related-predictor model; Model 3: Model with temporal *g* partly mediating the relationship between Hick *g* and psychometric *g*; Model 4: Model with Hick *g* partly mediating the relationship between temporal *g* and psychometric *g*.

METHOD

Participants

In order to achieve a sample size that provided reliable data for the SEM analyses, the data of Helmbold and Rammsayer (2006) and Rammsayer and Brandler (2002) were pooled. The pooled sample comprised 260 participants (130 male and 130 female). Only younger adults ranging in age from 18 to 39 years (mean ± standard deviation: 24.7 ± 5.5 years) were included in the sample. Education levels spanned a broad range, including 91 university students, 79 vocational school pupils and apprentices, as well as 14 persons who were unemployed. The 76 remaining participants were working persons of different professions. All participants reported normal hearing and had normal or corrected-to-normal sight. They were paid the equivalent of US$30 and offered a feedback about their performance on intelligence testing.

Intelligence Tests

In order to define a valid estimate of psychometric *g*, a comprehensive test battery was employed (cf. Brody, 1992; Jensen, 1998). The battery included 10 intelligence scales assessing various aspects of intelligence corresponding to Thurstone's (1938) primary mental abilities; verbal comprehension, word fluency, space, and flexibility of closure were assessed by subtests of the Leistungsprüfsystem (LPS; Horn, 1983). As a measure of reasoning abilities, the short version of the German adaptation of Cattell's Culture Fair Intelligence Test Scale 3 (CFT; Cattell, 1961) by Weiß (1971) was employed. Furthermore, scales measuring numerical intelligence and verbal, numerical, and spatial memory, respectively, were taken from the Berliner Intelligenzstruktur-Test (BIS; Jäger, Süß, & Beauducel, 1997). A brief description of the components of the battery is presented in Table 1.

Psychophysical Timing Tasks

Because temporal information processing is much more accurate with auditory stimuli than with visual ones, and because auditory stimuli are less prone to task-irrelevant, confounding influences (cf. Grondin, Meilleur-Wells, Ouellette, & Macar, 1998; N'Diaye, Ragot, Garneo, & Pouthas, 2004; Schab & Crowder, 1989), only auditory experimental tasks were used to measure timing-related abilities. Performance measures on interval timing, rhythm perception, and bimodal temporal-order judgment were obtained as psychophysical indicators of temporal resolution.

Interval timing I: Duration discrimination. With this type of task, the participant has to decide which of two successively presented intervals—a constant standard interval and a variable comparison interval—is longer. On each trial, the duration of the comparison can be shorter or longer than the duration of the standard interval. In the present study, two types of stimuli, filled and empty intervals, were used. In filled auditory intervals, a tone was presented continuously throughout the interval, whereas

Table 1
Description of the Psychometric Tests Applied for Measuring Primary Mental Abilities

Intelligence Test	Subscale/Ability	Task Characteristics
LPS	Verbal Comprehension (V)	Detection of spelling mistakes in nouns
LPS	Word Fluency (W)	Anagrams
LPS	Space (S)	Three-dimensional interpretation of two-dimensionally presented objects
LPS	Flexibility of Closure (C)	Detection of single elements in complex objects
CFT	Reasoning (R)	Evaluation of figural arrangements based on inductive and deductive thinking
BIS	Number 1 (N1)	Detection of numbers exceeding the preceding number by "three"
BIS	Number 2 (N2)	Solving of complex mathematical problems by means of simple mathematical principles
BIS	Verbal Memory (vM)	Reproduction of previously memorized nouns
BIS	Numerical Memory (nM)	Reproduction of two-digit numbers
BIS	Spatial Memory (sM)	Recognition of buildings on a city map

Note: LPS = Leistungsprüfsystem; CFT = Culture Fair Intelligence Test Scale 3; BIS = Berliner Intelligenzstruktur-Test.

in empty intervals only the onset and the offset of the interval were marked by clicks. In addition, two different base durations were employed, as there is some evidence that timing in the range of seconds and milliseconds might be functionally different to a certain extent (cf. Michon, 1985; Rammsayer, 1999; Rammsayer & Lima, 1991). The "long" base duration, however, was chosen not to exceed 1,200 ms as this duration represents a critical value above which explicit counting becomes a useful timing strategy (Grondin, Meilleur-Wells, & Lachance, 1999).

The duration discrimination task contained one block of filled and one block of empty intervals with a base duration of 50 ms each, as well as one block of filled intervals with a base duration of 1,000 ms. The order of the three blocks was counterbalanced across participants. Each block contained 64 trials and each trial consisted of one standard interval (= base duration) and one comparison interval. The duration of the comparison interval varied according to an adaptive rule referred to as the *weighted up-down procedure* (Kaernbach, 1991; for more details see Rammsayer & Brandler, 2004). As an indicator of discrimination performance, the difference limen (DL; Luce & Galanter, 1963) was determined. In previous studies performed to evaluate the sensitivity of assessment, Cronbach's alpha coefficients were shown to range from .82 to .99 for the duration discrimination tasks (Brandler & Rammsayer, 1999; Rammsayer, 1994; Rammsayer & Brandler, 2001).

Interval timing II: Temporal generalization. With this task, participants were required to identify a standard stimulus of a certain absolute duration among six deviant, nonstandard stimuli of different durations. Two temporal-generalization tasks with base durations of 75 and 1,000 ms, respectively were applied as an alternative measure of interval timing. Each task consisted of a learning and a test phase. In the learning phase, participants were instructed to memorize a standard stimulus duration, which was presented five times. In the subsequent test phase, both the standard and nonstandard stimuli were presented. In each trial the participants had to decide whether or not the presented stimulus was of the same duration as the standard stimulus. The test phase consisted of eight blocks. Within each block, the standard duration was presented twice, while each of the six nonstandard intervals was presented once. The stimuli were sine wave tones presented through headphones at an intensity of 67 dB. In the range of seconds, the standard stimulus duration was 1,000 ms, and the nonstandard durations were 700, 800, 900, 1,100, 1,200, and 1,300 ms. In the range of milliseconds, the nonstandard stimulus durations were 42, 53, 64, 86, 97, and 108 ms, and the standard duration was 75 ms.

As a quantitative measure of performance, an individual index of response dispersion (cf. McCormack, Brown, Maylor, Darby, & Green, 1999) was computed. For this purpose, the relative frequency of "standard" responses to the standard duration (e.g., 1,000 ms) was divided by the sum of the relative frequencies of "standard" responses to all seven stimulus durations. This measure would approach 1.0 (= best possible performance) if the participant only produced "standard" responses to the standard duration and no standard responses to the nonstandard stimuli. Although many recent studies of human timing have used temporal generalization tasks, the reliability of this type of task, to our knowledge, has not been reevaluated yet.

Temporal-order judgment. Temporal-order judgment refers to the question of how much time must intervene between the onsets of two different stimuli—for example, a tone and a light—for their order to be perceived correctly. Hence, for the temporal-order judgment task, auditory and visual stimuli were employed. Auditory stimuli were 1,000-Hz square waves presented via headphones at an intensity of 67 dB. Visual stimuli were generated by a red light-emitting diode in a black viewer box. The temporal-order judgment task was divided into two independent series of 32 trials each. In Series 1 the tone was preceded by the light, while in Series 2 the tone was presented first. Presentation of both stimuli was simultaneously terminated 200 ms after the onset of the second stimulus. Participants were required to decide whether the onset of the tone or the onset of the light occurred first. Trials from both series were presented randomly. Within each series, stimulus onset asynchrony varied from trial to trial depending on the participant's previous response according to the weighted up-down procedure that converged on a level of 75% correct responses. As an indicator of performance, the difference limen was determined. Rammsayer and Brandler (2002) reported a test-retest reliability coefficient of $r = .73$ for the temporal-order judgment task.

Rhythm perception. In psychophysical rhythm perception tasks, participants have to detect a deviation from regular, periodic, click-to-click intervals. In the present task, the stimuli consisted of 3-ms clicks presented through headphones at an intensity of 88 dB. Participants were presented with auditory rhythmic patterns, each consisting of a sequence of six 3-ms clicks marking five beat-to-beat intervals. Four of these intervals were of a constant duration of 150 ms, while one interval was variable ($150\,\text{ms} + x$). The participant's task was to indicate whether he or she had perceived a deviation from isochrony in the rhythmic pattern (i.e., one beat-to-beat interval was perceived as deviant) or not (i.e., all beat-to-beat intervals appeared to be of the same duration). Task difficulty was adapted by changing the magnitude of x from trial to trial depending on the participant's previous response. The adaptive rule was based on the weighted up-down procedure that converged on a probability of hits of .75. As an indicator of performance, the 75% threshold was determined based on 64 trials. In a previous study (Brandler & Rammsayer, 2000), a test-retest reliability coefficient of $r = .87$ was obtained for the rhythm perception task.

Hick Reaction Time Paradigm

As a measure of speed of information processing a typical ECT, the so-called Hick reaction time (RT) paradigm was used. The Hick paradigm is a visual simple and choice RT task in which participants have to react as quickly as possible to an upcoming visual stimulus. This task is based on

Hick's (1952) discovery of a linear relationship between an individual's RT and the number of stimulus alternatives among which a decision has to be made. In the case of simple RT, no decision between stimulus alternatives is involved (i.e., zero bits of information have to be processed). Analogously, deciding between two stimuli (two-choice RT) requires one binary decision, while, when four alternatives are presented (four-choice RT), two binary decisions are necessary (2-bit). The current version of the Hick paradigm was similar to the one proposed by Neubauer (1991), who was concerned with creating a version of this paradigm that is free of potential confounds such as order effects, response strategies, or changes in visual attention (Longstreth, 1984; Neubauer, Riemann, Mayer, & Angleitner, 1997).

Stimuli were rectangles (2 cm × 1 cm) and a plus sign (0.8 cm) displayed on a monitor screen. In the 2-bit condition (four-choice RT), four rectangles arranged in two rows were presented. After a variable foreperiod varying randomly between 700 and 2,000 ms, the imperative stimulus, the plus sign, was presented randomly in one of the four rectangles. The participants had to respond as quickly as possible to the imperative stimulus by pressing the response button on a "finger-on-keys" apparatus corresponding to the rectangle with the imperative stimulus. After each correct response, a 200-ms tone was presented followed by an intertrial interval of 1,500 ms. The 1-bit condition (two-choice RT) was identical to the 2-bit condition, except that two rectangles were presented arranged in a row. Accordingly, the participant had to choose between two response keys. Similiarly, in the 0-bit condition (no-choice or simple RT), only one rectangle was presented in the center of the screen and the participant had to react by pressing one designated response button. Each condition consisted of 32 trials preceded by 10 practice trials. Order of conditions was randomized across participants. As indicators of individual performance, median RT and intraindividual variability (standard deviation) were computed separately for the 0-, 1-, and 2-bit conditions.

Time Course of the Study

The intelligence tests and experimental tasks were implemented in two testing sessions of 90 minutes each. The order of testing sessions was counterbalanced across participants. Both testing sessions were separated by a 1-week interval. The experimental session was initiated by the three duration discrimination tasks, followed by temporal generalization, the temporal-order judgment task, rhythm perception, and the Hick task. Experimental trials of all tasks were preceded by practice trials to ensure that the participants understood the instructions and to familiarize them with the stimuli.

Data Analysis

For confirmatory factor analysis (CFA) and SEM analyses, Muthén and Muthén's (2005) M*plus* software and maximum likelihood methods were applied in the present study.

RESULTS

Descriptive Statistics

Descriptive statistics for all performance measures are presented in Table 2.

Confirmatory Factor Analysis: Specification of the Measurement Models

According to current factor-analytic conceptions of intelligence (cf. Carroll, 1993; Jensen, 1998; Johnson & Bouchard, 2005), psychometric *g* was conceptualized as a higher-order factor emerging at the top of a hierarchical model of several lower-order mental abilities. Modeling was based on the Berlin Intelligence Structure Model developed by Jäger (1982, 1984). According to this model, psychometric intelligence was extracted as a second-order factor based on the three first order factors of speed, processing capacity, and memory, each of which was operationalized in several ways. Residuals from subtests assigned to the same content category were allowed to covary as indicated by the corresponding arrows in the path diagrams. This model yielded a satisfactory degree of fit ($\chi^2 = 33.79$, $df = 20$, $p = .028$, CFI = .98, TLI = .96, RMSEA = .05).

The Hick data was also modeled in a hierarchical model with Hick *g* as second-order factor and central tendency of RT and intraindividual variability of RT as first-order factors. Extraction of these two first-order factors was based on considerations in the literature, which suggest that both these measures of RT reflect different aspects of information processing performance (cf. Deary & Caryl, 1997; Jensen, 1992, 2004; Slifkin & Newell, 1998). Because, at the same bit level, central tendency and intraindividual variability of RT cannot be considered independent of each other, residuals from both parameters were allowed to covary at each level of task complexity. Also for this model, an acceptable degree of fit was

Table 2

Mean (*M*), Standard Deviation (*SD*), Minimum (*Min*), and Maximum (*Max*) of All Performance Measures Obtained

Performance Measure	*M*	*SD*	*Min*	*Max*
Intelligence tests				
Verbal Comprehension [test score]	23.5	6.6	6	38
Word Fluency [test score]	29.4	8.0	5	40
Space [test score]	29.0	6.0	7	40
Flexibility of Closure [test score]	32.1	6.1	13	40
Reasoning [test score]	26.1	5.3	7	38
Number 1 [test score]	22.6	7.3	1	40
Number 2 [test score]	4.0	2.2	0	7
Verbal Memory [test score]	8.2	2.4	3	18
Numerical Memory [test score]	7.4	2.2	1	14
Spatial Memory [test score]	15.5	4.6	4	27
Temporal tasks				
DD1 [DL in ms]	9.6	5.6	3.3	51.4
DD2 [DL in ms]	18.7	9.3	4.1	70.8
DD3 [DL in ms]	150.1	81.4	44.2	745.0
TG1 [IRD]	.35	.11	.10	.73
TG2 [IRD]	.32	.11	.08	.78
TOJ [DL in ms]	93.0	32.6	22.9	200.2
RP [75%-threshold in ms]	54.9	20.2	6.1	142.4
Hick parameters				
RT 0 bit [ms]	244	32.1	179	355
RT 1 bit [ms]	308	38.4	227	460
RT 2 bit [ms]	390	58.5	269	581
RTSD 0 bit [ms]	65	28.3	21	164
RTSD 1 bit [ms]	58	23.4	23	221
RTSD 2 bit [ms]	75	26.8	30	298

Note: DD1 = duration discrimination of filled intervals (base duration = 50 ms); DD2 = duration discrimination of empty intervals (base duration = 50 ms); DD3 = duration discrimination of filled intervals (base duration = 1,000 ms); TG1 = temporal generalization (base duration = 75 ms); TG2 = temporal generalization (base duration = 1,000 ms); TOJ = temporal-order judgment; RP = rhythm perception; DL = difference limen; IRD = index of response dispersion; RT = median reaction time; RTSD = intraindividual standard deviation of reaction time.

obtained ($\chi^2 = 12.94$, $df = 5$, $p = .024$, CFI = .99, TLI = .96, RMSEA = .08).

Modeling of the data of temporal information processing was based on prior factor-analytic findings suggesting that performance on the several temporal tasks employed in the present study can exhaustively be described by a single general factor at the first level of aggregation (Rammsayer & Brandler, 2004, 2007). Therefore, based on all seven temporal measures, the first principal factor was extracted by means of CFA, referred to as temporal *g*. This model represented the data very well ($\chi^2 = 13.89$, $df = 14$, $p = .46$, CFI = 1.00, TLI = 1.00, RMSEA = .00).

Structural Equation Modelling: The Issue of Relatedness

A first issue is whether Hick *g* and temporal *g* are related to each other, a question that contrasts Model 1 (independence of predictors) with Model 2 (correlated predictors). As can be seen from Table 3, the unrelated-predictor model (Model 1) did not represent the data adequately, whereas for the related-predictor model (Model 2; see Figure 2), an acceptable degree of fit was observed. A significant χ^2 difference between both these nested models ($\Delta\chi^2 = 59.31$, $df = 1$, $p < .001$) clearly favored Model 2, which assumes a functional relationship between temporal *g* and Hick *g*.

Of further importance are the path coefficients in both models. In the unrelated-predictor model (Model 1), the path coefficient describing the direct effect from Hick *g* to psychometric *g* was $-.25$ ($t = -4.20$, $p < .001$), whereas the coefficient relating temporal *g* and psychometric *g* was .59 ($t = 11.59$, $p < .001$). When allowing both predictors to correlate (Model 2), a significant correlation of $-.65$ ($t = -13.81$, $p < .001$) between Hick *g* and temporal *g* was observed. With the correlation among predictors controlled, temporal *g* remained a highly significant independent predictor of psychometric *g* (estimated path coefficient = .59, $t = 11.65$, $p < .001$), whereas this was not true of the Hick *g* path coefficient ($t = -1.79$, $p = .07$). Thus, there is some initial indication that Hick *g* predicts psychometric *g* due to its shared variance with temporal *g*, whereas temporal *g* has independent predictive value.

Structural Equation Modeling: The Issue of Mediating Effects

Possible mediating effects among the predictors were examined in Models 3 and 4 (cf. Tabachnick & Fidell, 2001). Model 3 was supported because temporal *g* significantly mediated the relation between Hick *g* and psychometric *g* ($t = -6.64$, $p < .001$). This indirect

Table 3

Summary of Fit Statistics for Structural Equation Models

Model	χ^2	*df*	*p*	CFI	TLI	AIC	RMSEA
Model 1							
Unrelated-predictor model	384.54	209	.000	.90	.88	39720.66	.06
Model 2							
Related-predictor model	325.23	208	.000	.94	.92	39663.35	.05
Model 3							
Hick *g*—psychometric *g* partly mediated by temporal *g*	325.23	208	.000	.94	.92	39663.35	.05
Model 4							
Temporal *g*—psychometric *g* partly mediated by Hick *g*	325.23	208	.000	.94	.92	39663.35	.05
Model 5							
Hick *g*—psychometric *g* totally mediated by temporal *g*	325.87	209	.000	.94	.92	39661.99	.05
Model 6							
Hick *g* and temporal *g* related to speed, capacity, and memory	319.11	204	.000	.94	.92	39665.22	.05

Note. CFI = Comparative Fit Index; TLI = Tucker-Lewis Index; AIC = Akaike Information Criterion; RMSEA = Root Mean Square Error of Approximation.

effect was more pronounced than the direct effect of Hick *g* on psychometric *g,* which did not reach statistical significance in the mediation analysis. By contrast, Model 4 found that, with temporal *g* controlled, Hick *g* had no direct implications for predicting psychometric *g*. Furthermore, Hick *g* had no significant mediating influence on the relation between temporal *g* and Hick *g* ($t = 1.14$, $p = .25$).

