MECHANISMS OF TIMING ACROSS TASKS AND TEMPORAL INTERVALS

by

Ashley S. Bangert

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Doctoral Committee:

Professor Patricia A. Reuter-Lorenz, Co-Chair
Assistant Professor Rachael D. Seidler, Co-Chair
Professor David E. Meyer
Associate Professor J. Wayne Aldridge
Assistant Professor Cindy A. Lustig

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CHAPTER I

General Introduction

Timing is fundamental to many motor and cognitive processes. At the motor level, individuals temporally coordinate movements to perform actions, like hitting a ball. For cognition, timing is critical for conditioned learning and for representation of sequential relationships between stimuli in the environment as well as many other activities. Because there are no explicit sensory receptors for time, temporal information must be derived through the operation of some neural mechanism(s) whose properties are a point of much debate. Though there are many important timescales relevant for human behavior (Buhusi & Meck, 2005; Buonomano & Karmarkar, 2002), this paper focuses on timing on the order of milliseconds and seconds. Controversy abounds concerning the precise nature of the mechanism(s) responsible for timing at this scale, because movement requires millisecond level precision to achieve appropriate muscle responses (Mauk & Buonomano, 2004) and may, therefore, point to motor system specialization for timing milliseconds as opposed to seconds-length durations (Lewis & Miall, 2003b, 2003c). In addition, it is unclear whether motor and perceptual tasks that require explicit representations of given durations for performance are dependent on the same internal timing mechanism (Ivry & Hazeltine, 1995; Keele, Pokorny, Corcos, & Ivry, 1985; Lewis & Miall, 2003b). For example, tasks where individuals must translate a duration into a motor program for response (motor) may rely on a different, more precise timer than tasks where participants compare two duration representations in memory (perceptual).

Scalar Timing Theory

One idea that has dominated the animal and human timing literature is that a pacemaker-accumulator device serves as a ubiquitous clock, which, along with other processes, enables individuals to discriminate between different durations (Grondin, 2001, 2005). The most popular model of timing based on this type of clock is the information processing instantiation which developed out of scalar expectancy theory (SET). This theory emerged from the animal behavioral literature to explain performance regularities seen across experiments; it was eventually modified to explain regularities seen in humans as well (Allan, 1998; Gibbon, 1991; Grondin, 2001). One such example is the finding from peak-interval studies that response rate distributions superimpose when rate is normalized as a function of the interval being timed (Church, 2003; Gibbon, 1991). The information processing model of SET consists of several basic components. These include 1) a pacemaker which generates pulses at regular intervals and 2) an attentionally-mediated switch (Fortin, 2003; Grondin & Rammsayer, 2003; Meck, 1984; Meck & Benson, 2002) that closes at the onset of a relevant stimulus, allowing pulses to flow from the pacemaker to 3) an accumulator. Though attention was not specifically addressed in the initial model, psychopharmacological and behavioral studies have revealed its influence on the switch (Zakay, Block, Pastor, & Artieda, 1996). Once the stimulus terminates, the switch opens, halting pulse accumulation. With reinforcement, the representation of the pulses in the accumulator is transferred to 4) working memory and, eventually 5) reference or long-term memory. When a judgment about a particular duration must be made, individuals engage a 6) decision process in a comparator that uses a ratio comparison between the representation currently in working memory and a previously encoded representation pulled from reference memory (Allan, 1998; Church, 1984, 2003; Gibbon, Church, & Meck, 1984). Although not included in the original form of the model, motor preparatory responses must be engaged once a decision has been reached to enable the appropriate response. These basic components of SET are illustrated in figure 1.1 with additional modifications to show how components of this model can account for tasks that require individuals to directly reproduce an encoded duration via motor processes. In this case, the comparator may be bypassed, such that a representation currently in either working or reference memory is directly translated into a motor program that is executed at the response stage.

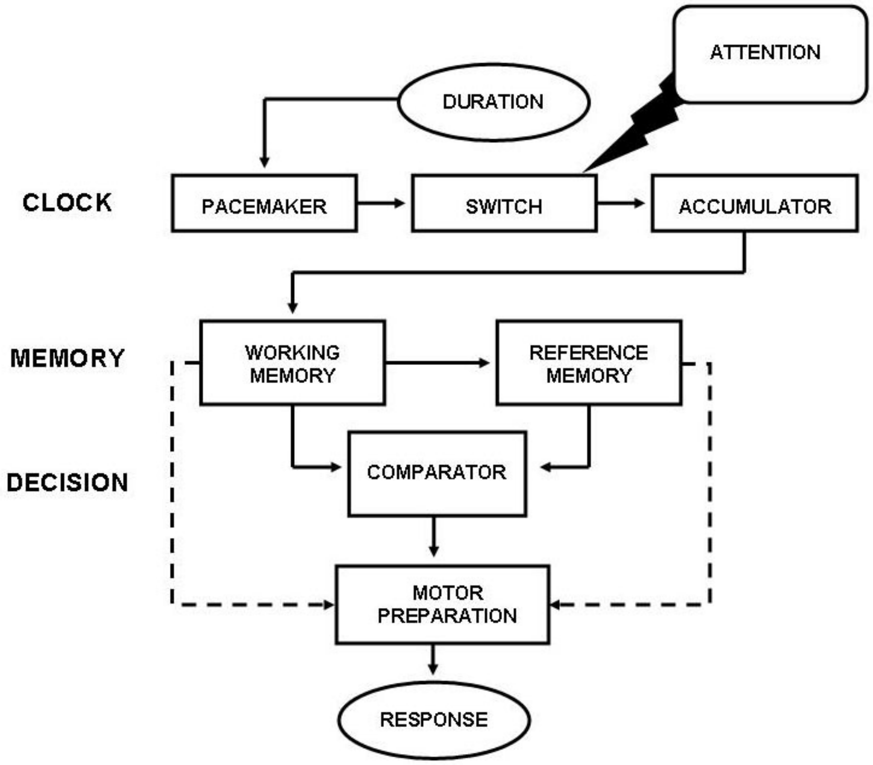


Figure 1.1. Modified information processing model of SET.

Variability in timing performance can arise from any part of the model. In its original instantiation, components of the SET pacemaker's function were proposed to lead to both Poisson (pulse rate) and scalar (drift rate across trials) sources of variance, while memory and decision threshold processes were modeled as scalar sources of variance (Gibbon et al., 1984). Scalar variance from memory and decision processes is thought to overwhelm all other sources of variance in the model (Allan, 1998; Gibbon et al., 1984; Grondin, 2001). Thus, SET predicts that the relationship between overall variability in timing performance and target duration follows Weber's law--standard deviation increases linearly with increasing target duration. Another way to express this prediction is that the coefficient of variation (CV), or standard deviation divided by the mean interval, will be constant across durations. Finally, this theory predicts mean accuracy--the average subjective estimate of a duration is close to its objective value (Wearden & Helfrich, 2003).

Scalar Timing in Humans

Early clock-counter models of timing argued that total performance variance on discrimination tasks in humans is dependent on a strictly Poisson process such that variance, not standard deviation, increases linearly with increasing target duration (Abel, 1972; Creelman, 1962; Wing & Kristofferson, 1973). However, over the last several decades scalar variability as predicted by SET has gained prominence in the timing literature due to its ability to explain timing performance in humans across a number of tasks developed as analogues to those used in the animal literature, including temporal generalization, temporal bisection, and the peak interval procedure (Rakitin et al., 1998; Wearden, 1991a; Wearden, Edwards, Fakhri, & Percival, 1998; Wearden, Rogers, & Thomas, 1997). Evidence of scalar timing has even been found for temporal generalization and roving bisection tasks where participants did not have to access representations stored in reference memory, because standard durations—those participants used as a guide for judging other durations throughout the task--were presented on every trial (Wearden & Bray, 2001). Recent investigations with tasks specially-developed for human research (e.g. temporal production, reproduction, and continuation tapping) also produced data that fit well with SET (Ivry & Hazeltine, 1995; Keele et al., 1985; Wearden & McShane, 1988). In addition, some evidence suggests that the same scalar clock operates for both motor and perceptual tasks (Ivry & Hazeltine, 1995; Keele et al., 1985). For example, Ivry & Hazeltine (1995) used slope analysis to separate timing performance variance into duration-dependent (slope) and duration independent (intercept) sources and compared the duration-dependent sources across motor and perceptual tasks; they determined that the data from their study, as well as those from a prior study by Alan Wing (1980), were best explained by functions conforming to Weber's law as opposed to those based on predictions associated with the operation of a stochastic, Poisson timing mechanism.