To further elucidate the mediating effect of temporal *g* on the relationship between Hick *g* and psychometric *g,* an additional model was tested. Model 5 was based on the assumption that Hick *g* only predicts psychometric *g* because of shared variance between Hick *g* and temporal *g*. This model resembles Model 3 but does not include a direct link between Hick *g* and psychometric *g* (see Figure 3). Though being somewhat more parsimonious, Model 5 fitted the data

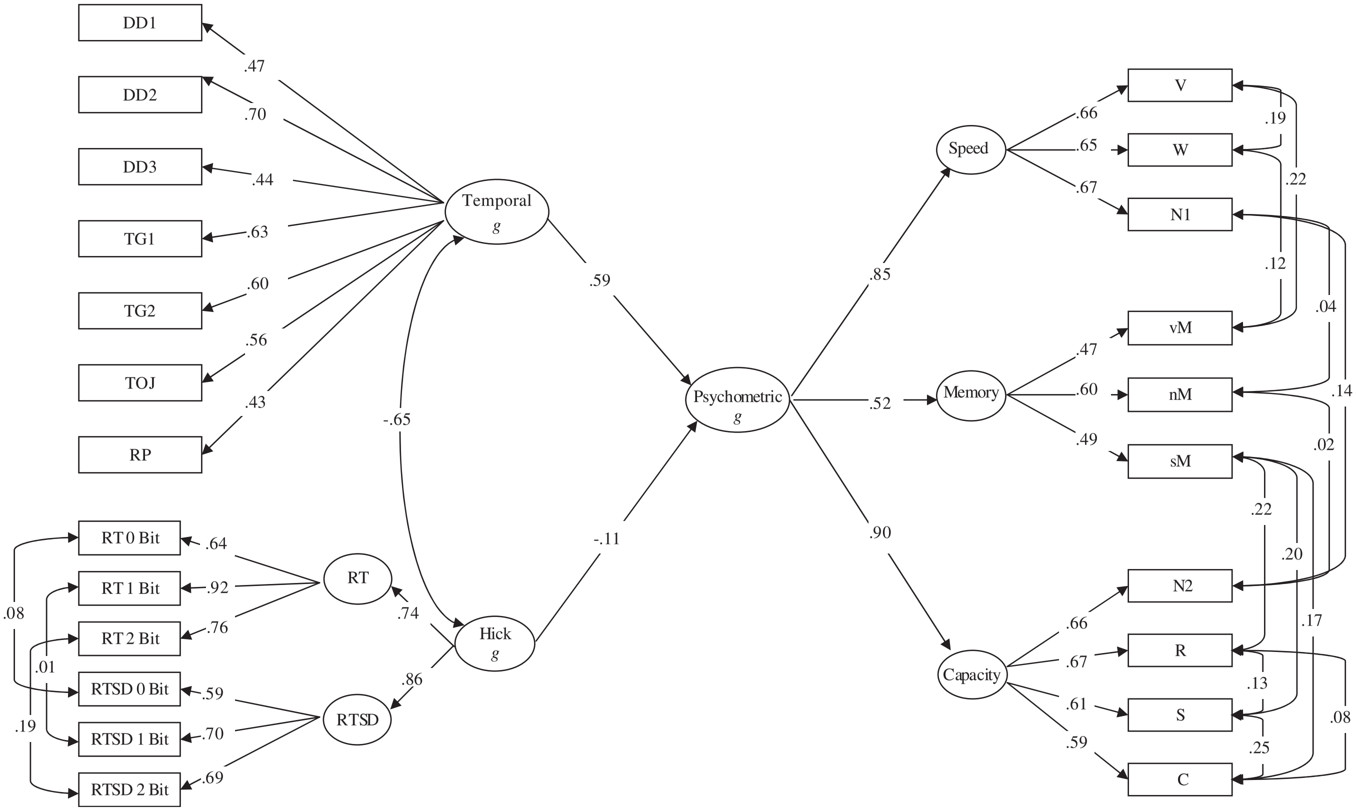

Figure 2
Related-predictor model (Model 2).

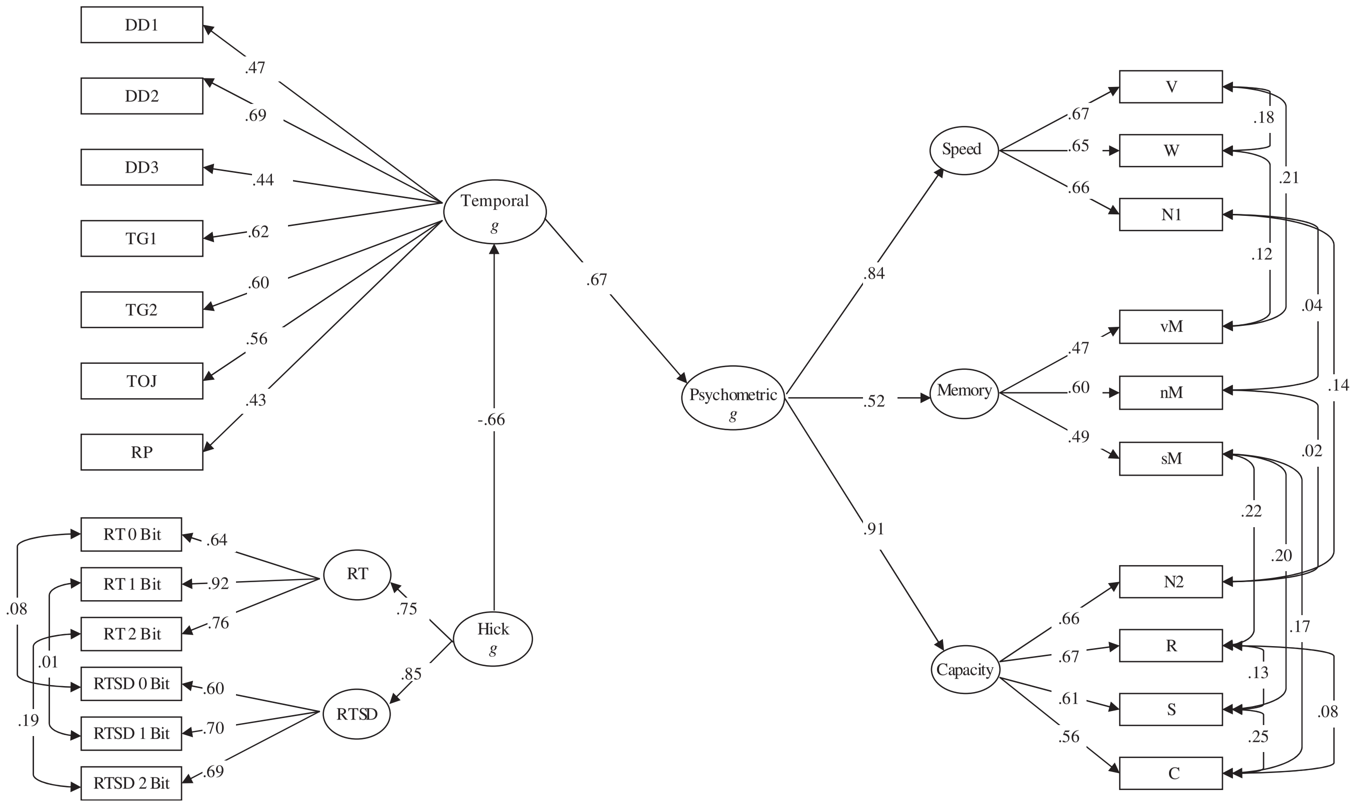

Figure 3

Model with temporal *g* totally mediating the relationship between Hick *g* and psychometric *g* (Model 5). (For abbreviations, see Tables 1 and 2).

as well as Model 3 (see Table 3). Deletion of the direct link from Hick *g* to psychometric *g* did not lead to a significant loss of model fit ($\Delta\chi^2 = .64$, $df = 1$, $p > .05$).

Additional Analyses Involving First-Order Factors of Intelligence

A final analysis (referred to as Model 6) decomposed psychometric *g* into its constituent factors related to speed, capacity, and memory ability. Because this model does not focus on possible mediating effects, a correlational relationship between temporal *g* and Hick *g* was assumed. Furthermore, the first-order factors of intelligence were allowed to correlate. This model obtained a satisfactory fit (see Table 3). Temporal *g* showed significant direct effects on each of the three first-order factors: speed (estimated path coefficient = .39, $t = 6.82$, $p < .001$), memory (estimated path coefficient = .54, $t = 10.17$, $p < .001$), and capacity (estimated path coefficient = .60, $t = 11.89$, $p < .001$). In contrast, Hick *g* proved to be exclusively related to the speed factor (estimated path coefficient = $-.22$, $t = -3.61$, $p < .001$). The path coefficients relating Hick *g* to memory (estimated path coefficient = .07, $t = 1{,}14$, $p = .25$) and capacity factors (estimated path coefficient = $-.02$, $t = -.32$, $p = .75$) were not significant.

DISCUSSION

The present study was designed to investigate the functional relationship between temporal acuity, speed of information processing as measured by the Hick paradigm, and psychometric intelligence. A large sample size and SEM procedures allowed us to make more definitive statements concerning relations between these constructs. The results illuminated the central role of temporal acuity as a predictor of psychometric intelligence, at least relative to the speed parameters assessed by the Hick paradigm. Implications of these results are discussed next.

Temporal Acuity and Information Processing Speed as Predictors of Psychometric Intelligence

SEM analyses reinforce some prior suggestions related to relations between basic cognitive performance and more general measures of intellectual performance. Replicating previous results, performance on both tasks of temporal information processing (Rammsayer &

Brandler, 2002, 2007; Watson, 1991) and the Hick paradigm (Deary, 2000a; Jensen, 1987, 2004, Juhel, 1991; Vernon, 1987) predicted individual differences in psychometric intelligence. The present findings also confirm the suggestions of Rammsayer and Brandler (2007) that temporal *g* may be more predictive of psychometric intelligence than are simple reaction times of the sort examined in the Hick paradigm. Perhaps of more importance, the large sample size and SEM approach used here allowed us to further this literature in several ways.

We were able to show that temporal acuity and information processing speed are correlated rather than independent factors. Such a substantial correlation further allowed us to characterize the independent predictive value of temporal *g* and Hick *g*, and in this context it was found that only temporal *g* was a significant predictor of psychometric intelligence when variance common to temporal *g* and Hick *g* were controlled for. These findings point to a mediating effect of temporal *g* on the relationship between Hick *g* and psychometric *g,* which was further examined in Model 3. As hypothesized, Model 3 results showed that the indirect path of Hick *g* on psychometric *g* (as mediated by temporal *g*) was larger than the direct or unmediated relation between Hick *g* and psychometric *g*. These results are consistent with the idea that temporal acuity is the more important variable in relation to psychometric intelligence and indeed appears to be sufficient to account for the well-replicated effects linking speed of information processing to the general intelligence-related abilities of the individual.

A more definite idea of a hierarchical relationship between temporal resolution power and mental speed was supported by Model 5, which was based on the assumption that the relationship between Hick *g* and psychometric *g* is entirely mediated by temporal *g*. Although this model, relative to Model 3, was more parsimonious, it provided an equal fit to the data. Thus, the present data provide a strong case for the idea that temporal abilities, relative to mere mental speed, are a more important predictor of performance on general intelligence tests (Rammsayer & Brandler, 2007).

This interpretation was corroborated by the finding that temporal acuity is significantly related to various aspects of psychometric intelligence as reflected by the first-order factors of intelligence referred to as speed, capacity, and memory. This outcome is in line with the results from a previous study (Helmbold & Rammsayer, 2006) demonstrating that timing performance is significantly associated with both speed and power/capacity measures of intelligence.

Study Limitations and Suggestions for Future Research

Some limitations of the present study, which in turn have implications for future research in this area, should be addressed. First, with regard to the reported superiority of timing performance over speed of information processing in predicting psychometric *g*, it should be noted that timing acuity was assessed by several temporal tasks, but speed of information was measured only by one task—the Hick paradigm. Because composite scores of performance will have more general and less specific variance if based on a large number of distinct tasks (Brody, 1992; Jensen, 1998), it cannot be excluded that superiority of temporal *g* in predicting psychometric *g* might be biased by the fact that this compound measure was based on a more diverse battery of tasks than Hick *g*. Therefore, further studies comparing timing acuity and speed of information processing as predictors of psychometric *g* should be based on more equivalent batteries of different tasks.

A second point concerns potential effects of sex and age on the relationship between both nonpsychometric domains and psychometric intelligence. Unfortunately, our sample size was too small to perform SEM for males and females separately. Therefore, future studies addressing this topic would be useful. Also, given the rather restricted age range of our participants, additional investigations are necessary to further elucidate the potential moderating effects of age on the relations observed here.

Finally, it is interesting to speculate on some of the other correlates of temporal processing acuity aside from those related to psychometric intelligence. In this connection, several studies have shown that dyslexic individuals have significant deficits in temporal resolution tasks (e.g., Rousseau, Hébert, & Cuddy, 2001; Tallal, Stark, & Mellits, 1985; Wolff, 1993). Also, psychological disorders such as those linked to affect and schizophrenic symptoms have been linked to temporal processing abilities in previous research (e.g., Bschor et al., 2004; Davalos, Kisley, Polk, & Ross, 2003; Rammsayer, 1990). Thus, temporal acuity may be an important personality variable quite aside from its apparent relation with psychometric intelligence. We therefore encourage such research in future studies.

Conclusion

The intelligence literature has displayed a great deal of interest in cognitive processing speed as a predictor of psychometric intelligence. The present study followed this general focus on performance in elementary cognitive tasks but further proposed that temporal acuity, relative to speed of processing, may be the more important elementary ability in predictions of psychometric intelligence. The results were in support of this suggestion. Thus, the present study contributes to the suggestion that more attention should be paid to individual differences in temporal resolution abilities relative to information-processing speed as temporal resolution abilities may be more important to predicting individual differences in intelligence-related abilities.

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Rhythm and reading development in school-age children: a longitudinal study

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Rhythm production in 53 children in grade 1 was investigated as a predictor of reading ability in the same children in grades 1–5. This paper reports the results of correlations and hierarchical regression analyses, controlling for shared variance between phonological awareness and naming speed. Rhythm was correlated significantly with both phonological awareness and naming speed. Rhythm predicted significant variance in reading ability at each grade level. Once phonological awareness was controlled, however, rhythm was a significant predictor only in grade 5. When naming speed was controlled, rhythm predicted unique variance in reading ability in grades 2, 3 and 5. Implications for the relationship between rhythm and the development of reading skills are discussed.

Recent research has concentrated on finding the underlying cognitive processes related to reading in order to determine possible predictors of reading ability (e.g. Schatschneider, Fletcher, Francis, Carlson & Foorman, 2004; Wagner & Torgesen, 1987). This is important because children who are poor readers in the primary grades have been found to remain poor readers in later grades (Francis, Shaywitz, Stuebing, Shaywitz & Fletcher, 1996). Currently, the most thoroughly researched cognitive processes are phonological awareness and naming speed, both of which are considered to be robust predictors of reading ability (Wolf & Bowers, 1999).

Phonological awareness has to do with the understanding that language can be broken down into smaller units of sound and manipulated (Shankweiler & Fowler, 2004). Furthermore, there are many levels at which this awareness can be realised. Children first develop awareness for syllables, followed by awareness for onset and rime (the onset is the initial consonant phonemes in any syllable, while the rime is the vowel plus the consonants that follow), and lastly, awareness for the smallest unit of speech, the phoneme (Goswami, 2002). Phonological awareness tasks include manipulations at all three levels.

There is a strong relationship between phonological awareness and reading ability as children who are poor readers are significantly worse than their peers on tests of phonological awareness (Wagner & Torgesen, 1987; Wagner, Torgesen & Rashotte, 1999). Children who demonstrate difficulty on tests of phonological awareness prior to formal schooling are at risk of becoming poor readers while those who do well on such tests are likely to become stronger readers (Bradley & Bryant, 1983). Even more, researchers have shown that the relationship between phonological awareness and reading continues throughout the school years (Shankweiler et al., 1995). A research consensus agrees that, with letter knowledge, phonological awareness is the strongest predictor of reading ability (Rayner, Foorman, Perfetti, Pesetsky & Seidenberg, 2001).

Another robust predictor of later reading is rapid automatised naming (RAN). Tests of RAN involve presenting a subset of familiar visual symbols from a certain category (i.e., alphanumeric, colours, objects) in a randomised serial array and having individuals name the items across the rows as quickly as possible (Savage, 2004). It has been argued that both naming speed and reading involve matching visual stimuli to phonological codes and saying them out loud in a specific timed manner (Wolf & Bowers, 1999). Not only has naming speed been found to relate directly to reading ability, but it has also been suggested that it plays a causal role in reading disability (Wolf & Bowers, 1999). There is no consensus on the fundamental nature of RAN, and why dyslexic readers are often slower than typical readers at rapid naming tasks. One hypothesis is that RAN is a linguistic process that is primarily phonological in nature (e.g. Bowey, McGuigan & Ruschena, 2005; Wagner & Torgesen, 1987), and therefore the slow naming speed observed in dyslexics is an expression of a larger phonological deficit. An alternative account has it that slow naming speed in dyslexics reflects a linguistic manifestation of a more general speed of processing deficit. Related to this is the notion that processing two or more stimuli presented sequentially, especially with short interstimulus intervals, is particularly problematic for dyslexics (Overy, Nicolson, Fawcett & Clarke, 2003; Tallal, Merzenich, Miller & Jenkins, 1998). Evidence for such a deficit has been observed in the auditory (Tallal et al., 1993), visual (Farmer & Klein, 1993) and motor (Nicolson & Fawcett, 1994; Wolff, 1993) domains.

Researchers have debated whether naming speed and phonological awareness are fundamentally part of the same construct, in that naming speed is primarily a phonological task that can be seen as the 'retrieval of phonological codes from a long-term store' (Wolf & Bowers, 1999). Evidence supporting a relationship between naming speed and phonological awareness is somewhat inconsistent, as some researchers have found strong correlations (e.g. Wagner, Torgesen & Rashotte, 1994), while the majority have found only moderate ones (e.g. Morris et al., 1998; Savage, 2004). Nonetheless, Wagner et al. (1994) found that the strong correlations between phonological awareness and naming speed disappeared over time. Evidence supports the notion that naming speed and phonological awareness measure different constructs as both uniquely predict and contribute to reading ability (Morris et al., 1998; Savage, 2004; Wolf & Bowers, 1999). Functional magnetic resonance imaging has shown that both phonological awareness and naming speed activate neurological networks in the brain that are related to reading, and yet different from each other (Misra, Katzir, Wolf & Poldrack, 2004).

Despite the substantial literature showing the power of phonological awareness and RAN to predict reading performance, research continues to investigate the nature of these factors and to search for other factors that can explain the remaining variance in reading that these factors cannot account for. A candidate for further investigation is rhythm. There are a number of reasons for us to consider rhythm as a potentially influential factor in reading development.

Rhythm is an important part of language, becoming salient almost from birth, as evidenced by newborns' ability to discriminate languages based on their rhythmic class (i.e., English, Dutch [stress-based] vs Japanese [mora-based], Nazzi, Bertoncini & Mehler, 1998). Researchers suggest that the strong–weak pattern of stressed syllables typical of English is used by infants as young as 7.5 months to segment words in continuous speech (Jusczyk, Houston & Newsome, 1999). Verbal communication with an infant has been termed musical speech as it consists of high pitch, slow tempo, repetition and changes in tone (Anvari, Trainor, Woodside & Levy, 2002), and newborn infants tend to respond better to the inviting rhythm of musical speech (Balkwill & Thompson, 1999). Linguistic rhythm manifested through stress is also used as a cue to facilitate speech segmentation in adults, especially in stress-timed languages such as English and Dutch (e.g. Cutler & Norris, 1988). Rhythmic information can also be lexically contrastive, as can be seen in the minimal pair *dessert/desert*, which differ only in the relative emphasis of the syllables. There is increasing interest in the notion that rhythm may play a role in reading development.

A handful of studies have investigated the role of rhythm in reading directly. Wood and Terrell (1998) conducted a study investigating relationships among a variety of speech perception tasks and reading ability. They had three groups in their study: poor readers (mean age = 9 years), age-matched controls (mean age = 9 years) and reading-age-matched controls (mean age = 6.4 years). The authors examined children's ability to match a low-pass-filtered sentence to a sentence with the same stress pattern. A low-pass-filtered sentence is one where the phonemic and lexical characteristics of the sentence are removed and only the prosodic contour of the utterance remains. The participants were presented with a low-pass-filtered sentence, followed by two regular sentences with the same number of syllables, one of which also matched in terms of metrical stress pattern. Wood and Terrell found that the poor readers had the lowest scores on this task, followed by the reading age controls and then the age-matched controls. After controlling for vocabulary, a significant difference still remained between the poor readers and the age-matched controls, but not between the poor readers and reading-age-matched controls, thus suggesting that a maturational lag might exist. Wood and Terrell concluded that sensitivity to lexical rhythm in speech is necessary before progressing to phonemic awareness and reading. In addition, Wood (2004) found that children's sensitivity to changes in stress was related to reading ability.

Goswami and her colleagues have also demonstrated that sensitivity to rhythm is related to reading ability in good and poor readers. This work suggests that, in order to achieve phonological awareness, children must be sensitive to the rise time of the amplitude envelope in speech (Goswami et al., 2002). Rise time is associated with the perceptual centre (p-centre) of the syllable; for the speaker/hearer, it captures the 'subjective moment of occurrence' (Scott, 1998) of syllabic rhythm. In the studies conducted by Goswami and her colleagues (e.g. Goswami et al., 2002; Muneaux, Ziegler, Truc, Thomson & Goswami, 2004; Richardson, Thomson, Scott & Goswami, 2004), the percept associated with changes in rise time was variation in rhythmic beat. The beat detection task used in Goswami's studies was associated with significant amounts of variance in a variety of literacy and literacy-related tasks including word reading, spelling and phonological awareness (rime oddity). Poor readers were significantly less sensitive to changes in rise time than their chronological- and reading-age-matched peers, and precocious readers were the most sensitive of all groups to beat variation (Goswami et al., 2002). Interestingly, this phenomenon does not appear to be restricted to stress-timed languages like English; the effect was also observed in French, a syllable-timed language (Muneaux et al., 2004).

A more common approach to the study of rhythm and reading is mediated through musical tasks. Peynircioglu, Durgunoglu and Oney-Kusefoglu (2002) found that musical aptitude has a strong link with phonological awareness in children between the ages of 3 and 6 years, as they further proposed that having a high musical aptitude appears to enhance children's ability to manipulate sound. Adult musicians with dyslexia report particular difficulties with rhythm (Ganschow, Lloyd-Jones & Miles, 1994).

Anvari et al. (2002) presented preschool children with two computer-generated rhythmic patterns with instructions to determine whether the two rhythms were the same or different and also had children orally reproduce rhythmic patterns (e.g. la la LA la), among other tasks measuring melody discrimination, chord discrimination and chord analysis. Factor analysis revealed a single music factor for 4-year-old children, and two factors relating to pitch perception and rhythm perception for the 5-year-old children. In terms of reading ability, factor analysis revealed one factor for phonemic awareness tasks in both 4- and 5-year-olds. Overall, Anvari et al. found that reading awareness and phonological awareness were correlated, as were the musical factors with phonemic awareness in both age groups. However, the music factor was related to reading in the 4-year-olds, while in the 5-year-olds, pitch perception was related to reading while rhythm perception was not. Furthermore, a hierarchical regression revealed that music was predictive of reading ability beyond phonological awareness in 4-year-olds as was pitch perception in 5-year-olds (rhythm was not entered in the 5-year-olds' regression analysis as it was not correlated with reading ability). The researchers noted that within the context of their study, it is unclear as to why rhythm was not related to the latter age group. We suggest that one possibility for this negative finding is the nature of the reading outcome measures. Anvari et al. measured reading ability with the WRAT-3, which begins with a string of 15 letters to be identified before moving on to word identification. That is, even though there is variability on the measure, the majority of scores represent letter identification as opposed to actual word-reading ability. Therefore, it might be the case that rhythm ability plays a stronger role in relation to reading ability when the task involves decoding or word recognition rather than letter identification. This notion is supported by the findings of Atterbury (1985) and Douglas and Willats (1994). In the former, studying children between the ages of 7 and 9 years, the authors found that poor readers, compared with normal readers, were impaired in rhythm production, measured by the ability to clap back a set rhythm. Also, Douglas and Willats (1994), using the same task later used by Anvari et al. (2002), found that rhythm discrimination correlated with reading ability in 7- and 8-year-old children. Similarly, Overy et al. (2003) found that dyslexic children were significantly less able to perform musical rhythm tasks than age-matched controls, although they were significantly better than control children at tasks involving musical pitch.

In sum, evidence supports the notion of a relationship between rhythm and reading, but little attention has been paid to the question of whether sensitivity to rhythm can predict reading development beyond the contribution of more traditional variables. The present research seeks to determine whether rhythm does uniquely predict young children's reading, beyond phonological awareness and naming speed, through a 5-year longitudinal study. No known study has investigated such a longitudinal relationship controlling for, and examining the relationships with, phonological awareness and naming speed. Therefore, an original contribution of this study is the ability to track the contribution of rhythm to reading as it develops over 5 years of school, and the role of rhythm as a predictor in combination with the more traditional variables of phonological awareness and RAN. Of interest is whether a relationship exists between rhythm in grade 1 and concurrent tasks of phonological awareness, naming speed, word reading and pseudoword reading. Based on current research evidence supporting a link between rhythm and both phonological awareness and RAN, it is hypothesised that correlations between these factors will be observed in the present study. We also expect to uncover a relationship between rhythm and reading, consistent with the findings of the studies reviewed here.

Method

Participants

Fifty-three children (31 males, 22 females; mean age = 76.1 months, *SD* = 3.4 months) began the study in the fall of grade 1. The children were tested again in the fall of grades 2–5. Over the last 3 years, attrition reduced the sample to 47, 44 and 38. The participants were drawn from three schools in Eastern Ontario, Canada, representing a range of socioeconomic backgrounds. The majority of the participants were Caucasian, which is in line with the population residing in the region that was investigated. All participants had informed parental consent and were able to understand task instructions.

Measures and procedure

All tests were administered at a time convenient to the classroom teacher. The researcher worked one on one with the participant in a quiet place so as to ensure minimal distraction. All tests involved practice trials and no test was administered until the researcher was positive that the participant fully understood the instructions.

Phonological awareness. In grade 1, five measures of phonological awareness were administered (Sound Oddity was taken from Bradley & Bryant, 1983, and the remaining four were taken from Wagner, Torgesen, Laughon, Simmons & Rashotte, 1993). *Sound Oddity* requires the participant to listen to three words, two of which share a phoneme, and to identify which word out of the three was the 'odd one' (e.g. *pig*, *pen*, *hall*). There were six practice items and 30 test items. *Blending Phonemes* requires the participant being asked to combine individual phonemes together to form a complete word (e.g. 'What word does /ch/ - /ai/ - /r/ say?'). This task consisted of six practice items and 15 test items. For *Blending Onset and Rime*, the participant is presented with the first consonant in a word (onset) and then the rime with the instructions to put the two together to form one complete word (e.g. 'What word does /d/ - /og/ say?'). This task consisted of six practice items and 15 test items. *Phoneme Elision* requires the participant to repeat a word without a specific phoneme. All the phonemes that were to be deleted were consonants and the remaining phonemes formed a new word (e.g. 'Say the word /bat/. Now say the word /bat/ without the /b/'). The location of the deleted phoneme varied. This task consisted of six practice items and 15 test items. For *Sound Isolation*, the participant identifies the first, middle or last sound in a word. The task consisted of six practice items and 15 test items. With the exception of Sound Oddity, each of the phonological awareness tasks was discontinued after four mistakes were made in the last seven items. The number of items that were correctly answered became the score.

Naming speed. Two tests of naming speed were administered in grade 1. These measures were developed based on colour naming and picture-naming tasks described in Wolf, Bally and Morris (1986). Colours and pictures were chosen over alphanumeric stimuli as the predictors were measured in the fall of grade 1 before children had much formal reading instruction and the researchers were not confident that all the children would be familiar with the letters and digits. Each task consisted of a series of 32 randomly ordered colours or pictures, each taken from a set of four (colours: blue, green, red and yellow; pictures: bird, horse, pig and cat). The participants had time to practise and to make sure that they were familiar with the colours and pictures. Stimuli items were presented in two four-by-four matrices. The number of seconds it took the child to name the stimuli correctly was the child's score. If an error was made, the experimenter pointed to the incorrect stimulus immediately, with the child having to start again from that spot as the time continued to be recorded without stopping.

Reading ability. Two subtests from the Woodcock Reading Mastery Tests – Revised (Woodcock, 1987) were used in all grades. Word Identification requires that the participant read aloud words in isolation (e.g. *is*, *you*, *and*) that continuously increase in difficulty, with a total of 106 possible items. Word Attack measures participants' ability to read pseudo-words through the application of phonic and structural analysis skills (e.g. *dee*, *apt*, *ift*), with a total of 45 items.

Rhythm. In Grade 1, Weikart's (1989a) Rhythmic Competency Analysis test was used. The instrument is reported to have an internal consistency (alpha) ranging from .70 to .79 (Weikart, Schweinhart & Larner, 1987). This test includes five different rhythmic production tasks, which are conducted to two different sets of music. The first musical selection was 'Soldier's Joy' from the recording *Rhythmically Moving 2* (Weikart, 1989b) and the second musical selection was 'Oh, How Lovely' from *Rhythmically Moving 1* (Weikart, 1989a). The second musical selection was slower in tempo. Task one requires that the child tap the beat of the musical selection on his/her lap using both hands simultaneously. Task two requires that the child tap on his/her lap to the beat using alternating hands. Task three requires that the child move his/her legs in a walking manner to the beat while seated. Task four requires that the child walk the beat while standing in one place. Task five requires that the child walk the beat in a forward direction. If the child accurately produced at least eight consecutive beats in unison with the underlying steady beat of the music, one point was given. This provided for an 11-point scale with the range from 0 to 10, as up to 1 point could be achieved on each task for both musical selections. Two raters, proficient in this test, marked all participants.

Results

Alpha was set to .05 for all analyses. Because the scores were not dichotomous (right vs wrong), but instead represented a range of values from 1 to 10, inter-rater reliability for the rhythm task was calculated using the split-half method, with each rater's scores representing alternating halves of the total score for each participant. Reliability was determined to be high and acceptable at .92. Given that both raters also had similar means ($M = 5.38$ and 5.08) and standard deviations ($SD = 2.97$, 3.11), both raters' scores were combined for a possible total of 20 points on the task. Preliminary analyses were performed to determine whether there were any gender differences on the measures used. *T*-tests revealed no significant differences, so the data for males and females were combined.

The means and standard deviations for all the measures used across grades 1–5 are presented in Table 1. All five phonological awareness test scores were significantly correlated with one another (see Table 2), so they were converted to *z*-scores and averaged into a single score, PA ($M = 0.0$, $SD = 0.83$). Both colour-naming and picture-naming scores were significantly correlated ($r = .55$, $p < .001$), so they were converted to *z*-scores and averaged into a single score ($M = 0.0$, $SD = 0.88$). These composite scores for phonological awareness and RAN are used for all further analyses.

T-test analyses were run to determine that no differences existed between the participants who remained in the study until grade 5 and those who were lost to attrition on their performance on the PA, RAN and rhythm tasks taken in grade 1. No significant differences were found on any of the three measures between the two groups (*t*-values ranged from .01 to 1.45, and *p*-values ranged from .15 to .99).

Simple correlations among rhythm, phonological awareness, naming speed and reading were examined and are reported in Table 3. Concurrent correlations showed grade 1 rhythm correlated significantly with RAN, phonological awareness and Word Identification. The lack of significant relation between rhythm and Word Attack is likely due to the fact that the majority of the participants scored 0 on Word Attack, thereby causing the distribution to be extremely skewed and resulting in a restriction of range. Longitudinal correlations showed that each of the three predictors measured in grade 1, RAN, phonological awareness and rhythm, maintained a significant relationship with both Word Identification and Word Attack over the following 4 years. The strength of these relationships ranged from $r = .63$ to .73 for phonological awareness, from $r = .39$ to .53

Table 1. Means and standard deviations of all measures used across grades 1 and 2.

Measure	*N*	*M*	*SD*
Rhythm – Grade 1	53	10.45	5.96
Sound Oddity – Grade 1	53	14.91	5.71
Sound Isolation – Grade 1	53	6.30	4.59
Blending Phonemes – Grade 1	53	8.85	4.45
Blending Onset and Rime – Grade 1	53	9.49	4.73
Phoneme Elision – Grade 1	53	4.89	4.69
Phonological Awareness – Grade 1	53	0.00	0.83
Naming Speed Colours – Grade 1	53	32.70	9.52
Naming Speed Pictures – Grade 1	53	35.66	11.27
Naming Speed – Grade 1	53	68.40	18.34
Word Identification – Grade 1	53	7.19	11.60
Word Attack – Grade 1	53	1.68	4.25
Word Identification – Grade 2	53	35.19	16.50
Word Attack – Grade 2	53	10.04	9.51
Word Identification – Grade 3	47	52.09	14.60
Word Attack – Grade 3	47	17.21	10.48
Word Identification – Grade 4	44	59.09	12.25
Word Attack – Grade 4	44	22.27	10.44
Word Identification – Grade 5	38	69.05	11.99
Word Attack – Grade 5	38	28.24	9.30

Table 2. Intercorrelations between all five phonological awareness tasks in grade 1 ($N = 53$).

Measure	1	2	3	4	5
1. Sound Oddity	–	$.55^{**}$	$.45^{**}$	$.64^{**}$	$.58^{**}$
2. Sound Isolation		–	$.77^{**}$	$.63^{**}$	$.67^{**}$
3. Blending Phonemes			–	$.48^{**}$	$.57^{**}$
4. Blending Onset and Rime				–	$.69^{**}$
5. Phoneme Elision					–

$^{**}p < .01$.

Table 3. Intercorrelations between rhythm, phonological awareness (PA), naming speed (NS) and reading across grades ($N = 53$).

Measure	1	2	3	4	5	6	7	8	9	10	11	12	13
1. MR		$-.41^{**}$	$-.30^{*}$	$.28^{*}$	.26	$.42^{**}$	$.39^{**}$	$.37^{**}$	$.41^{**}$	$.31^{*}$	$.37^{*}$	$.40^{*}$	$.50^{**}$
2. PA		–	$-.57^{**}$	$.55^{**}$	$.48^{**}$	$.70^{**}$	$.73^{**}$	$.69^{**}$	$.67^{**}$	$.67^{**}$	$.68^{**}$	$.63^{**}$	$.64^{**}$
3. NS			–	$-.36^{**}$	$-.28^{*}$	$-.52^{**}$	$-.46^{**}$	$-.50^{**}$	$-.39^{**}$	$-.53^{**}$	$-.49^{**}$	$-.49^{**}$	$-.48^{**}$
4. WID – Grade 1				–	$.86^{**}$	$.62^{**}$	$.62^{**}$	$.53^{**}$	$.55^{**}$	$.47^{**}$	$.47^{**}$	$.38^{*}$	$.44^{**}$
5. WA – Grade 1					–	$.58^{**}$	$.65^{**}$	$.50^{**}$	$.53^{**}$	$.44^{**}$	$.43^{**}$	$.38^{*}$	$.44^{**}$
6. WID – Grade 2						–	$.89^{**}$	$.92^{**}$	$.80^{**}$	$.86^{**}$	$.78^{**}$	$.78^{**}$	$.74^{**}$
7. WA – Grade 2							–	$.82^{**}$	$.84^{**}$	$.77^{**}$	$.78^{**}$	$.70^{**}$	$.71^{**}$
8. WID – Grade 3								–	$.86^{**}$	$.94^{**}$	$.87^{**}$	$.87^{**}$	$.83^{**}$
9. WA – Grade 3									–	$.84^{**}$	$.91^{**}$	$.82^{**}$	$.88^{**}$
10. WID – Grade 4										–	$.89^{**}$	$.96^{**}$	$.88^{**}$
11. WA – Grade 4											–	$.87^{**}$	$.88^{**}$
12. WID – Grade 5												–	$.89^{**}$
13. WA – Grade 5													–

Notes: MR = Musical Rhythm, WID = Word Identification, WA = Word Attack.
$^{*}p < .05$, $^{**}p < .01$.

for RAN and from r =.31 to .50 for rhythm. Overall, these relationships among the variables support the prediction that rhythm would show a sustained relation with reading.

Regression analyses were conducted in order to determine rhythm's predictive power with respect to reading. Of interest was whether rhythm has enough power to predict reading ability uniquely, or whether its ability to predict reading is a result of shared variance with phonological awareness and/or naming speed. Hierarchical regressions were performed first with the two grade 1 reading scores as the dependent variables and then with the two reading scores from grades 2–5 as the dependent variables. The first 10 regressions examined the predictive ability of rhythm on its own (see Table 4). Overall, the regression analyses here demonstrate that rhythm in grade 1 significantly predicts both word reading and pseudo-word reading as far as grade 5 (with the exception of grade 1 Word Attack), and that the longitudinal measurements account for more variance than do the concurrent measurements.

The next 10 regressions looked at the predictive ability of rhythm, removing any shared variance with phonological awareness (see Table 5). Overall, rhythm did not account for unique variance in reading, with one exception in grade 5. In grade 5, rhythm predicted nearly 9% of variance in Word Attack, after the contribution of phonological

Table 4. Percentage of variance in word identification and word attack in grades 1–5 accounted for by Grade 1 rhythm.

Measure	*N*	% Variance rhythm accounted for in Word Identification	% Variance rhythm accounted for in Word Attack
Grade 1	53	7.5^{*}	6.5
Grade 2	53	17.3^{**}	15.1^{**}
Grade 3	47	13.8^{**}	16.8^{**}
Grade 4	44	9.7^{*}	13.4^{*}
Grade 5	38	15.9^{*}	24.6^{**}

$^{*}p<.05$, $^{**}p<.01$.

Table 5. Hierarchical regression predicting reading in grades 1–5 from phonological awareness (PA) and rhythm.