There are circumstances, however, unique to humans, which affect the validity of SET and have influenced the design choices for studies with human versus animal participants. While human studies focus on durations in the range of milliseconds to seconds, animal studies typically involve longer durations (several seconds to minutes); one justification for this difference is to prevent humans from counting to judge duration length. Counting involves subdividing a given duration into smaller components that are timed with less variability than the overall value (Grondin, Meilleur-Wells, & Lachance, 1999; Grondin, Ouellet, & Roussel, 2004; Wearden, 1991a). It becomes an effective strategy starting with durations slightly longer than 1 second (Grondin et al., 2004) and leads to departures from scalar variability such that variance remains constant as durations increase (Grondin et al., 1999; Grondin et al., 2004; Hinton & Rao, 2004; Wearden, 1991a).

Despite evidence that SET is useful for explaining human timing in the absence of counting, there are challenges to the notion of a unitary scalar clock for timing across milliseconds and seconds in perceptual and motor tasks. Behavioral studies with humans typically investigate a few values within only the milliseconds or the seconds range, and task and timescale are often confounded--motor tasks are used to examine milliseconds timing, while perceptual tasks are used with longer durations (Allan, 1998; Gibbon, Malapani, Dale, & Gallistel, 1997). Also, studies that compare performance across timescales usually test a single duration in each (Droit-Volet, 2002; Lavoie & Grondin, 2004; Rammsayer, 1999; Rammsayer & Lima, 1991). To determine whether a unitary mechanism conforming to the properties of SET controls timing in motor and perceptual tasks across both milliseconds and seconds, it is not sufficient to test a few widely-spaced durations for each task. Instead, one must use a larger duration set spanning both timescales to search for nonlinearities and determine whether they indicate transitions between different timing mechanisms or some other critical feature of the internal clock, memory, or decision processes (Collyer, Broadbent, & Church, 1992; Crystal, 1997, 1999, 2001, 2003; Rammsayer, 1999).

Role of cognitive processes in short and long duration timing

Aside from performance changes associated with counting, researchers have proposed functional transitions at several points on the temporal scale. Yet, there is little consensus about where they occur. For example, Michon (1985) argued for a transition around 500 ms between a system that processes information about time in an automatic, perceptual fashion (< 500 ms) and one that is cognitive in nature (> 500 ms). Lavoie & Grondin (2004) proposed a critical transition in the region of 2 seconds, which marks the upper bound of the “psychological present,” which is the period of time in which successive stimuli can be presented and still be perceived as part of the same group or overall stimulus. A transition point between motor and cognitive timing systems has also been proposed in the region of 1 second (Lewis & Miall, 2003a, 2003b, 2003c, 2006b).

Findings from some behavioral studies are consistent with the notion of a specialized role for executive processes, such as attention and working memory, in timing longer as opposed to shorter durations. Rammsayer and Lima (1991) found that increased cognitive load interfered with processing of durations ranging from 1 to 2 seconds but not 50 to 98 ms in length. Dual-task studies have shown interference effects for durations of about 2 to 5 seconds when individuals were asked to time while performing a concurrent task, such as mental arithmetic, visual search, mental rotation, or maintenance of a memory set (Brown, 1997; Fortin, 2003; Fortin & Breton, 1995; Fortin & Rousseau, 1998). However, other studies have shown that executive functions may have a similar effect on timing of both short and long durations. Rammsayer and Ulrich (2005) revealed similar interference effects of mental arithmetic for 100 ms and 1000 ms standards. Likewise, Grondin and Rammsayer (2003) and Macar and colleagues (1994) manipulated the influence of controlled attention on temporal discrimination and found that estimates of perceived duration were similarly affected for both milliseconds and seconds durations.