	Step	Predictor variable	β	R^2 change	*F*	Significant *F* change
Grade 1 WID	1	PA	.55	.30	21.57	<.001
	2	PA	.52			
		Rhythm	.06	.00	10.73	.64
Grade 1 WA	1	PA	.48	.23	15.62	<.001
	2	PA	.46			
		Rhythm	.07	.00	7.82	.62
Grade 2 WID	1	PA	.70	.49	49.41	<.001
	2	PA	.64			
		Rhythm	.15	.02	26.20	.16
Grade 2 WA	1	PA	.73	.53	57.19	<.001
	2	PA	.68			
		Rhythm	.11	.01	29.16	.31
Grade 3 WID	1	PA	.69	.48	41.49	<.001
	2	PA	.64			
		Rhythm	.14	.02	21.70	.23
Grade 3 WA	1	PA	.67	.45	37.15	<.001
	2	PA	.60			
		Rhythm	.19	.03	20.65	.11
Grade 4 WID	1	PA	.67	.44	33.49	<.001
	2	PA	.64			
		Rhythm	.07	.00	16.61	.59
Grade 4 WA	1	PA	.69	.47	37.05	<.001
	2	PA	.64			
		Rhythm	.12	.01	19.05	.32
Grade 5 WID	1	PA	.63	.40	24.18	<.001
	2	PA	.56			
		Rhythm	.21	.04	13.78	.13
Grade 5 WA	1	PA	.64	.41	24.53	<.001
	2	PA	.53			
		Rhythm	.32	.09	17.12	.02

Notes: *N* = 53 in grades 1 and 2, 47 in grade 3, 44 in grade 4 and 38 in grade 5; WID = Word Identification, WA = Word Attack.

awareness. For Word Identification, rhythm never survived control for phonological awareness.

Shared variance in reading between naming speed and rhythm was also examined. The next 10 regression analyses look at the predictive ability of rhythm, removing any shared

Table 6. Hierarchical regression predicting reading in grade 1 and grade 2 from naming speed (NS) and rhythm.

	Step	Predictor variable	β	R^2 change	*F*	Significant *F* change
Grade 1 WID	1	NS	– .35	.13	7.30	<.05
	2	NS	– .30			
		Rhythm	.19	.03	4.66	.18
Grade 1 WA	1	NS	– .28	.08	4.28	<.05
	2	NS	– .22			
		Rhythm	.19	.03	3.10	.18
Grade 2 WID	1	NS	– .52	.27	18.66	<.001
	2	NS	– .43			
		Rhythm	.29	.08	13.10	.02
Grade 2 WA	1	NS	– .46	.21	13.81	<.001
	2	NS	– .38			
		Rhythm	.28	.07	9.88	.03
Grade 3 WID	1	NS	– .50	.25	15.07	<.001
	2	NS	– .44			
		Rhythm	.26	.07	10.14	.05
Grade 3 WA	1	NS	– .39	.15	8.17	<.01
	2	NS	– .31			
		Rhythm	.33	.10	7.62	.02
Grade 4 WID	1	NS	– .53	.28	16.63	<.001
	2	NS	– .49			
		Rhythm	– .19	.03	9.49	.17
Grade 4 WA	1	NS	– .49	.24	13.05	<.001
	2	NS	– .42			
		Rhythm	.26	.06	8.74	.06
Grade 5 WID	1	NS	– .49	.24	13.05	<.001
	2	NS	– .41			
		Rhythm	.27	.07	7.83	.08
Grade 5 WA	1	NS	– .48	.23	10.5	<.01
	2	NS	– .35			
		Rhythm	.38	.13	9.76	.01

Notes: $N = 53$ in grades 1 and 2, 47 in grade 3, 44 in grade 4 and 38 in grade 5; WID = Word Identification, WA = Word Attack.

variance with naming speed (see Table 6). Overall, once the shared variance from naming speed is removed, rhythm does play a significant role in explaining variance in grade 1 reading and predicting reading in subsequent grades. Specifically, rhythm predicts unique variance in grades 2 and 3 Word Identification and in grades 2, 3 and 5 Word Attack.

In summary, grade 1 rhythm on its own significantly predicts reading ability in grades 1–5. However, once the shared variance with phonological awareness is removed, rhythm only predicts a significant amount of variance in grade 5 Word Attack. When the shared variance with naming speed is removed, rhythm does not account for a significant amount of variance in grade 1 reading, and yet it still predicts a significant amount of variance in grades 2 and 3 Word Identification and Word Attack, as well as in grade 5 Word Attack.

Discussion

This study investigated the relations among rhythm, phonological awareness, naming speed and reading in a longitudinal sample of children in grades 1–5. The correlations indicate that rhythm in grade 1 is significantly related to not only the two main predictors of reading ability, phonological awareness and naming speed but also to reading ability in the same year and up to 4 years later. Furthermore, once shared variance with phonological awareness was removed, rhythm uniquely predicted Word Attack in grade 5. When naming speed was controlled, rhythm predicted variance in Word Identification in grades 2 and 3, and in Word Attack in grades 2, 3 and 5.

An essential primary finding in the present study is that rhythm and reading, both real words and pseudo-words, are related in a sample of typically developing readers. This is noteworthy because the majority of studies demonstrating such a relationship have involved poor readers of different ages, and the evidence has rested primarily on comparisons of good and poor readers on rhythm tasks (e.g. Atterbury, 1985; Overy et al., 2003; Wood & Terrell, 1998). Studies that have not selected out poor readers have often used measures of literacy, which, while appropriate for the age of the participants, are perhaps inadequate in scope to allow the relationship with rhythm to emerge. For example, Anvari et al. (2002), which did not find a significant correlation between reading and rhythm for their older children, measured primarily letter knowledge in preschoolers. One notable exception is the study by Whalley and Hansen (2006), which found significant relationships between word-level rhythm and decoding, and between sentence-level rhythm and reading comprehension. Our findings are broadly consistent with those of Atterbury (1985), Douglas and Willats (1994), Goswami (2002), Overy et al. (2003) and Wood and Terrell (1998), who found significant reading–rhythm correlations in older children. What is new is the evidence that this relationship is sustained over 5 years of schooling, and its strength does not diminish substantially. Indeed, the simple correlations between rhythm and word reading show that the concurrent reading–rhythm relationship is the weakest ($r = .28$), while the strongest is in Grade 5 ($r = .40$). A similar trend is seen for pseudo-word reading; the concurrent relationship does not reach significance, while the strongest relationship is seen between rhythm and Word Attack measured in grade 5 ($r = .50$).

What could account for the increase in the strength of such a relationship? In grade 1, the demands of reading are fairly simple as children are mostly reading monosyllabic words. Indeed, a glance at the Woodcock Word Identification items shows that there are only two polysyllabic words within the first 30 items (*little*, item 17, and *after*, item 30). As children progress, however, reading increasingly requires the ability to tackle polysyllabic words, which involve the rhythmic alternation of strong and weak syllables. As the participants advanced in grade, the average number of words they were reading, and the complexity of those words, increased. Metrical and rhythmic intonation is necessary for reading polysyllabic words, as it is required in order to assign stress properly and achieve the proper alternation (in English) of full and reduced (schwa) vowels in words. Therefore, one possibility is that those children who were more sensitive to the demands of the rhythm task in grade 1 were also those who developed a greater facility for using the linguistic rhythm of stress to help decode more difficult words.

Another important finding is that much of the variance in reading ability provided by rhythm overlaps almost completely with that provided by phonological awareness. Only in the case of grade 5 Word Attack does rhythm predict significant variance in excess of that explained by phonological awareness. While this is in keeping with an account that sees rhythm as developmentally more important as the demands of reading increase, we are reluctant to overinterpret this result in the light of the other nonsignificant regression results involving phonological awareness and rhythm. In this study, therefore, it appears that rhythm is not related to reading beyond the cognitive, auditory and linguistic skills required by phonological awareness. This contrasts with Goswami et al. (2002), who found that the beat detection task predicted a significant 9% of variance in reading after the contribution of phonological awareness. However, at least two points make direct comparisons impossible; first, there are vast methodological differences between the rhythm tasks used in Goswami et al. and the current study; and second, the phonological awareness task in Goswami et al. was a rime oddity task, where four of the five phonological awareness tasks in this study required phoneme-level manipulation. Lamb and Gregory (1993) have suggested that some auditory skills used in language processing are also related to music perception skills (i.e. blending and segmenting sounds, and melodic and rhythmic discrimination). As Anvari et al. (2002) point out, these abilities require temporal sequencing abilities, which may be the key factor common to the reading, rhythm and phonological awareness tasks used in this study.

A final interesting finding relates to the role of rhythm in reading once naming speed was removed. In these analyses, rhythm proves to have relatively robust predictive power. Although it was no predictor of reading in grade 1, rhythm still predicted a modest but significant amount of unique variance in grades 2 and 3 Word Identification and grades 2, 3 and 5 Word Attack. Unlike the case observed for phonological awareness, the results indicate that, overall, rhythm is related to reading beyond the cognitive demands of rapid naming. One challenge to this interpretation may lie in the choice of RAN task administered in grade 1. Several studies have shown that alphanumeric RAN is more predictive of reading development than colour and object RAN. Therefore, the robust role played by rhythm in the presence of RAN may have been attenuated, had alphanumeric RAN measures been employed. Although Scarborough's (1998) meta-analysis found that naming speed for colours and pictures was comparable to naming speed for alphanumeric stimuli for children who are learning to read (median $r = -.39$ for colours and pictures, median $r = .38$ for letters and digits), this is clearly an area for future research.

While both phonological awareness and naming speed have been shown to predict reading development in many studies, they do not predict all the variance in reading development. It would be valuable to discover a process that added to the amount of variance accounted by phonological awareness and naming speed. Finding that rhythm is correlated with reading development over 5 years is interesting, but in order to be useful for theory building, it is necessary to determine whether the variance contributed by rhythm is unique, or whether it is shared by other, more traditional predictors. Many studies that have investigated the role of rhythm in reading have failed to consider the role of rhythm in combination with rapid naming or phonological awareness, and none have considered the contribution of these variables over time. The findings from this study suggest that rhythm plays a role that is largely distinct from naming speed, but is subsumed by phonological awareness. This is interesting when considered in light of previous research linking rhythm to phonological awareness (e.g. Goswami, 2002). We also observe that the contribution of rhythm appears to increase over time, when it is considered alone, and also in the context of naming speed.

There are several limitations within the context of this study that require acknowledgment and constrain the interpretation of our data. First, the rhythm task measured rhythm production only; a measure of rhythm discrimination would have allowed a more comprehensive analysis and integration of these findings relative to the literature. For example, the conflicting findings of Atterbury (1985) and Douglas and Willats (1994) regarding the relationship between reading and rhythm may be due to the fact that the former measured only rhythm production and the latter measured only rhythm discrimination. Relatedly, the score on the rhythm task was a combined score of the participants' abilities to tap the rhythm with both hands, alternating hands, march the rhythm while seated, standing and walking. Insofar as the tasks involve different amounts of coordination and balance beyond that of rhythm production, scores may reflect these extraneous influences. A measure of the participants' exposure to music would have allowed for a discussion of whether rhythm related to reading is heightened by musical experience. A further limitation is the relatively small sample size; attrition lowered the sample size from 53 to 38, which may have prevented some of the regression analyses from reaching conventional levels of significance in the later grades.

Overall, our findings provide evidence that rhythm is a factor that deserves greater research attention. The present study focuses on non-speech rhythm; given the importance of speech rhythm in oral language, especially in stress-timed languages such as English and Dutch, perhaps speech rhythm, such as stress or prosody, would be a productive area of investigation (Wade-Woolley & Wood, 2006). This is particularly true for older readers, as the results of this study show that the strongest correlations between reading and rhythm are in the older grades. Further research is required to determine whether the greatest impact of rhythm is domain general, or more tightly constrained within the linguistic system.

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Time Reproduction in Children With ADHD and Their Nonaffected Siblings

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ABSTRACT

Objective: Time reproduction is deficient in children with attention-deficit/hyperactivity disorder (ADHD). Whether this deficit is familial and could therefore serve as a candidate endophenotype has not been previously investigated. It is unknown whether timing deficits are also measurable in adolescent children with ADHD and nonaffected siblings. **Method:** These issues were investigated in 226 children with ADHD, 188 nonaffected siblings, and 162 normal controls ages 5 to 19. Children participated in a visual and auditory time reproduction task. They reproduced interval lengths of 4, 8, 12, 16, and 20 seconds. **Results:** Children with ADHD and their nonaffected siblings were less precise than controls, particularly when task difficulty was systematically increased. Time reproduction skills were familial. Time reproduction deficits were more pronounced in younger children with ADHD than in older children. Children with ADHD could be clearly dissociated from control children until the age of 9. After this age, group differences were somewhat attenuated, but were still present. Differences between nonaffected siblings and controls were constant across the age range studied. Deficits were unaffected by modality. **Conclusions:** Time reproduction may serve as a candidate endophenotype for ADHD, predominantly in younger children with (a genetic risk for) ADHD. *J. Am. Acad. Child Adolesc. Psychiatry,* 2007;46(5):582–590. **Key Words:** attention-deficit/hyperactivity disorder, siblings, endophenotype, time reproduction, development.

Attention-deficit/hyperactivity disorder (ADHD; American Psychiatric Association, 1994) is a highly heritable disorder. On average, 73% of the phenotypic variance of this disorder can be explained by heritable factors (Faraone et al., 2005; Willcutt, in press). Consequently, siblings of an affected individual have a six- to eightfold higher risk for developing ADHD (Willcutt, in press). The identification of susceptibility genes, however, has proved troublesome, partly because of the heterogeneity at both the genotypic and phenotypic levels (Buitelaar, 2005; Gottesman and Gould, 2003).

Endophenotypic research has attempted to contribute to overcoming these difficulties. Endophenotypes are defined as heritable, quantitative, vulnerability traits (Almasy and Blangero, 2001; Castellanos and Tannock, 2002; Waldman, 2005) that form a more direct expression of disease genes than behavioral symptoms (Gottesman and Gould, 2003). The key criteria of an endophenotype are (Doyle et al., 2005) that it should co-occur with the condition of interest and preferably that its neurobiological substrate is plausible, that it should appear in individuals who carry genes for the disorder but do not express the disorder itself, and that it should show evidence of heritability, among others indicated by significant familiality. Here, we investigate these characteristics to determine whether time reproduction may be a candidate endophenotype of ADHD.

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The first criterion of an endophenotype seems to be met for time reproduction because deficits in this function co-occur with the condition of interest. Time reproduction deficits have frequently been observed in individuals with ADHD who are less precise in temporal reproduction tasks (Baldwin et al., 2004; Barkley et al., 1997, 2001; Bauermeister et al., 2005; Kerns et al., 2001; McInerney and Kerns, 2003; Meaux and Chelonis, 2003; Smith et al., 2002; Toplak et al., 2003; West et al., 2000). Time reproduction is, for example, essential for time-dependent tasks, such as planning, waiting, and organizing (Baldwin et al., 2004; Smith et al., 2002; Toplak et al., 2003). In temporal reproduction tasks an interval length is presented either visually (e.g., by switching a light bulb on and off) or auditorily (tone) and has to be reproduced. The reproduction paradigm accurately represents the subjective sense of time (Zakay, 1990) and seems the most taxing aspect of subjective timing (Barkley et al., 2001) because it loads heavily on working memory, attention, and inhibition processes; processes identified as deficient in ADHD (Baldwin et al., 2004; Biederman and Faraone, 2002; Kerns et al., 2001; Nigg, 1999, 2001; Oosterlaan and Sergeant, 1996).

There also appears to be at least some plausibility in the neurobiological substrate of time reproduction. Mainly the frontal lobe, basal ganglia, and cerebellum seem to be involved in time reproduction (Handy et al., 2003; Lewis and Miall, 2003a,b; Mangels et al., 1998) and have also been identified as being smaller in children with ADHD (Durston, 2003). Dopaminergic systems seem to play an important role in time reproduction (Handy et al., 2003) and have also been shown to be dysfunctional in ADHD (Swanson et al., 2000). Thus, time reproduction deficits appear to co-occur with ADHD, and there is some indication of a plausible neurobiological substrate.

The second and third criteria, the presence of time reproduction deficits in individuals who carry genes for the disorder but do not express the disorder itself and the heritability of time reproduction deficits, have not been investigated before. Therefore, the main aims of the present study were to investigate possible time reproduction deficits in nonaffected siblings of children with ADHD and whether these deficits are familial. Previously, Schachar et al. (2005) reported on an intermediate phenotype in nonaffected siblings of children with ADHD: Although these siblings did not fulfill the *DSM-IV* (American Psychiatric Association, 1994) criteria for ADHD, they showed more ADHD symptoms than did normal controls. It may be suggested that time reproduction deficits found in nonaffected siblings are associated with this intermediate phenotype. To investigate whether endophenotypic deficits in nonaffected siblings are independent of phenotypic symptoms, symptom level could be used as a covariate, as was done in this study.

A related issue that deserves attention studying cognitive deficits in children with ADHD (and their nonaffected siblings) is the issue of age-dependent changes in cognitive deficits. ADHD is a developmental disorder that is by its nature not a static entity. A substantial number of children with ADHD eventually no longer meet criteria for the diagnosis (Biederman et al., 2000; Faraone et al., 2006). This may indicate that the disorder can be characterized by a delayed yet normal development (Satterfield and Braley, 1977). However, there is also strong evidence of the persistence of some structural brain abnormalities during development (Castellanos et al., 2002), and time reproduction deficits have been reported in both adolescents and young adults with ADHD (Barkley et al., 2001). How this fits into the theoretical framework of an endophenotype has yet to be determined. For instance, a predominantly genetically based deficit, such as an ADHD endophenotype, may not be fully outgrown and may still be measurable in adults with ADHD. Alternatively, heritable deficits, although inherent to the disorder, may become less evident because of compensatory mechanisms acquired during brain development (Halperin and Schulz, 2006). The influence of genes is not constant during the development: Genes can “switch on” and “off,” and their influence strongly depends on the expression of other genes and their interaction with environmental influences (Brown, 2002). Therefore, another aim of this study, aside from determining whether time reproduction meets the criteria of an endophenotype, was to study time reproduction skills in relation to age in a cross-sectional design.

The presence of time reproduction deficits in children with ADHD and their nonaffected siblings can be most reliably studied using a systematic increase in the lengths of the intervals to be reproduced. This task design appears to be the most adequate to study deficits in time reproduction. As the demands on the ability to reproduce time increase, the performance deficit of the patient, as compared to normal controls, would become more prominent (Sergeant and Van der Meere, 1990). This finding would translate into a significant group × difficulty level interaction, in which increasing difficulty level would enhance group differences. This interaction between group and difficulty level exposes the underlying vulnerability more clearly than studying only a group main effect. This systematic increase in difficulty level has, however, only been infrequently implemented (Barkley et al., 1997), but is implemented in the present study. To rule out the possibility that findings were the result of the modality in which time intervals were presented (West et al., 2000), we studied time reproduction both visually and auditorily. The majority of the studies have focused on the visual modality (Toplak et al., 2006). A few studies have targeted the auditory modality (Toplak et al., 2003; West et al., 2000), and only one study directly compared the modalities (West et al., 2000). West et al. reported deficits only in the visual modality, not in the auditory modality. This finding, however, awaits replication.

METHOD

Subjects

Families with at least one child with the combined subtype of ADHD and at least one additional sibling (regardless of possible ADHD status) were recruited to participate in the Amsterdam part of the International Multicenter ADHD Genes study (IMAGE). The IMAGE project is an international collaborative study that aims to identify genes that increase the risk of ADHD using QTL linkage and association strategies (Brookes et al., 2006). Additional control families were recruited from primary and high schools from the same geographic regions as the participating ADHD families. Controls and their first-degree relatives had no formal or suspected ADHD diagnosis. A total of 178 ADHD families and 100 control families fulfilled inclusion and exclusion criteria. In the ADHD families 226 children with ADHD and 188 nonaffected siblings participated. Control families consisted of 162 children. For 51 control children no additional control sibling could be recruited for the study because the additional sibling did not want to participate or because there was only one child in the control family.