Pharmacological studies, however, have shown that agents known to specifically interfere with working memory processing also selectively interfere with seconds but not milliseconds timing (Rammsayer, 2006); these agents include the dopamine antagonist, remoxipride, (Rammsayer, 1997), benzodiazepines (Rammsayer, 1992, 1999), and N-methyl-D-Aspartate (NMDA) receptor antagonists (Rammsayer, 2006). Conflicting results from the behavioral and pharmacological literature leave the role of executive processes for milliseconds and seconds timing somewhat unclear. However, evidence that manipulation of attention similarly affects these durations suggests that the attentionally-mediated SET model may operate across both duration ranges.

Neural substrates for short and long duration timing

Evidence for a separation between neural structures responsible for millisecond versus second timing came from studies of Parkinson's disease and cerebellar stroke patients whose timing deficits suggested specialized roles for the cerebellum and the basal ganglia in timing milliseconds versus seconds, respectively (Gibbon et al., 1997; Ivry, 1996). However, recent patient studies have muddied this dissociation. Cerebellar patients have shown impairments for both motor and perceptual timing on the order of milliseconds (Casini & Ivry, 1999; Franz, Ivry, & Helmuth, 1996; Ivry & Keele, 1989; Mangels, Ivry, & Shimizu, 1998; Nichelli, Alway, & Grafman, 1996) and perceptual timing on the order of seconds (Malapani, Dubois, Rancurel, & Gibbon, 1998; Mangels et al., 1998; Nichelli et al., 1996). Though some studies indicate that Parkinson's patients are not deficient at motor and perceptual timing on the order of milliseconds (Aparicio, Diedrichsen, & Ivry, 2005; Ivry & Keele, 1989), more recent studies suggest they have motor and perceptual timing deficits for both seconds-length (Pastor & Artieda, 1996; Smith, Harper, Gittings, & Abernethy, 2007) and milliseconds-length durations (Artieda, Pastor, Lacruz, & Obeso, 1992; Harrington, Haaland, & Hermanowitz, 1998; Pastor & Artieda, 1996; Thomas H. Rammsayer & Classen, 1997). Contemporary work proposes that the cerebellum and basal ganglia play specialized roles in a general timing network; the cerebellum times durations that have a salient event structure, while the basal ganglia serve as a threshold mechanism during the decision stage of temporal processing (Ivry & Spencer, 2004; Spencer & Ivry, 2005).

Lewis and Miall's (2003b; 2003c; 2006b) argument for a transition around 1 second between automatic, or "motor", and cognitively-mediated timing is largely based on a meta-analysis of neuroimaging studies of timing, as well as their own study, which revealed that different neural substrates are activated for timing above and below 1 second (Lewis & Miall, 2003b, 2003c). The meta-analysis showed that brain regions typically associated with milliseconds timing included motor control areas, such as left primary motor (M1) and primary somatosensory (S1) cortices, bilateral supplementary motor area (SMA), right superior temporal gyrus (STG), right lateral cerebellum and right premotor (PM) cortex, along with some hint of basal ganglia (BG) and thalamic involvement. Timing of durations longer than 1 second engaged regions associated with executive processes, such as bilateral dorsolateral prefrontal cortex (DLPFC) and right insular cortex, as well as other areas, including bilateral intraparietal sulcus (IPS), bilateral PM cortices, left lateral cerebellum, and bilateral SMA (Lewis & Miall, 2003b). Again, there was some indication of BG activation for timing in this duration range, but neither the BG nor the cerebellum demonstrated specificity for either timescale. Other characteristics of the tasks used in these studies may have influenced the mechanisms engaged for timing. Indeed, Lewis and Miall (2003b; 2003c; 2006b) argue that two other factors (continuous versus discrete measurement, and whether temporal response requires translation of the standard into movement) affect whether mechanisms engaged for timing are reliant on more automatic or attentionally-mediated processes. Given the modified version of the SET model introduced in figure 1.1, this latter difference may reflect task-differences in either engaging or bypassing decision processes.

Recent neuroimaging studies investigating timing of durations shorter and longer than 1 second have led to more questions regarding the regions that subserve timing for these different scales. In a study where individuals discriminated standard intervals of 450 ms and 1300 ms, the preSMA, ACC, and right caudate were commonly activated for both standards but also showed greater activity in the 1300 ms condition when compared with the 450 ms condition. This study did not examine regions of greater activity for the shorter standard, but it does implicate a role for the basal ganglia across milliseconds and seconds timing. In a similar vein, Jahanshahi and colleagues (2006) used positron emission tomography (PET) to directly compare activations for short (500 ms) and long (2000 ms) standards during temporal reproduction. Areas of greater activation for the long standard included right cerebellum and right putamen; activation for the short standard was in the left caudate and a slightly more inferior region of the right cerebellum. Areas commonly activated by both durations included the substantia nigra and the left lateral PM cortex, suggesting that the basal ganglia play an important role in timing regardless of the timescale. However, evidence for dissociable neural regions for timing milliseconds versus seconds comes from a repetitive transcranial magnetic stimulation (rTMS) study (Koch et al., 2007) which showed that lesions of the cerebellum disrupted reproduction of milliseconds but not seconds durations; right DLPFC lesions showed the opposite effect.

Nonlinearities in timing

Nonlinearities in timing behaviors have been observed for both animals and humans. Gibbon and colleagues (1997) reviewed a number of studies and found that 100 ms and 1500 ms marked changes in the coefficients of variation (CV). Specifically, CVs decreased up to 100 ms, stayed constant until 1500 ms and then increased again for longer durations. Some studies have found points of maximal sensitivity in the data which indicate that certain durations are timed with greater precision than their neighbors. Crystal (1999) found such points at 300 ms and 1200 ms when testing rats on a temporal discrimination task. Similar departures have been seen in studies using intervals of many seconds in length (Bizo, Chu, Sanabria, & Killeen, 2006; Crystal, 1997, 1999, 2001, 2003); in some cases, the CV changed as a U-shaped function with increasing standard durations (Bizo et al., 2006). Studies with human participants have also found evidence of regions of maximal sensitivity in the range of 300 to 800 ms (Drake &

Botte, 1993) and 250 to 500 ms (Fetterman & Killeen, 1990; Grondin, 1992), as well as at 272 ms, 450 ms (Collyer, Broadbent, & Church, 1994) and 500 ms (Friberg & Sundberg, 1995).

Timing Across Different Tasks

Temporal reproduction and discrimination epitomize the distinction between motor and perceptual timing. In reproduction, individuals encode a target duration and transform it into a motor program to produce the duration via movement. For discrimination, individuals merely compare representations of two or more temporal durations in memory and judge whether they differ. Few studies have directly assessed whether the same timing mechanism(s) operate across temporal tasks with different response demands; one such study found a correlation between motor and perceptual task variability using a standard duration of 400 ms (Keele et al., 1985). Ivry and Hazeltine (1995) used Weber slope analysis to determine whether discrimination and production of durations in the milliseconds range rely on a common timer; they found equivalent performance slopes for these tasks when they were modified to make cross-task constraints more parallel (e.g., both tasks involved performing a discrete event for the response), suggesting a common inter-task timer. However, in the above studies, production and discrimination were presented in paired blocks corresponding to a specific standard duration, and the production block always preceded the discrimination block in each pair (Ivry & Hazeltine, 1995). It is, therefore, possible that similarities in performance were due to participants using a strategy or representation developed in the production task to assist with discrimination. It is not clear that evidence for a common clock would persist in the absence of this order confound.