All of the children were between the ages of 5 and 19 years and were of European white descent. Participants were excluded if they had an IQ <70 or a diagnosis of autism, epilepsy, general learning difficulties, brain disorders, or known genetic disorders, such as Down syndrome or fragile X syndrome.

In an ADHD family both the children already clinically diagnosed with ADHD as well as their siblings were similarly screened using the standard procedures of the IMAGE project described fully elsewhere (Brookes et al., 2006). Briefly, screening questionnaires (parent and teacher Conners long-version rating scales [Conners, 1996], parent and teacher Strengths and Difficulties Questionnaires [Goodman, 1997], and Social Communication Questionnaire [Berument et al, 1999]) were used to identify children with ADHD symptoms. *T* scores ≥63 on the Conners ADHD subscales (L, M, and N) and scores >90th percentile on the SDQ Hyperactivity subscale were considered clinical. Concerning all of the children in a family scoring clinically on any of the questionnaires completed either by the parents or the teachers, a semistructured, standardized, investigator-based interview was administered separately for each child: the Parental Account of Children's Symptoms (PACS; Taylor, 1986; Taylor et al., 1991). The PACS covers *DSM-IV* symptoms of ADHD, conduct disorder, oppositional defiant disorder, and anxiety, mood, and other internalizing disorders. The section on autistic behavior traits was administered if a clinical score was obtained on the Social Communication Questionnaire (raw score ≥15). A standardized algorithm was applied to the PACS to derive each of the 18 *DSM-IV* ADHD symptoms, providing operational definitions for each behavioral symptom. These were combined with items that were scored 2 (pretty much true) or 3 (very much true) in the teacher-rated Conners ADHD subscales (L, M, and N) to generate the total number of hyperactive-impulsive and inattentive symptoms of the *DSM-IV* symptom list. Situational pervasiveness was defined as at least one symptom occurring in two or more different situations, as indicated by the parents in the PACS interview, as well as the presence of at least one symptom scoring 2 or 3 from the ADHD subscales (L, M, and N), as indicated by the teachers on the Conners questionnaire. For purposes of analysis here, siblings were regarded as nonaffected if they obtained scores in the nonclinical range on both the parent and teacher questionnaires (Conners N scale: *T* score ≤62, SDQ: <90th percentile). No PACS interview was administered concerning nonaffected siblings.

The Conners long version for both parents and teachers was completed for control children. Control children had to obtain nonclinical scores on both the parent and teacher versions (Conners N scale: *T* score ≤62). Table 1 provides the characteristics of the three groups.

Measures

Time Reproduction. Time reproduction was measured with the Timetest Application version 1.0 (Barkley, 1998) in which subjects were required to reproduce temporal intervals with different interval lengths (4, 8, 12, 16, 20 seconds). The task was administered first in the visual modality and thereafter in the auditory modality. Standardized verbal and visual instructions were used. In both modalities testing started following a practice session of three trials. Thereafter, 20 experimental trials were administered. The five interval lengths were randomly presented four times. Children were not informed about the length of the intervals and did not receive feedback concerning their performance.

In the visual modality two lights bulbs appeared on the screen. After the left light bulb had been switched on for a specific interval length, the right light bulb had to be kept lit for the same interval length by pressing the space bar. In the auditory modality a tone was presented that had to be reproduced by pressing the space bar. Administration of both modalities required 15 minutes. The dependent measure was the precision of the reproduction (operationalized as the absolute discrepancy between the response length and the stimulus length).

Intelligence. Full Scale IQ was estimated by four subtests of the WISC-III or WAIS-III (depending on the child's age): Vocabulary, Similarities, Block Design, and Picture Completion (Wechsler, 2000, 2002). These subtests are known to correlate between 0.90 and 0.95 with the Full Scale IQ (Groth-Marnat, 1997).

TABLE 1

Sample Characteristics

	ADHD (n = 226)		Nonaffected Siblings (n = 188)		Normal Controls (n = 162)				
	Mean	SD	Mean	SD	Mean	SD	$F_{2,573}$	p	ηp^2
Age, mo	143.1	34.3	137.7	44.5	136.9	38.0	1.55	.21	.01
Gender									
% Male	80.5		46.8		39.5		79.50[a]	<.001[b]	.14
IQ	99.8	11.8	103.4	11.4	105.9	9.2	15.03	<.001[b]	.05
Handedness									
% Right-handed	92.0		88.8		84.0		8.46[a]	.21	
Conners Parent									
DSM-IV: Inattentive	71.3	8.6	49.3	7.9	46.7	4.9	658.94	<.001[b,c]	.70
DSM-IV: Hyperactive-impulsive	77.4	10.7	50.8	8.8	48.0	5.5	680.91	<.001[b,c]	.70
DSM-IV: Total	76.2	9.4	50.0	7.9	47.0	4.9	860.82	<.001[b,c]	.75
Oppositional	66.2	11.7	50.9	9.9	47.7	7.3	200.02	<.001[b,c]	.41
Anxious-shy	58.7	13.8	49.7	9.1	49.3	8.5	48.05	<.001[b]	.14
Conners Teacher									
DSM-IV: Inattentive	66.7	8.4	49.3	6.7	46.0	4.4	526.31	<.001[b,c]	.65
DSM-IV: Hyperactive-impulsive	69.8	10.8	50.0	8.5	46.5	4.3	430.95	<.001[b,c]	.60
DSM-IV: Total	70.3	9.5	49.7	6.8	45.9	4.0	639.63	<.001[b,c]	.69
Oppositional	62.5	13.1	50.9	8.7	48.3	5.6	114.52	<.001[b,c]	.29
Anxious-shy	63.9	11.3	55.8	10.1	55.3	10.4	39.99	<.001[b]	.12

Note: ADHD = attention-deficit/hyperactivity disorder.

[a] χ^2.

[b] The ADHD group differs significantly from the nonaffected siblings group and the control group ($p < .05$).

[c] The nonaffected siblings group differs significantly from the control group ($p < .05$).

Procedure

Testing of children with ADHD and their siblings took place at the Vrije Universiteit Amsterdam and was conducted simultaneously for all of the children in the same family. Psychostimulants were discontinued for at least 48 hours before testing took place (Pelham et al., 1999). Children were motivated with small breaks. At the end of the session, a gift worth approximately \$5 was given. Control children were tested in a similar way in a quiet room at their school. The study had medical/ethical approval.

Data Analyses

The percentage of data missing was <5% and appeared to be nonsystematic. Missing data were replaced by means of expectation maximization (Tabachnick and Fidell, 2001). Cronbach α was set at .05. None of the dependent variables was normally distributed. Therefore, a natural log transformation was applied.

A linear mixed model was used to examine the effects of modality, interval length, and age, to test whether these effects should be incorporated in the additional analyses. Group (three groups: ADHD, nonaffected siblings, and controls) as fixed factor, modality (two modalities: visual and auditory) and interval length (five intervals: 4, 8, 12, 16, and 20 seconds) as repeated measures, age as a covariate, and family as a random effect to account for within family correlation. Also, the interactions between group and the three other variables (modality, interval length, and age) were implemented in the initial model. Dependent measure was the absolute discrepancy between stimulus length and response length.

Modality was eventually not entered into the analyses because it had no effect on the absolute discrepancy scores ($F_{1,575.4} = 0.06$; $p = .80$) and the two-way interaction group by modality was not significant ($F_{2,575.4} = 0.92$, $p = .40$). Data were, therefore, averaged across modalities. Main effects were examined by means of pairwise comparisons; interaction effects were examined by repeating the analyses with the two groups of interest. To examine whether differences between nonaffected siblings and controls survived statistical adjustment for ADHD symptom level differences, analyses were repeated with Conners' N raw score (averaged across parent and teacher) as a covariate.

The hypothesis was tested that children with ADHD and nonaffected siblings would be less precise in their reproductions than normal controls (main effect of group). Furthermore, whether time reproduction skills would show familiality, indicated by significant covariances between siblings, was analyzed. We hypothesized that with increasing task difficulty, group differences would become more manifest (interaction group × interval length). Last, whether group differences would be smaller in the older children compared to the younger children (interaction group × age) was tested.

RESULTS

Group Differences and Familiality

A significant effect for group was found ($F_{2,553.6} = 16.88$, $p < .001$). Pairwise comparisons revealed that children with ADHD and their nonaffected siblings performed worse than controls (both $p < .001$). The difference between nonaffected siblings and controls remained significant after controlling for symptom severity ($p < .001$). Children with ADHD performed worse than their nonaffected siblings ($p < .004$). These group differences are in line with endophenotype-like group patterns. Furthermore, siblings within families resembled each other in their time reproduction skills (Wald $Z = 0.55$, $p < .001$, estimate of covariance = .12 [95% confidence interval 0.10–0.14]). Even though significant familiality does not implicate heritability, it is at least consistent with it.

Group Differences as Modulated by Increasing Task Difficulty

A significant main effect of interval length was found ($F_{4,576.0} = 456.94$, $p < .001$), indicating that precision deteriorated as interval length increased. This finding indicated that our task manipulation was successful. Furthermore, a significant group × task difficulty interaction was found, in which increasing interval length had a differential effect on the three groups ($F_{8,576.0} = 2.11$, $p = .03$). Group contrasts indicated that children with ADHD and their nonaffected siblings performed worse with increasing interval length than controls ($F_{4,388.0} = 4.02$, $p < .003$ and $F_{4,350.0} = 2.59$, $p = .04$, respectively). The difference between nonaffected siblings and controls remained significant after controlling for symptom severity ($F_{4,350.0} = 2.59$, $p = .04$). Both the children with ADHD and the nonaffected siblings were equally affected by the increase in interval length ($F_{4,414.0} = 0.37$, $p = .83$). This implied that the increase in task difficulty differentiated children with ADHD and their nonaffected siblings from controls (Fig. 1).

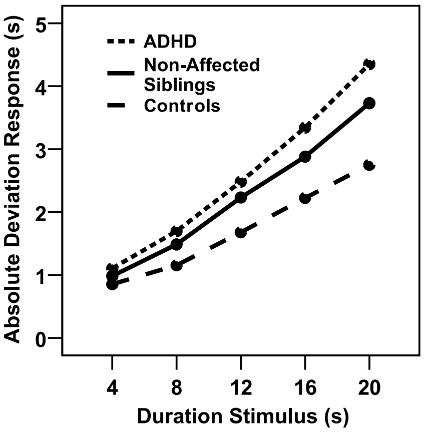

Fig. 1 The effect of increasing task difficulty on time reproduction in children with attention-deficit/hyperactivity disorder (ADHD), nonaffected siblings, and controls.

Group Differences as Modulated by Age

A significant effect of age was found on time reproduction ($F_{1,531.2} = 127.46$, $p < .001$), which indicated older subjects performed more precisely than younger subjects. Also, the group × age interaction was significant ($F_{2,539.5} = 867$, $p < .001$), indicating that the effect of age was not comparable across groups. Group contrasts indicated that the effect of age on time reproduction was greater in the ADHD group than in the control group ($F_{1,316.5} = 15.96$, $p < .001$) and the nonaffected siblings group $F_{1,403.8} = 9.44$, $p < .002$, respectively). The effect of age was comparable in nonaffected siblings and controls ($F_{1,350.0} = 1.14$, $p < .29$; Fig. 2).

The effect of age on time reproduction was not comparable across groups. This raised the possibility that after a certain age, no differences could be detected in time reproduction skills between children with ADHD, their nonaffected siblings, and controls. To investigate this possibility and to stipulate from what age the group × age interaction would become nonsignificant, the ADHD group was compared to the control group with respect to this interaction by first excluding children 5 years of age, then children of 6 years and younger, and so on.

In children with ADHD compared to controls, the group × age interaction was still significant when 5-, 6-, 7-, 8-, and 9-year-olds were excluded, but failed to reach significance when 10-year-old children were removed from the analyses ($F_{1,388.4}$) = 2.81, $p = .10$). The main effect of group remained, however, significant ($F_{1,403.4} = 5.17$, $p = .02$), indicating that the children with ADHD at age 11 still performed less precisely than controls.

Because the group × age interaction was comparable across the nonaffected siblings group and control group, group differences were stable across the age range studied. Nonaffected siblings were less precise than controls.

Reported results remained unchanged when possible confounders (IQ, gender) were implemented in the model and when anxiety or oppositional disorder as assessed by the Conners rating scales (averaged across

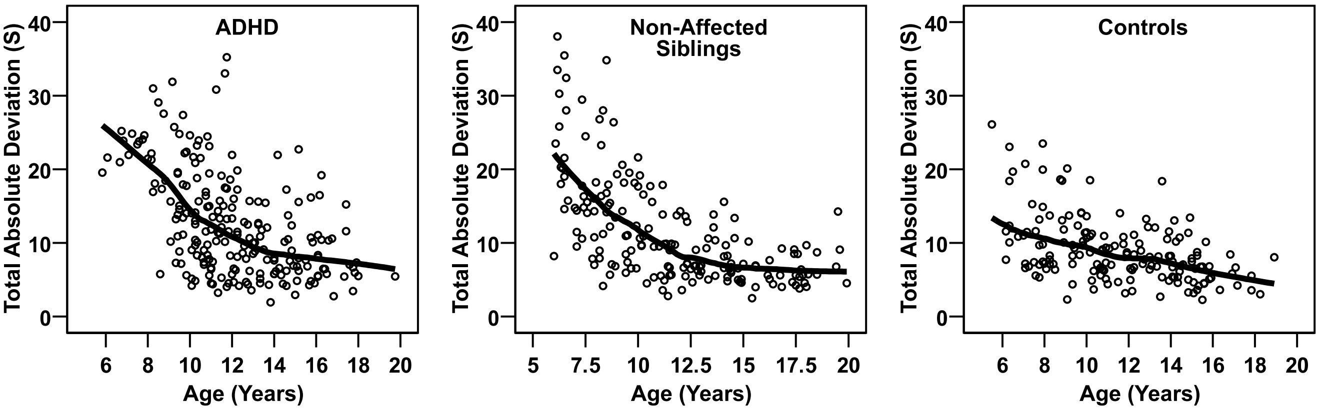

Fig. 2 Time reproduction precision in children with attention-deficit/hyperactivity disorder (ADHD), nonaffected siblings, and normal controls between the ages of 5 and 19.

parent and teacher) were implemented in the model. Means and SDs of the untransformed absolute discrepancy scores are presented in Table 2.

DISCUSSION

The present study showed that children with ADHD and their nonaffected siblings were clearly less precise in time reproduction than controls. This imprecision in children with ADHD agrees with findings of previous studies (Toplak et al., 2006), but the timing imprecision of nonaffected siblings has not been previously reported. Moreover, siblings resembled each other in their time reproduction skills, indicating familiality of the measure. The presence of deficiencies in time reproduction not only in children with ADHD but also in their nonaffected siblings indicates that time reproduction fulfills two important criteria of an endophenotype (Doyle et al., 2005): it co-occurred with the disorder and it was manifested in individuals who carry the genes for ADHD but did not express the disorder. Although the significant familiality of time reproduction skills does not implicate the measure to be heritable (as is required by the third criterion), it is at least consistent with it. The finding of time reproduction deficits in nonaffected siblings could not be explained by a possible intermediate phenotype (Schachar et al., 2005) because implementing symptom severity as a covariate in the analyses did not eliminate group differences between nonaffected siblings and controls. As we expected, increasing task difficulty (interval length) differentiated children with ADHD and nonaffected siblings even further from controls. When task difficulty was systematically increased, the vulnerability to time reproduction deficiencies in

TABLE 2

Means and SDs of the Untransformed Absolute Deviation Scores on the Five Different Interval Lengths

	ADHD (*n* = 226)		Nonaffected Siblings (*n* = 188)		Normal Controls (*n* = 162)				
	Mean	SD	Mean	SD	Mean	SD	*F*	*df*	*p*
4 s	1.32	1.51	1.15	1.03	0.93	0.71	5.63	2,549.24	.004[a]
8 s	1.96	1.84	1.79	1.81	1.24	0.85	10.25	2,541.00	<.001[a,b]
12 s	2.83	2.52	2.61	2.56	1.82	1.31	10.22	2,545.75	<.001[a,b]
16 s	3.70	3.12	3.30	3.03	2.37	1.38	12.07	2,534.92	<.001[a,b]
20 s	4.62	3.47	4.44	4.52	2.91	2.03	12.43	2,576.00	<.001[a,b]

[a] The ADHD group differs significantly from the control group ($p < .05$).
[b] The nonaffected siblings group differs significantly from the control group ($p < .05$).

children with ADHD and their nonaffected siblings was more clearly exposed. Therefore, the systematic increase in task difficulty seems particularly useful in dissociating groups of children with (a risk for) ADHD from groups of children without (a risk for) ADHD (Sergeant and van der Meere, 1990). Furthermore, time reproduction deficits in children with ADHD and in their nonaffected siblings were not modality specific, which implies a generalized deficit in time reproduction.

Studying age in relation to time reproduction as endophenotype revealed interesting results. In line with previous research on the development of executive functions, time reproduction improved during development in all children (Halperin and Schulz, 2006). This is probably related to the development of the prefrontal cortex (Halperin and Schulz, 2006) and frontally mediated processes involved in time reproduction, such as attention, working memory, and inhibition. The effect of age, however, was greater in the ADHD group as compared with the nonaffected siblings and control group. As a result group differences were large when young children were compared, but attenuated when older children were compared; yet, even though group differences became smaller, they were still present. These findings seem to agree with both the delayed maturation hypothesis (Satterfield and Braley, 1977) and the observations of nonprogressive brain volume abnormalities in children with ADHD (Castellanos et al., 2002). On the one hand, older children with ADHD performed relatively better than younger ADHD subjects compared with controls, which may suggest an age-related improvement in deficits in time reproduction, as has been found for other frontal functions and ADHD symptoms (Biederman et al., 2000; Faraone et al., 2006; Halperin and Schulz, 2006). On the other hand, older ADHD subjects (and nonaffected siblings) still performed worse as compared with controls, which seems to agree with the persistence of brain volume abnormalities in children with ADHD (Castellanos et al., 2002).

Limitations

Some limitations of this study should be noted. First, this study employed a cross-sectional design, which is not the optimal approach for studying the effects of age on cognitive deficits. The present findings await replication in a longitudinal study. Second, only subjects of white ethnicity were included in this study, which limits the generalization of our findings to other ethnic groups. Third, boys were overrepresented in the ADHD group, whereas they were underrepresented in the control group. This was due to the fact that ADHD is more frequently diagnosed in boys than in girls and because healthy girls are more willing to participate than healthy boys. We do not believe, however, that this affected the results because gender did not appear to affect time reproduction, and implementing gender in the model did not change the results. Fourth, we did not administer the PACS interview to nonaffected siblings. This may have resulted in undetected ADHD cases in the nonaffected siblings group, which in turn may explain the time reproduction deficits of this group. However, we do not believe this to be the case, because (1) all siblings were thoroughly screened and if they scored clinically on any of the screening questionnaires, the PACS interview was administered, and (2) even when symptom severity was used as a covariate, group differences between nonaffected siblings and controls remained significant. A final limitation is that we did not determine whether time reproduction is indeed heritable, which is a required criterion for an endophenotype (Gottesman and Gould, 2003). Future research, applying designs tailored to this question, should clarify this.