Another way to elucidate whether the same mechanism is invoked for timing across motor and perceptual tasks is to examine patient groups with damage to timing-specific brain regions and observe whether damage leads to pervasive deficits on motor and perceptual tasks. Ivry and Keele (1989) found that cerebellar patients were impaired at motor and perceptual timing of millisecond durations. Other researchers have found only motor timing deficits in cerebellar stroke patients (Harrington, Lee, Boyd, Rapcsak, & Knight, 2004), but common deficits on motor and perceptual timing tasks in Parkinson’s patients (Harrington et al., 1998). Given these differing findings, it is not clear whether specific temporal tasks are reliant on different neural structures, and, possibly, different timers.

Lewis and Miall (2003b; 2003c) have proposed that tasks that require individuals to construct motor representations of temporal intervals in the service of recreating those intervals via movement may rely on a different timing system than discrimination tasks that require a comparison of two abstract temporal representations in memory (Lewis & Miall, 2003b, 2003c, 2006b). A recent meta-analysis of neuroimaging studies has implicated motor regions of cortex, such as left M1, left S1, bilateral SMA, right lateral cerebellum, right PM cortex, and right IPL for motor timing tasks, and executive processing regions, such as right DLPFC, left PM cortex, right IPL, left lateral cerebellum, right BG, and left PM cortex for perceptual timing tasks (Lewis & Miall, 2003b, 2003c). However, a review of the literature by another research group argues that the same brain regions are involved in timing for both motor and perceptual tasks (Macar et al., 2002), with a more detailed investigation highlighting involvement of the SMA for both (Coull, 2004; Macar, Anton, Bonnet, & Vidal, 2004; Macar, Coull, & Vidal, 2006).

Mounting evidence from behavioral, neuroimaging, and pharmacological studies suggests that a single scalar timer may not adequately explain timing behaviors across motor and perceptual tasks requiring judgments of durations spanning milliseconds and seconds. This dissertation takes the systematic approach of testing a large number of durations spanning the milliseconds and seconds ranges to examine the feasibility of a unitary scalar timer across these timescales for both motor and perceptual tasks. Of particular interest is what the interaction between task type and duration length will reveal about the properties of the mechanism(s) responsible for timing under these different circumstances.

THE CURRENT INVESTIGATION

Participants completed temporal discrimination and reproduction tasks across a set of durations spanning milliseconds and seconds. The first experiment investigated whether a common mechanism can account for performance across durations within a temporal reproduction task. In the second experiment, we extended our investigation to include a perceptual timing task. We also added more durations to the task, including endpoint pairs designed to counteract anchoring effects. The two tasks were performed by different participant groups in this study. The third experiment examined similarly structured temporal reproduction and discrimination tasks in a within-subjects design, eliminating certain procedural differences between the tasks presented in experiment 2. This study allowed us to investigate individual differences in timing performance.

If a single scalar mechanism controls timing of both milliseconds and seconds durations in task conditions where individuals time implicitly, without counting, Weber plots of performance variance against the square of the mean target durations should reveal a positive linear function with a constant slope across the durations tested. This means that the Weber fractions across the shortest and longest durations should be equivalent. Moreover, constant CVs should be observed across all tested durations within a task. The presence of equivalent Weber fractions for data obtained across different timing tasks would, likewise, suggest the operation of a common timer across these tasks (Ivry & Hazeltine, 1995). Given that the tasks used in these studies involve different response demands, this latter claim is predicated on the assumption that task differences associated with the motor preparation stage are not associated with changes in duration-dependent variance. Rather, variance arising from this stage is expected to be related to peripheral or implementation processes.

This exercise is vital to formulation of an accurate theory of timing which can enlighten researchers about how individuals use temporal representations to perform complex tasks, such as bimanual coordination. It is also important for helping develop appropriate diagnostic tools and treatments for specialized groups (e.g. Parkinson's patients; older adults) who exhibit deficits in timing behaviors crucial to motor and cognitive activities of daily living.