Clinical Implications

Time reproduction seems to be sufficiently sensitive to discover cognitive deficits in children with ADHD and to discover cognitive deficits in the absence of behaviorally detectable problems in their nonaffected siblings, especially when a systematic increase in task difficulty is applied and when young children are assessed. In daily life time reproduction deficits may translate into difficulties with tasks that require a timing component, such as waiting, planning, and organizing (Rubia et al., 2003), reflected by impulsive behavior.

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Exposure and Gender Differences in Childhood Mental Health Problems: A Longitudinal Population-Based Study Kapil Sayal, PhD, Jon Heron, PhD, Jean Golding, DSc, Alan Emond, MD

Objectives: High levels of alcohol use during pregnancy can lead to adverse physical and neurodevelopmental outcomes in children. It remains uncertain whether there is a safe level of drinking during pregnancy. In this study we investigate whether very low levels of alcohol consumption (<1 drink per week) are independently associated with childhood mental health problems (assessed at 3 time points between ages 4 and 8 years) and whether these effects are moderated by gender. We expected that only higher levels of alcohol consumption would be associated with later mental health problems and that any associations might be more readily detectable in boys. *Methods:* This prospective, population-based study used data from the Avon Longitudinal Study of Parents and Children. We investigated the relationship between self-reports of the amount and frequency of alcohol use in the first trimester and the presence of clinically significant mental health (behavioral and emotional) problems at 47 and 81 months (parental report: n = 9086 and 8046, respectively) and at 93 to 108 months (teacher report: n = 5648). *Results:* After controlling for a range of prenatal and postnatal factors, the consumption of <1 drink per week during the first trimester was independently associated with clinically significant mental health problems in girls at 47 months. This gender-specific association persisted at 81 months and was confirmed by later teacher ratings. *Conclusions:* Very low levels of alcohol consumption during early pregnancy may have a negative and persistent effect on mental health outcomes. Given the lack of a clear dose-response relationship and unexpected gender effects, these findings should be considered preliminary and need additional investigation. **Pediatrics** 2007;119:e426–e434.

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WRITTEN BY Kevin McGrew, PhD @ ***http://ticktockbraintalk.blogspot.com/2008/05/genetics-study-links-brain-clock-and.html***

Tuesday, May 13, 2008

Genetics study links brain clock and autism

This press release was sent to me by a friend of the Brain Clock blog. It is a press release from Corporate Communications and Marketing Athrolys College Road Bangor. The hyperlinks and additional reference information (including link to original research article and other Autism-related timing article) at the end of this post have been added by the Time Doc blogmaster.

Whenever I can find the time, I'll be adding autism to the *"Group differences and clinical disorders"* branch of the IQ Brain Clock EWOK. The complete list of possible clinical disorders research has suggested may involve aspects of mental timing (although not reflected at the current EWOK) are listed in my 2007 brain clock keynote address PPT show. This working list includes P*arkinson's, Huntington's, Schizophrenia, ADHD, reading development and disorders (dyslexia), certain speech and language development related disorders, motor timing disorders, Aspergers, and now Autism*.

I'm also soon be adding Dr. Wimpory to the *Mental Timing Scholars* blogroll of the IQ Brain Clock blog.

Publication date: 7/03/2007

Research by scientists in Wales reported in Molecular Psychiatry (advance online issue 30th Jan 07) has identified that Autistic Disorder is associated with two genes involved in timing and biological clocks: per1 and npas2. Cross species research shows that these two clock genes regulate timing mechanisms that control such things as sleep cycle, memory and communicative timing, a less familiar concept. The work, identifying a link between autism and these clock genes, was led by Dr. Dawn Wimpory, Lecturer-Practitioner/Consultant Clinical Psychologist for Autism, practising with the NWWales NHS Trust and Bangor University. She collaborated with Bangor University colleagues in both the School of Psychology and the North West

Cancer Research Fund Institute (NWCRFI), together with Professor Michael J Owen's team from Cardiff University's Department of Psychological Medicine.

Dr. Wimpory's clinical work and observations of the lack of social/communicative timing in Autistic Disorder was complemented by colleague Brad Nicholas of The NWCRFI suggesting that clock genes may be involved. This idea waited many years to be tested but new information from the human genome project, developments in the field of biological clocks and the construction of autism gene banks has recently allowed the experiment to be carried out.

Autistic Disorder is characterised by three areas of abnormality: impairment in communication (verbal and non-verbal) and reciprocal social interactions together with a markedly restricted repertoire of activities and interests, all in evidence before three years of age. (Autistic Spectrum Disorders or ASDs include milder and more varied related difficulties.) Dr. Wimpory works on the hypothesis that a deficiency in social timing contributes greatly to the difficulties faced by people with Autistic Disorder.

"Timing is quintessential to normal infant development. In Autistic Disorder, malfunction of adaptive timing may lead to a cascade of other developmental problems. In the first few months an unaffected infant can take part in social exchanges, sharing eye contact and babbling in what we'd recognise as 'natural' communication patterns. This facility for preverbal communication appears lacking or diminished in Autistic Disorder," explains Dr. Wimpory.

It is through such preverbal communication that an unaffected infant anticipates and predicts others' behaviour, progressing to increasingly sophisticated social participation, for example, in teasing exchanges. Mutually enjoyable preverbal teasing games (e.g. 'peep-bo!') are timing-dependent. They appear as an early stage in the development of empathy and social pretence. Empathy and pretending are among the life-long difficulties for individuals with Autistic Disorder. These may be developmentally linked to early difficulties in synchronising with the inbuilt rhythms of communication including eye-contact.

The study analyzed genetic markers in 11 clock related genes from 110 individuals with Autistic Disorder and each of their parents (avoiding the more varied ASD subjects and those with additional substantial learning/intellectual impairments often included in autism genetic studies). The results showed that markers in two of the genes, npas2 and per1, had significant association with Autistic Disorder. These two genes had already been identified as regulating complex emotional memory, communicative timing and sleep patterns in the mouse and the fruit fly; organisms that are used by scientists to study the role of clock genes. Problems in sleep, memory and timing are all characteristic of Autistic Disorder; each may play an important role in its development.

"Autism is a disorder of complex inheritance where several interacting genes may be involved. This is the first autism study to identify interacting genes, it is also the first to identify genes that regulate behaviour recognised as affected in autism: timing and memory. It adds further evidence for the role of the biological clock in autism".

The research was funded by the Baily Thomas Charitable Fund with additional support from Autism Cymru; the researchers now intend to replicate their study with a larger sample.

Time Doc blogmaster comments: I pulled the following two mental timing publications from Dr. Wimpory's web page:

- Nicholas B, Rudrasingham V, Nash, S., Kirov G, Owen MJ, Wimpory, D. (2007). Association of Per1 and Npas2 with Autistic Disorder:Support for the Clock Genes/Social Timing Hypothesis *Molecular Psychiatry,12,(6)* 581-592 (click here to view)
- Wimpory, D., Nicholas, B., Nash, S. (2002). Social Timing, Clock Genes and Autism: A New Hypothesis *Journal of Intellectual Disability Research, 46,(4)* 352-358. (click here to view; note that date is listed incorrectly as 2005 on Dr. Wimpory's web page)

Posted by Kevin at 10:50 AM

Genetics Study links Autism to timing mechanism

Publication date: 7/03/2007

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Cross species research shows that these two clock genes regulate timing mechanisms that control such things as sleep cycle, memory and communicative timing, a less familiar concept. The work, identifying a link between autism and these clock genes, was led by Dr. Dawn Wimpory, Lecturer-Practitioner/Consultant Clinical Psychologist for Autism, practising with the NWWales NHS Trust and Bangor University. She collaborated with Bangor University colleagues in both the School of Psychology and the North West Cancer Research Fund Institute (NWCRFI), together with Professor Michael J Owen’s team from Cardiff University’s Department of Psychological Medicine.

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Neuron
Article

Timing in the Absence of Clocks: Encoding Time in Neural Network States

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SUMMARY

Decisions based on the timing of sensory events are fundamental to sensory processing. However, the mechanisms by which the brain measures time over ranges of milliseconds to seconds remain unclear. The dominant model of temporal processing proposes that an oscillator emits events that are integrated to provide a linear metric of time. We examine an alternate model in which cortical networks are inherently able to tell time as a result of time-dependent changes in network state. Using computer simulations we show that within this framework, there is no linear metric of time, and that a given interval is encoded in the context of preceding events. Human psychophysical studies were used to examine the predictions of the model. Our results provide theoretical and experimental evidence that, for short intervals, there is no linear metric of time, and that time may be encoded in the high-dimensional state of local neural networks.

INTRODUCTION

All forms of sensory processing are ultimately based on decoding the spatial and/or temporal structure of incoming patterns of action potentials. The elucidation of the neural mechanisms underlying the processing of spatial patterns has advanced considerably in the past 40 years. For example, the coding and representation of simple spatial patterns, such as the orientation of a bar of light, are well characterized in primary visual cortex (Hubel and Wiesel, 1962; Ferster and Miller, 2000). Indeed, much has been discovered about the mechanisms underlying the emergence of orientation-selective cells and their role in perception (e.g., Miller et al., 1989; Ferster and Miller, 2000; Gilbert et al., 2000; Schoups et al., 2001; Yang and Maunsell, 2004).

In comparison with spatial stimuli, there is a significant gap in our understanding of how the brain discriminates simple temporal stimuli, such as estimating the duration of time for which a light or tone is presented. Recent studies have begun to examine the neural (Kilgard and Merzenich, 2002; Hahnloser et al., 2002; Leon and Shadlen, 2003) and anatomical (Rao et al., 2001; Lewis and Miall, 2003; Coull et al., 2004) correlates of temporal processing. However, the neural mechanisms that allow neural circuits to tell time and encode temporal information are not clear. Indeed, it has not yet been determined if timing across different time scales and modalities relies on centralized or locally independent timing circuits and mechanisms (Ivry and Spencer, 2004).

Timing is critical in both the discrimination of sensory stimuli (Shannon et al., 1995; Buonomano and Karmarkar, 2002; Ivry and Spencer, 2004; Buhusi and Meck, 2005) and the generation of coordinated motor responses (Mauk and Ruiz, 1992; Ivry, 1996; Meegan et al., 2000; Medina et al., 2005). The nervous system processes temporal information over a wide range, from microseconds to circadian rhythms (Carr, 1993; Mauk and Buonomano, 2004; Buhusi and Meck, 2005). We will focus on the scale of milliseconds and seconds, in which the dominant model of temporal processing is the internal clock model. A prototypical clock model includes an oscillator (pacemaker) that emits pulses that are counted by an accumulator (Creelman, 1962; Treisman, 1963; Church, 1984; Gibbon et al., 1997). Within this framework, the pulse count provides a linear metric of time, and temporal judgments rely on comparing the current pulse count to that of a reference time. This model has proven effective in providing a framework for much of the psychophysical data relating to temporal processing (Church, 1984; Meck, 1996; Rammsayer and Ulrich, 2001). However, electrophysiological and anatomical support for the putative accumulator remains elusive, and mounting evidence indicates that clock models are not entirely consistent with the experimental data (for reviews see Mauk and Buonomano, 2004; Buhusi and Meck, 2005).

A number of alternate models of timing have been suggested (see Discussion; for reviews see Gibbon et al., 1997; Buonomano and Karmarkar, 2002; Buhusi and

Meck, 2005). One such class of models, state-dependent networks (SDNs), propose that neural circuits are inherently capable of temporal processing as a result of the natural complexity of cortical networks coupled with the presence of time-dependent neuronal properties (Buonomano and Merzenich, 1995; Buonomano, 2000; Maass et al., 2002). This framework, based on well-characterized cellular and network properties, has been shown to be able to discriminate simple temporal intervals on the millisecond scale, as well as complex spatial-temporal patterns (Buonomano and Merzenich, 1995; Buonomano, 2000; Maass et al., 2002). Here we examine the mechanisms and nature of the timing in this model and show that it encodes temporally patterned stimuli as single ‘‘temporal objects,’’ as opposed to the sum of the individual component intervals. This generates the counterintuitive prediction that we do not have access to the objective (absolute) time of a given interval if it was immediately preceded by another event. This prediction is tested and confirmed using independent psychophysical tasks. Together, our results provide a mechanistic account of the distinction between millisecond and second timing and suggest that within the millisecond range, timing does not rely on clock-like mechanisms or a linear metric of time.

RESULTS

State-Dependent Networks

An SDN composed of 400 excitatory (Ex) and 100 inhibitory (Inh) recurrently connected integrate-and-fire units was simulated using NEURON. The synapses in the network exhibit short-term forms of synaptic plasticity and both fast and slow IPSPs (see Experimental Procedures). Short-term synaptic plasticity (Zucker, 1989) plays a critical role in SDNs by altering the state of the network in a time-dependent fashion after each input, which in turn produces time-dependent neuronal responses. In essence, in the same manner that long-term plasticity may provide a memory of a learning experience (Martin et al., 2000), SDNs use short-term synaptic plasticity to provide a memory trace of the recent stimulus history of a network (Buonomano, 2000).

The functional properties of an SDN can be understood if we consider the sequential presentation of two brief and identical events (e.g., two auditory tones) 100 ms apart (Figure 1A). When the first event arrives in the network, it will trigger a complex series of synaptic processes resulting in the activation of a subset of neurons. When the same event is repeated 100 ms later, the state of the network will have changed from S_0 to S_{100}. Due to the time-dependent changes in network state (imposed by short-term synaptic plasticity), the population response to the second stimulus inherently encodes the fact that an event occurred 100 ms before. In this fashion the network implements a temporal-to-spatial transformation—i.e., the presence, absence, or number of spikes from a given subset of neurons will depend on the temporal structure of the stimulus. The model is stochastic in the sense that determining which neurons will be interval sensitive is a complex function of the network's random connectivity, assigned synaptic strengths, and short-term plasticity (Buonomano, 2000). Once time is encoded in a spatial code, it can be read out by a set of output neurons (see below; Buonomano and Merzenich, 1995; Buonomano, 2000; Maass et al., 2002; Knüsel et al., 2004).

In this model, there is no explicit or linear measure of time like the tics of an oscillator or a continuously ramping firing rate (see Discussion; Durstewitz, 2003). Instead, time is implicitly encoded in the state of the network—defined not only by which neurons are spiking, but also by the properties that influence cell firing, such as the membrane potential of each neuron and synaptic strengths at each point in time. Thus, even in the absence of ongoing activity, the recent stimulus history remains encoded in the network. The simulation in Figure 1 consists of 500 neurons and a total of 12,200 synapses, allowing us to define the network's state in 12,700-dimensional space. Since the state of the network ultimately determines the response to the next input, we can think of its evolving trajectory through this space as encoding time. Principal component analysis was performed to provide a visual representation of this trajectory (see Experimental Procedures). In response to a single stimulus, the first three principal components establish a rapidly evolving neural trajectory through state-space, followed by a much slower path settling back toward the initial state (Figure 1B). When a second event is presented at t = 100 ms, it produces a perturbation in state-space different from the t = 0 event (Figure 1C). Similarly, additional presentations of the same stimulus at varying delays would continue to produce cumulative changes in network state.

The time it takes for the network to return to its initial state—its reset time—is a function of the longest time constants of the time-dependent properties. For short-term synaptic plasticity, this is on the order of a few hundred milliseconds (Zucker, 1989; Markram et al., 1998; Reyes and Sakmann, 1998). The dynamics of short-term plasticity must run its course; thus, the network cannot return to its initial state on command. As addressed below, this property has important implications for temporal processing.

Temporal Objects

An important feature of SDNs is that they naturally extend beyond simple interval discrimination to the processing of complex temporal sequences. This is due to the cumulative nature of changes in network state (Buonomano and Merzenich, 1995; Maass et al., 2002). However, potential weaknesses in SDNs arise because of both the absence of an explicit metric of time and their sensitivity to changes in initial state.

To examine these issues we investigated the ability of the network to discriminate between 100 and 200 ms intervals (we will use the notation [100] × [200] ms), as well as two simple patterns that contain these intervals, namely

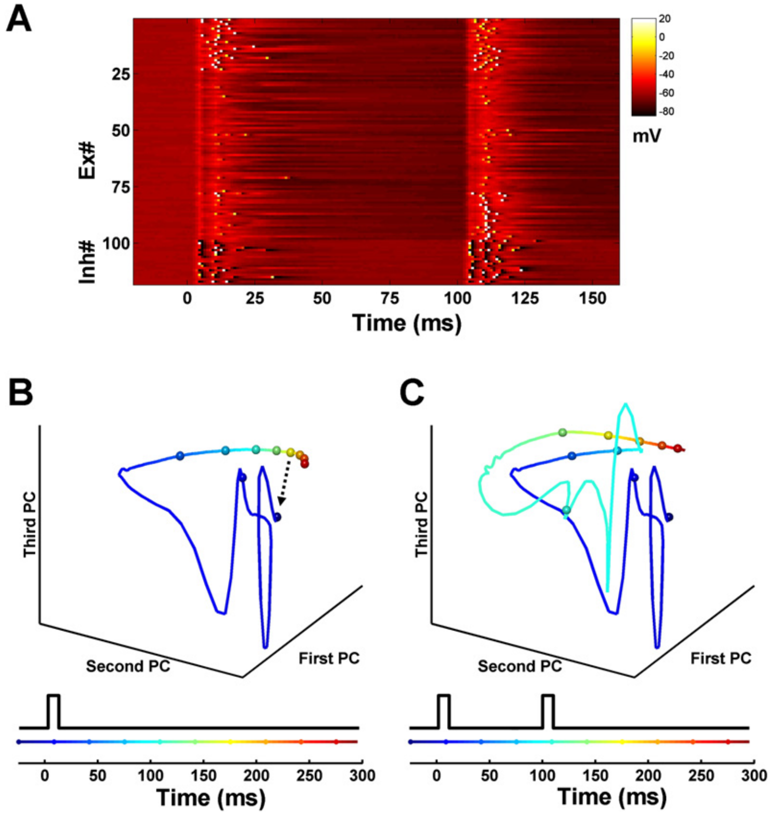

Figure 1. State-Dependent Network Simulation

(A) Voltage plot of a subset of neurons in the network. Each line represents the voltage of a single neuron in response to two identical events separated by 100 ms. The first 100 lines represent 100 Ex units (out of 400), and the remaining lines represent 25 Inh units (out of 100). Each input produces a depolarization across all neurons in the network, followed by inhibition. While most units exhibit subthreshold activity, some spike (white pixels) to both inputs, or exclusively to the first or second. The Ex units are sorted according to their probability of firing to the first (top) or second (bottom) pulse. This selectivity to the first or second event arises because of the difference in network state at t = 0 and t = 100 ms.

(B) Trajectory of the three principal components of the network in response to a single pulse. There is an abrupt and rapidly evolving response beginning at t = 0, followed by a slower trajectory. The fast response is due to the depolarization of a large number of units, while the slower change reflects the short-term synaptic dynamics and slow IPSPs. The speed of the trajectory in state-space can be visualized by the rate of change of the color code and by the distance between the 25 ms marker spheres. Because synaptic properties cannot be rapidly “reset,” the network cannot return to its initial state (arrow) before the arrival of a second event.

(C) Trajectory in response to a 100 ms interval. Note that the same stimulus produces a different fast response to the second event. To allow a direct comparison, the principal components from (B) were used to transform the state data in (C).

a 100 or 200 ms interval preceded by a 150 ms interval ([150; 100] and [150; 200]). We calculated the information each neuron in the network contains for the discrimination of both sets of stimuli. Mutual information was determined based on the number of spikes in each neuron (see Experimental Procedures). The neurons containing information for the [100] × [200] and the [150; 100] × [150; 200] discriminations fall in largely nonoverlapping populations (Figure 2A). This occurs even though the discrimination could in principle be based on the same [100] × [200] interval. Since the individual intervals are encoded in the context of the whole stimulus, the network cannot recognize that the [100] and [150; 100] patterns share a common feature. Nevertheless, it can discriminate between all four stimuli (Figure 2B). Each stimulus is coded as a distinct temporal object regardless of its component features.

Reset Task

The prediction that emerges from the model is that if a distractor precedes a 100 ms target interval at random intervals, discrimination of the target should be impaired in comparison to a 100 ms interval with no distractor (or one preceded by a fixed distractor). This prediction was examined using psychophysical studies. We designed a task (Figure 3A) in which each trial consisted of a randomly interleaved presentation of a single two-tone (2T) or three-tone (3T) stimulus, and participants were asked to judge the interval between the last two tones. In the 3T case the first tone acts as a distractor. By independently and adaptively varying the intervals, discrimination thresholds were calculated for the 2T and 3T tracks (see Experimental Procedures). The randomly interleaved—and thus unpredictable—presentation of the 3T stimuli also ensured that the subjects did not adopt strategies to ignore the distractor. The standard interval (SI) was presented at the beginning of a trial and maintained implicitly as a result of feedback to each response (Grondin and Rammsayer, 2003; Karmarkar and Buonomano, 2003). Subjects were asked to judge whether the target interval was shorter or longer than the standard. Two classes of distractors, fixed (FIX) and variable (VAR), were examined. In the FIX condition, the distractor was always presented at a fixed interval before the target interval. In the VAR condition, the distractor was presented at a range of times (±50% of the standard).

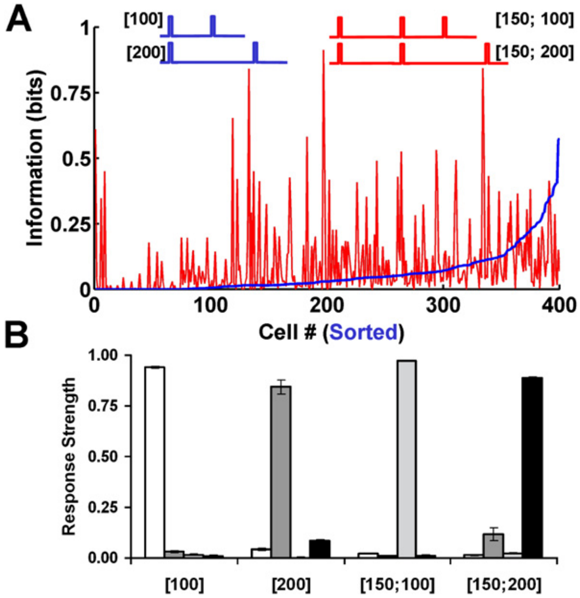

Figure 2. Encoding of Temporal Patterns

(A) Information per neuron. The blue trace displays the mutual information that each Ex unit provides for the discrimination of a 100 versus 200 ms interval (sorted). The red line shows the information for the same intervals preceded by a 150 ms interval; that is, discrimination of the pattern [150; 100] versus [150; 200]. While individual neurons contain significant information for both stimuli, a different population of neurons encodes each one.

(B) Discrimination of all four stimuli. All Ex units were connected to four output neurons trained to recognize the network activity produced by the last pulse of all four stimuli. Average responses were calculated from six independent (different random number generator seeds) simulations. Note that a mutual information measure based on total spike count to each stimulus, as in (A), would introduce a confound because the number of spikes is also a function of the number of events (see Experimental Procedures). Each group of four bars represents the responses of the four output neurons.

This task was termed the "Reset task" based on the unique constraints it places on the temporal encoding mechanisms. If a subject were using a simple stopwatch strategy, he or she would have to start the stopwatch at the first tone, even though it is irrelevant in the 3T trials. The true role of the second tone can only be determined retroactively by the presence or absence of a third tone. With a stopwatch, one approach could be to quickly record the time at t_2 and then reset the watch. Alternately, the time at t_2 and t_3 could be noted and then t_2 subtracted from t_3 to obtain the interval between the second and third tones. We will refer to the first strategy as a clock reset mechanism and the second as temporal arithmetic. Both can be implemented with internal clock models, either because the accumulator could be reset, or because the presence of a linear temporal metric would allow for temporal arithmetic. Both clock-based models predict that performance on the 2T and 3T tracks should be similar in both the FIX and VAR conditions because the predictability of the distractor should not affect the encoding of t_1-t_2 and t_2-t_3.

In contrast, in the SDN model, a reset strategy cannot be implemented because short-term plasticity cannot be reset on cue. Temporal arithmetic cannot be performed due to the absence of a linear metric of time. SDNs predict that performance on the FIX condition will be similar for the 2T and 3T stimuli because the feedback at the end of each trial can be used to establish consistent states on which to build internal temporal representations for both stimuli. However, they also predict an impaired performance in the 3T-VAR trials compared with the 2T or FIX conditions since the state of the network will not be reproducible across trials.

Subjects were first tested with a target interval of 100 ms (SHORT). Consistent with previous studies, thresholds for the 2T conditions were in the range of 20% of the target (Wright et al., 1997; Karmarkar and Buonomano, 2003). A two-way analysis of variance (ANOVA) revealed a significant interaction between conditions (FIX × VAR) and tone number (2T × 3T; $F = 57.75$; $n = 15$; $p < 0.0001$), demonstrating a dramatic impairment in the 3T-VAR condition only (Figure 3B). Indeed, the threshold in the 3T-VAR condition for a 100 ms interval was similar to that observed in independent (2T only) experiments on a 200 ms interval (46 ± 3.4 ms versus 45 ± 7 ms; data not shown). Thus, under the SHORT condition, the psychophysics supported the predictions of the SDN. In contrast, when the Reset task involved a target of 1000 ms (LONG), there was no effect of the variable distractor, as evident in the lack of interaction in the ANOVA (Figure 3C; $F = 0.087$; $n = 12$; $p > 0.5$). Importantly, the point of subjective equality (PSE) was approximately equal to the target intervals in both the SHORT and LONG experiments, independent of the presence or absence of the distractor in both the FIX and VAR conditions (Figures 3D and 3E). Therefore, a memory component of the task cannot account for the differences observed between the two target lengths.

The specific effect of the variable distractor on the SHORT group is consistent with the prediction of the SDN model. It is unlikely that this result is due to effects such as the increased uncertainty caused by the variable distractor, as the same degree of uncertainty was present in the LONG trials without an accompanying timing impairment. Additionally, the randomly interspersed presentation of the 2T and 3T stimuli ensures the same level of uncertainty for both stimuli (in both conditions), but the 2T-VAR performance was not affected. However, to further examine the general psychophysical effects of a variable distractor, we conducted two additional controls. The first was a task in which the distractor interval was 100 (FIX) or 50–150 ms (VAR) coupled with a 1000 ms target (Short-Long). In addition, subjects performed a frequency discrimination task in which the target frequency was preceded by a tone either at a fixed or variable interval (see Experimental Procedures). Neither the Short-Long [$F = 0.18$; $n = 10$; $p > 0.5$] or frequency [$F = 0.23$; $n = 14$; $p > 0.5$] experiments revealed a decrement in performance produced by the variability of the distractor (Figures 4A and 4B).

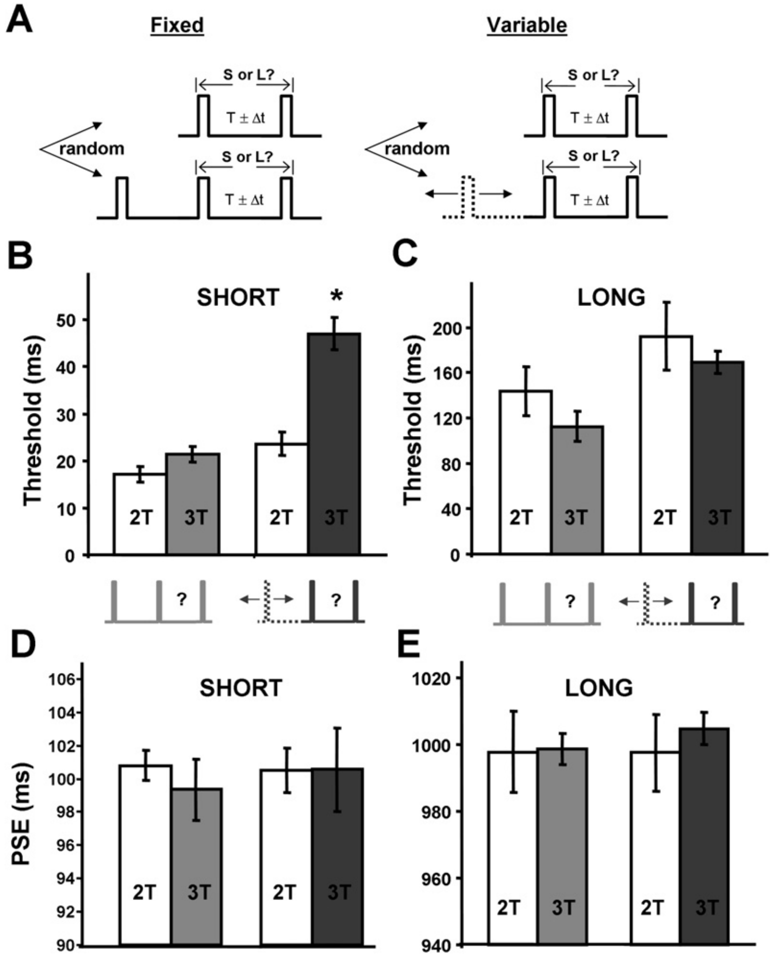

Figure 3. Reset Task: a Variable Distractor Impairs Discrimination of a Short, But Not a Long, Interval

(A) Reset task. Top rows represent the standard 2T interval discrimination task in a single stimulus protocol. Subjects are asked to press different mouse buttons if they judged the interval to be short (S) or long (L). The feedback across trials results in the creation of an internal representation of the target interval. Bottom rows represent the 3T task in which a distractor is presented at a fixed or variable (dashed) interval across trials.

(B) Thresholds for the 100 ms (SHORT) Reset task. (Left) Thresholds for the 100 ms 2T interval discrimination (open bars) and the 100 ms interval preceded by a distractor presented at the same interval across trials (3T-FIX, gray). (Right) Threshold for the standard 100 ms task (open) and 3T task in which the distractor was presented at variable intervals across trials (3T-VAR; gray). Error bars = SEM. The asterisk represents a significant difference from the other three groups.

(C) Reset task (represented as in A), using a 1000 ms (LONG) target interval. Neither of the main effects nor the interaction was significant.

(D and E) Point of subjective equality (PSE) values for the same experiments shown in (B) and (C), respectively. The PSE was not significantly different from the target intervals of 100 (D) and 1000 ms (E) in any condition.

Effect of the Interstimulus Interval on Performance

It is important to rule out the possibility that the impairments observed in the Reset task were not produced by some complex interaction between uncertainty and the intervals being judged, or that the distractor in the FIX condition was serving as a reference interval (see Discussion). Thus, we examined the prediction of the SDN model using a second independent psychophysical test. The SDN model predicts impaired performance under conditions when the network state at the time of the target stimulus varies across trials. This condition can also be produced by insufficient reset time before the next stimulus is presented. To test this directly, we examined performance on a traditional two-interval two-alternative forced-choice task (Wright et al., 1997) in which the interstimulus interval (ISI) was varied. In this paradigm, subjects heard both the 100 ms target and a longer comparison interval, then made a judgment as to whether the longer stimulus occurred first or second. We presented the two intervals with a mean ISI of either 250 or 750 ms. Since experimental data suggests that short-term plasticity operates on the time scale of a few hundred milliseconds (Markram et al., 1998; Reyes and Sakmann, 1998), the state-dependent model predicts that the network will not have completely returned to its initial state in the ISI_{250} condition, thus impairing temporal discrimination. Indeed, a comparison of the ISI_{250} to the ISI_{750} condition showed a significant decrease in performance for the shorter ISI [$t = 3.53$; $n = 10$; $p < 0.01$] **(**Figure 5A**)**. Subjects also performed a frequency discrimination task under the short and long ISI conditions, for which they reported if the tone pitch was higher for the first or second stimulus. There was no difference between the two conditions [$t = 0.53$; $n = 10$; $p > 0.5$] (Figure 5A), indicating that the effect of the shorter ISI was specific to time discrimination.

The state-dependent framework predicts that the two intervals are more difficult to compare, resulting in higher temporal discrimination thresholds, because their state-space trajectories have different starting points which vary from trial to trial. The total length of time from the first tone of the first stimulus to the first tone of the second is determined by the exact duration of the ISI (250% ± ≤25%). As a result, the variability in the initial state for the second stimulus is caused by the first—the first interval interferes with the second. However, if the target and comparison stimuli were presented at the same ISI, but

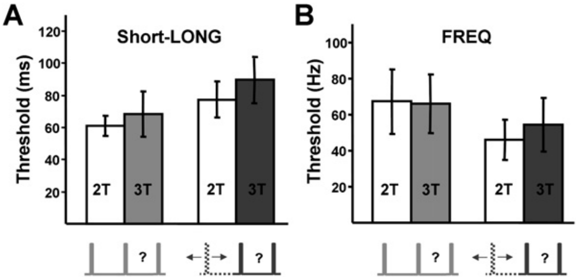

Figure 4. Control Interval and Frequency Discrimination Tasks

(A) Short-Long Reset task. The variable distractor in these trials was between 50–150 ms, and the target interval was 1 s. When a short unpredictable distractor preceded a long target interval, there was no effect of whether the distractor was fixed or variable.

(B) Frequency task. A tone was presented in the absence of a distractor (open bars) or in the presence of a distractor tone presented at a fixed (gray bar, left) or variable (gray bar, right) interval before the target tone. Conventions as in Figure 3.

to different local networks, the impairment produced by the short ISI should be decreased or absent. To examine this prediction, we took advantage of the known tonotopic organization of the auditory system. We performed interval discrimination tasks under two experimental conditions: (1) as above, a 100 ms standard and a comparison (100 + ΔT ms) played at 1 kHz at ISI_{250} and ISI_{750}; (2) a similar condition except that one of the stimulus intervals was played at 4 kHz and the other at 1 kHz. Replicating the above results, Figure 5B shows that there was a significant increase in the threshold of the ISI_{250} compared with the ISI_{750} tasks [$t = 6.85$; $n = 9$; $p < 0.001$] in the same frequency condition. However, using different frequencies for the standard and comparison intervals eliminated any impairment in performance on the short ISI [$t = 0.85$; $n = 9$; $p > 0.3$].

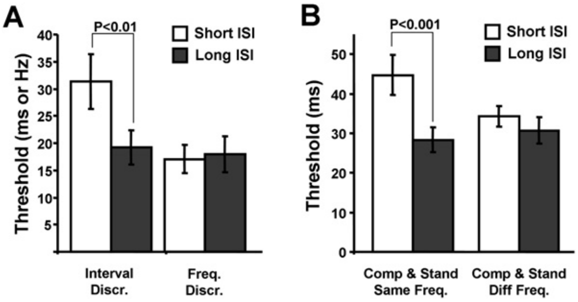

Figure 5. Short Interstimulus Intervals Impair Interval, but Not Frequency, Discrimination

(A) Bars on the left show the thresholds for a two-interval two-alternative forced-choice discrimination with a 100 ms target. When the interval between the stimuli was short (250 ms), performance was significantly worse compared with that in the long ISI condition (750 ms). In contrast, performance on a frequency discrimination task was unaltered by the ISI.

(B) Bars on the left illustrate the results for short (250 ms) and long (750 ms) ISI when both the standard and comparison intervals were presented at the same frequency. Bars on the right represent the interval discrimination thresholds when the standard and comparison stimuli were presented at different frequencies. We believe the difference in absolute interval discrimination between both studies (right bars in A and B) reflects interference between the different task and stimulus sets in both studies, as well as the inherent subject variability observed in timing tasks.

Interval Discrimination despite Differences in Initial State

While the insufficient reset time in the above experiments (Figure 5A) impaired discrimination thresholds, it did not entirely prevent subjects from performing the task. We were thus interested in returning to the theoretical model to determine how performance varied as a function of ISI and whether some degree of timing was still possible with only a partial reset of the network. First, the trajectory of the network in state-space was calculated in response to two 100 ms intervals separated by a 250 or 750 ms ISI. As shown in (Figure 6A), a 750 ms ISI allows the network to return to a point very close to its "naive" initial state. As a result, the trajectory produced by the second stimulus closely traces that produced by the first one. In contrast, for the 250 ms ISI, the network does not return to the neighborhood of the initial state, and its trajectory for the second interval is significantly different. Measures of these distances are presented in Figure 6B.

To quantify the effect of initial state on interval discrimination, output units were trained to discriminate 100 ms from other intervals in the range of 50–150 ms. We then determined the ability of the model to perform this discrimination when the comparison intervals followed the 100 ms target by ISIs that varied from 250–750 ms. Performance worsened with decreasing ISIs (Figure 6C). Importantly, performance changed in a graded manner, indicating that the reset effect is not expected to be all or none. Thus, the behavior of the theoretical model is consistent with the results seen in the human psychophysical data.

DISCUSSION

The standard model of temporal processing postulates a single centralized internal clock, which relies on an oscillator and an accumulator (counter) (Creelman, 1962; Treisman, 1963; Church, 1984; Grondin, 2001). The clock concept is generally taken to imply that the passage of time is counted in units that can be combined or compared linearly. In contrast, SDN models propose that for spans on the scale of tens to hundreds of milliseconds, time may be represented as specific states of a neural network. Within this framework, a 50 ms interval followed by a 100 ms interval is not encoded as the combination of the two. Instead, the earlier stimulus interacts with the processing of the 100 ms interval, resulting in the encoding of a distinct temporal object. Thus, temporal information is encoded in the context of the entire pattern, not as conjunctions of the component intervals.

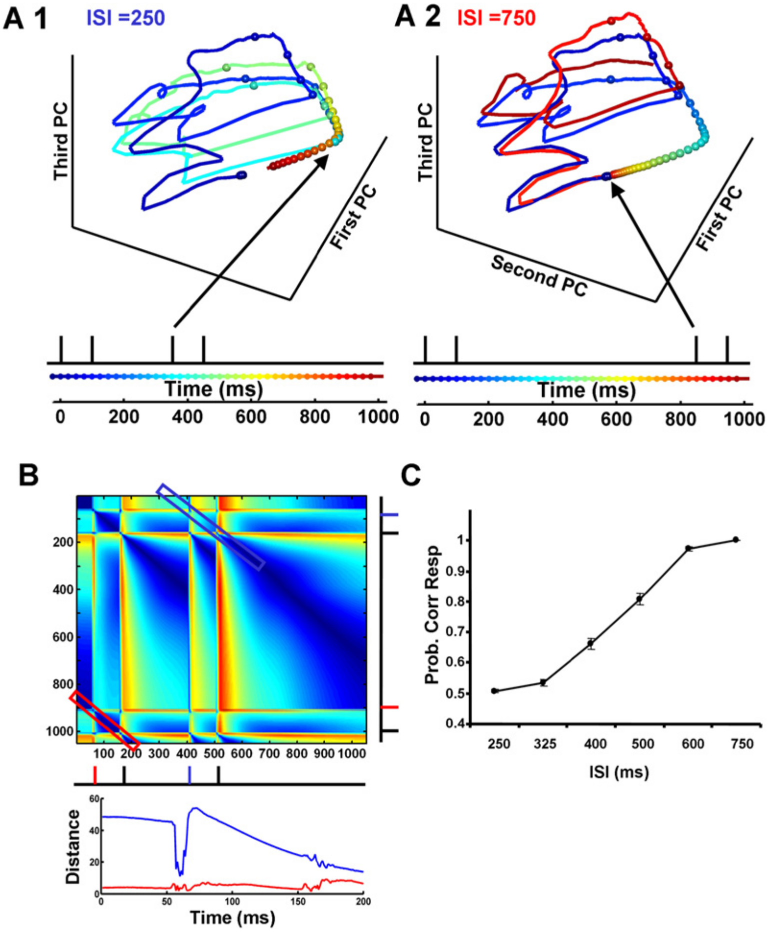

Figure 6. Dependence of the State-Dependent Network on Initial State

(A) Trajectory of the same network shown in Figure 1 and Figure 2, in response to two 100 ms intervals separated by a 250 (A1) or 750 (A2) ms ISI. Note that the trajectories under the 750 ms ISI are much closer to overlapping than they are in the 250 ms condition. Arrows indicate the times of the onset of the second interval.

(B) Distance matrix. The diagonal represents the distance in Euclidean space between the trajectories shown in (A1) and (A2) starting at 0. The distance is zero until the onset of the second tone (the noise "seed" was the same for both simulations). The secondary diagonals permit the visualization of the distances between two trajectories shifted in time. This allows the comparison of the trajectory starting at the onset of the second interval (for the 250 ms ISI) with that of the first interval (blue rectangle and blue line in lower panel), or the second interval of the 750 ms ISI with the first interval (red rectangle and red line in lower panel). These distances, shown in the lower panel, allow for quantification of the effect of the network not returning to its initial (resting) state before presenting the next stimulus. Note that while the initial distance is lower in the 750 ms ISI, it is not zero.

(C) Percent correct performance of networks trained to discriminate two intervals separated by varying ISIs. Average data from four stimulations. Output units were trained to discriminate intervals ranging from 50–150 ms. Performance was then tested by examining generalization to these same intervals when presented at varying ISIs after the presentation of a 100 ms interval. Results for the 100 × 150 ms discrimination are shown. Performance is highly dependent on the initial state of the network.

State-Dependent Networks and the Reset Task

SDN models propose that timing is a ubiquitous component of neural computations, and that local cortical circuits are inherently capable of processing both temporal and spatial information (Buonomano and Merzenich, 1995; Buonomano, 2000; Maass et al., 2002). In these models timing relies on mechanisms analogous to using the evolving state of a physical system—like the ripples on the surface of a lake—to tell time. However, as shown here (Figure 1 and Figure 2), reliance on the state of a complex system to tell time creates potentially serious limitations due to the resulting dependence on the initial state and the lack of a linear metric of time.

Interestingly, our psychophysical results reveal the same limitations—interval discrimination is impaired by the presence of a distractor that appears at unpredictable times. However, interval discrimination was not altered if the distractor occurred at a fixed time prior to the target. Thus, internal representations of the target interval can develop across trials for the 2T and 3T-FIX stimuli, but not for the target interval of the 3T-VAR stimuli. This is because the state of the system at the onset of the second tone is variable. The impairment in the 3T-VAR condition is not due to the unpredictability of the distractor's presence itself; since the 2T and 3T stimuli are randomly intermixed, the unpredictability is the same under all conditions. Rather, the impairment in the 3T-VAR condition is limited to the predictability (consistency) of the *interval* of the distractor.

An alternate interpretation of the 3T-VAR impairment is that in the 3T-FIX condition, the distractor interval served as a reference cue for the target interval. The two-interval discrimination task, in which both a standard and comparison interval are presented on each trial, was used to rule out this possibility (Grondin and Rousseau, 1991; Rammsayer, 1999; Wright et al., 1997). Performance was impaired if the time between the stimuli was 250 ms, but not 750 ms (Figure 5A). It could be argued that the impairment for short ISIs reflects a difficulty in segmenting or attending to rapidly presented stimuli. We find this interpretation unlikely since performance on the short and long ISI conditions did not differ when the two intervals were presented at different frequencies.

The influence of preceding stimuli on temporal judgments is surprising because much of the timing performed by the nervous system on the scale of hundreds of milliseconds is based on a continuous barrage of incoming stimuli, such as speech or Morse code recognition. The subjects in the current study were naive; thus, a critical issue relates to the effect of learning. We speculate that training would allow subjects to improve their discrimination of intervals independent of temporal context. Indeed, SDN models do not predict that spatial-temporal patterns preceded by other events are impossible to process. Rather, they propose that there must be previous exposure to a large number of instances of the stimuli so that a correspondence between the target information in a number of different contexts can be learned.

Clock Models

The standard clock models predict a linear metric of time, which implies that the clock can time the sequential intervals independent of the presence of a variable distractor across trials. However, most of these models do not explicitly address the issue of the clock reset properties. Thus, it seems reasonable to consider whether a clock with some state-dependent properties could account for the impaired timing of short ISIs or intervals with a distractor. For example, one could assume that resetting or reading the time of the clock is state-dependent, and thus, the reset process could inject noise into the system or be delayed dependent on the initial state.

There are two aspects of our results which could argue against a state-dependent clock mechanism. First, though a state-dependent reset of a centralized clock could explain impaired timing in the short ISI condition (Figure 5A), it would not predict the lack of impairment in the short ISI condition with different frequencies (Figure 5B). The second issue concerns the specificity of the reset problem. In our Reset experiments (Figure 3), a clock would be started by the first tone and stopped and reset (restarted) by the second. The third tone would again stop the clock. As mentioned above, a state-dependent reset would take time or inject noise into the process, and impair the 3T-VAR sequence compared with the 2T one. However, such a clock would also be expected to impair timing of 3T stimuli in the FIX condition. In both cases, the second tone would stop and reset the clock, because there is a 50% chance that the second tone would be the end versus the beginning of the target interval. This prediction is counter to our psychophysical results. One might then propose the use of multiple clocks, in which the first tone activates a primary clock, the second tone activates a secondary clock (and stops the first), and the third tone stops the second clock. This explanation would correctly suggest that timing is not impaired in the FIX condition, but would also hold for the VAR, again violating the dissociation found in our data.

Nevertheless, we cannot eliminate the possibility that there exists a set of assumptions which can enable clock models to account for the observed millisecond timing results. However, we argue that the SDN model provides the most parsimonious explanation of the current psychophysical data on the processing of short intervals.

Other Models of Temporal Processing

A number of other mechanistic models have been put forth to account for measuring and encoding time. These include climbing firing rate models (Durstewitz, 2003; Reutimann et al., 2004), multiple oscillator models (Miall, 1989; Matell and Meck, 2004), and those based on ongoing network dynamics (Medina and Mauk, 2000; Buonomano, 2005). The latter focus primarily on generating appropriately timed motor responses and will not be discussed here.

The climbing or ramping firing rate models suggest that, like many other stimulus features, time is encoded in the firing rate of neurons. Experimentally it is established that some cortical neurons undergo a more or less linear ramping in their firing rate over time (Niki and Watanabe, 1979; Brody et al., 2003; Leon and Shadlen, 2003). In their simplest form climbing models propose that firing rate represents a linear metric of absolute time. However, recent data suggests that, at least in some cases, these neurons are coding expectation rather than absolute time (Janssen and Shadlen, 2005). Climbing rate models have been discussed primarily in relation to timing of intervals or durations; how they would account for timing of temporal patterns has not yet been addressed. Thus, their predictions for our tasks are not immediately clear. For the Reset task it could be argued that ramping would begin at the first stimulus. Time could be read out in the firing rate at the onset of the second and third tone, assuming activity is not reset by the second tone. However, climbing models would not predict the dramatic impairment observed in the 3T-VAR condition or the effect of short ISIs. We would speculate that ramping firing rates are likely to play an important role in the timing of expected motor responses, but less likely to be involved in the timing of rapid sensory stimuli, particularly for complex tasks such as speech or interpretation of Morse code.

The multiple oscillator model suggests that time is encoded in a population of oscillators with different base frequencies (Miall, 1989; Matell and Meck, 2004; Buhusi and Meck, 2005). Time can be read out by a set of coincidence detectors. This model has the advantages of not requiring an accumulator and being capable of timing multiple consecutive intervals once the oscillators have been triggered. However, how this model will behave in the tasks examined here is again dependent on its assumptions. If each event does not reset the oscillators, this model would be expected to produce a decrease in performance in the 3T-VAR condition, consistent with our results. However, it would not necessarily predict the decrease in performance observed with the short ISIs observed in Figure 5, since its reset mechanisms could be all or none. Furthermore, this model posits that timing is centralized. Thus, it would not predict that any effect of a short ISI would be dependent on whether the frequencies of the comparison stimuli were the same. We would concur that a multiple oscillator model could contribute to timing in the range of seconds (Matell and Meck, 2004; Buhusi and Meck, 2005), but would argue that it is unlikely to account for the timing on the scale of a few hundred milliseconds.

Millisecond versus Second Timing

Timing in both the range of milliseconds and seconds has often been considered to rely on the same underlying mechanisms (Church, 1984; Macar et al., 2002). The results described here demonstrate qualitative differences in the processing of short and long intervals. Unlike the millisecond range, timing of intervals lasting one second or longer appears consistent with mechanisms that generate a linear metric of time. For a 1 s target subjects could accurately judge the first or second of two consecutive intervals in the Reset task, even though they did not know a priori which was the target. Performance was also independent of both fixed and variable distractors preceding the target interval. This implies that subjects could independently keep track of the objective time of two sequential second-long intervals and implies the presence of a linear metric of time. As described above, two simple strategies that a standard clock model could utilize to perform this task are resetting a clock at the second tone, or contributing values to the performance of temporal arithmetic. For the long intervals we did not observe any decrease in timing accuracy in the 3T versus 2T stimuli. We would suggest that this observation is more consistent with the temporal arithmetic scenario. Specifically, that timing on the order of seconds relies on a linear metric of time, and that the second of two consecutive intervals can be calculated by subtracting the first interval from the final count.

The theoretical framework and psychophysical results described here, together with previous psychophysical (Rammsayer and Lima, 1991), pharmacological (Rammsayer, 1999), and imaging studies (Lewis and Miall, 2003), support the existence of distinct loci for subsecond and second processing. The precise boundary between these forms of temporal processing cannot yet be established. However, it seems likely that they are highly overlapping, and that timing in intermediary ranges (e.g., 400–800 ms) may be accurately performed by both the mechanisms underlying time perception and time estimation. Based on the time constants of short-term synaptic plasticity and other time-dependent neural properties, we suggest that the SDN model is limited to intervals below 500 ms. Additionally, even within a specific time scale, there may be multiple mechanisms contributing to timing, and thus the above models are not mutually exclusive.

Relation to Previous Psychophysical Data

A comprehensive model of temporal processing should provide a detailed description of the neural mechanisms underlying timing, generate novel testable predictions, and account for existing experimental data. Two of the most robust features of temporal processing determined experimentally relate to the scalar property and the role of attention in subjective time estimation. The scalar property refers to the observation that the ratio of the absolute criterion interval and the standard deviation of temporal estimates tends to be constant for long intervals (Gibbon, 1977; Gibbon et al., 1997; Buhusi and Meck, 2005). However, this is not the case for interval discrimination in the range of a few hundred milliseconds (Wright et al., 1997; Mauk and Buonomano, 2004). Thus, we examined how performance scales with short intervals in the SDN model. Results showed that, consistent with the human psychophysical data, temporal resolution is proportionally worse for short intervals (see Figure S1 in the Supplemental Data).

Attention has been widely reported to alter estimates of time in the range of seconds (Hicks et al., 1976; Macar et al., 1994; Brown, 1997; Coull et al., 2004). Internal clock models can account for attention-dependent effects in the second range by assuming a gating mechanism that controls the number of events generated by the oscillator that are counted by the accumulator (Meck, 1984; Zakay and Tsal, 1989). In contrast, on the shorter time scale, divided attention or cognitive load does not appear to specifically alter temporal judgments (Rammsayer and Lima, 1991; Lewis and Miall, 2003). Therefore, the SDN model would be expected to be fairly insensitive to shifts in attention. However, recent studies have revealed that temporal distortions of short intervals can be produced by saccades or stimulus features (Morrone et al., 2005; Johnston et al., 2006). These studies suggest that on short scales, timing is local, and are generally consistent with the SDN model that predicts that temporal processing could occur in a number of different cortical areas on an as-needed basis.

Conclusion

We propose here that cortical networks can tell time as a result of time-dependent changes in synaptic and cellular properties, which influence the population response to sensory events in a history-dependent manner. This framework is applicable to the processing of simple intervals as well as more complex spatial-temporal patterns, and does not invoke any novel hypothetical mechanisms at the neural and synaptic level. Additionally, we propose that timing is not centralized, and can potentially occur locally at both early and late stages of cortical processing. The psychophysical experiments examined here emerged as a direct prediction of this model, and the results are supportive of this general framework. However, establishing the neural basis for timing will ultimately require the accumulation of converging evidence from a number of different fields; of particular relevance will be the use of more complex temporal stimuli in conjunction with in vivo electrophysiology to determine if the population response to ongoing sensory events also contains information about the preceding stimuli.

EXPERIMENTAL PROCEDURES

Neural Network Simulations

The simulated network was composed of 400 Ex and 100 Inh recurrently connected Hodgkin-Huxley units (Buonomano, 2000). Excitatory neurons were randomly interconnected with a probability of 0.2. The mean synaptic weights were adjusted so that neurons responded with zero to three spikes to a short stimulus, as is typical for primary sensory cortex in awake animals (Brody et al., 2002; Wang et al., 2005). Short-term dynamics of excitatory synapses were simulated according to Markram et al. (1998). Short-term synaptic plasticity of Ex→Ex synapses was facilitatory, based on experiments suggesting that paired-pulse facilitation is present in adult cortex (Reyes and Sakmann, 1998; Zhang, 2004). The mean U (utilization), τ_{rec} (recovery from depression), and τ_{fac} (facilitation) parameters were 0.25, 1 ms, and 100 ms, respectively. All three values were randomly assigned using a normal distribution with an SD of 20% of the mean. Short-term plasticity IPSPs in the form of paired-pulse depression was implemented as previously described (Buonomano, 2000).

Mutual Information and Network Readout

Mutual information was calculated using the total number of spikes in response to a stimulus, thus providing an assumption-independent estimate of the amount of information available (Buonomano, 2005). For the discrimination between stimuli with different numbers of pulses (Figure 2A), training of the output units was based on previously described supervised learning rules (Buonomano, 2000; Maass et al., 2002) using only the pattern produced by the last pulse. Training was performed on a set of 25 stimulus presentations and tested on 10 novel test presentations. In the stimulations shown in Figure 6, the outputs were trained to discriminate pairs of intervals (100 ms versus intervals ranging from 50–150 ms). In each case the shortest interval was defined as the short stimulus and the longest as the long stimulus.

Principal Component Analysis

The data set was comprised of the voltage of all Ex and Inh neurons, as well as the synaptic weights (which were time-varying) of excitatory and inhibitory synapses. To reduce the dimensionality of the data set, only 20% of all synaptic weights were used. The data were normalized and the principal components were calculated using the PRINCOMP function in Matlab. Although the dimensionality is very high, the dimensions are highly correlated during the silent period between events (if one cell is hyperpolarized, most cells are hyperpolarized). As a result, the first three principal components can account for a significant amount of the total variability (approximately 75% in Figure 1B). As expected, these components do not account well for the actual response to each event, which is dominated by highly nonlinear dynamics.

Psychophysics

Subjects consisted of graduate and undergraduate students between the ages of 18 and 30 from the UCLA community. All subjects had normal hearing.

Reset Task

These experiments were based on a single-stimulus two-alternative forced-choice protocol as described previously (Karmarkar and Buonomano, 2003). A within-subject design was used; thus, each subject performed the two distractor conditions (FIX and VAR) with each condition having two tracks (2T and 3T). Sessions of the FIX and VAR conditions were given on alternating days over a 1 day period (counterbalanced). Each block within a session consisted of 120 trials: 60 2T and 60 3T. Each tone (1 kHz) was 15 ms in duration and included a 5 ms linear ascending and descending ramp. In the FIX condition, a distractor tone was presented at a fixed interval equal to that of the SI prior to the target. In the VAR condition the distractor occurred before the target at an interval uniformly distributed between SI ± (0.5 × SI). Thresholds for the 2T and 3T tracks were obtained by presenting the target interval as SI ± ΔT, where ΔT varied adaptively according to a three-down one-up procedure (Levitt, 1971; Karmarkar and Buonomano, 2003). Threshold was defined as two times the mean of the reversal values, which corresponds to a 79% correct performance level.

In each trial subjects made a forced choice decision as to whether the stimulus seemed shorter or longer than the target interval by pressing one of two buttons on a computer mouse. They were provided with immediate visual feedback. All stimuli were generated in Matlab and presented through headphones.

The 2T and 3T stimuli were randomly interleaved to ensure that subjects did not develop a strategy that involved ignoring the distractor tone. Additionally, the simultaneous measure of performance on a conventional 2T task and a task with the presence of a distractor provided a control for nonspecific effects such as difficulty of the overall task, attention, and memory. Target intervals were either 100 or 1000 ms.

A similar protocol to the one used above was also used for the frequency discrimination task. Rather than adaptively varying the interval of the tones, their frequency was varied according to F ± ΔF (where F, the target frequency, was 1 kHz). Tone duration was 25 ms.

Two-Interval Forced Choice Procedure

In this task subjects were presented with two intervals on each trial: an SI and the comparison interval (standard + ΔT) (Allan, 1979; Karmarkar and Buonomano, 2003). Subjects were asked to press one of two buttons depending on whether they judged the first stimulus or the second interval to be longer. The SI was 100 ms, and the ISIs for the short and long ISI conditions were 250 and 750 ms, respectively.

The frequency task in the ISI experiments used the same type of stimuli, but shifted the frequency of both tones of the comparison stimulus. Note that in contrast to the single stimulus protocol, subjects could reference the target frequency on each trial as opposed to developing an internal representation of it across trials. We believe this difference, together with the absence of a distractor, is responsible for the improvement in the frequency thresholds as compared with the Reset task. All subjects performed all four tasks in a counterbalanced manner.

Statistics

In the Reset task, the key analysis was the performance on the 3T-VAR task in comparison with *both* the 2T-VAR and 3T-FIX tasks. A difference between only one of these comparisons would suggest a "cross-track" effect of the variable distractor independent of whether it was in the 2T or 3T condition, or impairment of 3T discriminations independent of whether the distractor was presented at a fixed or variable interval. Thus, we performed a two-way ANOVA to determine if there was an interaction between the 2T/3T and FIX/VAR factors.

Supplemental Data

The Supplemental Data for this article can be found online at http://www.neuron.org/cgi/content/full/53/3/427/DC1/.

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