CHAPTER II

Reproduction: 5 Durations

Objective

This study tests whether a common, scalar mechanism is responsible for reproduction of temporal durations across several hundred milliseconds to just below two seconds in length. Participants also completed a simple reaction time (SRT) task so that we could investigate whether individual differences in SRT explain differences in temporal reproduction performance.

Method

Participants

Seventeen (7 females, Age = 19.35 ± 1.06 years) college-aged participants from the University of Michigan completed the experiment for course credit. All participants were right-handed, as determined by the Edinburgh Handedness Inventory (Oldfield, 1971) and reported no hearing problems. They gave informed consent as approved by the University of Michigan Institutional Review Board and completed a health history and activity level questionnaire.

Procedure

The temporal reproduction and SRT tasks were implemented using E-Prime software. Tones were presented binaurally via Koss UR-29 headphones.

Simple reaction time (SRT). Prior to each set of reproduction blocks, participants completed the SRT task. For this task, participants were seated at a computer and asked to focus on a black fixation cross in the center of the computer screen. On each trial, participants heard a 50 ms 1000 Hz tone and were asked to respond as quickly to the tone as possible with a right-index finger press on the space bar. The participant's reaction time was displayed to them after each trial. Any trials where SRT was greater than 800 ms or less than 100 ms were repeated at the end of the run. This procedure was adopted to eliminate trials where individuals were not paying attention or anticipated the tone instead of reacting to it.

Temporal reproduction. Participants reproduced five different standard durations (300 ms, 650 ms, 1000 ms, 1350 ms, and 1700 ms) over the course of the experiment. They completed a short set of practice trials with two standard durations not used in the actual experiment (475 ms and 1175 ms) to make sure that they were acclimated to the task. For each standard, participants completed 2 blocks of 5 runs, with 12 trials per run. One block of reproduction was completed for each of the standards before the second block of any duration was presented to participants. Within each block set, presentation order of the standard durations was randomized. Participants were seated at a computer and, on each trial, were asked to focus their eyes on a black fixation cross. At the start of each trial, they heard a pair of 50 ms 1000 Hz tones separated by an empty interval the length of the specified standard duration. After presentation of the standard and a variable delay of 400, 600 or 800 ms, the fixation cross turned green to cue participants to reproduce the standard with two right-index finger taps on the space bar of the keyboard. Figure 2.1 illustrates a single trial from the task. Participants were not told the value of any of the durations prior to completion of the study. Also, participants were instructed not to count or produce any other movements aside from those required for reproducing the standard interval during the task.

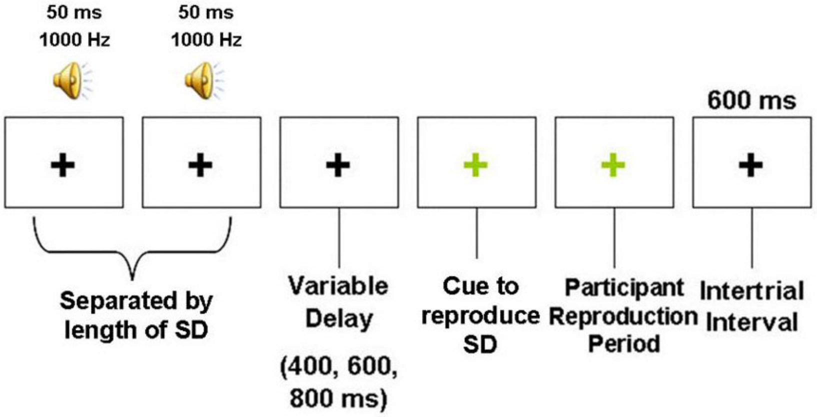


Figure 2.1. Schematic of the temporal reproduction task.
SD = Standard Duration

During the first run of each duration block, participants received visual feedback about their performance after every trial. The feedback showed a horizontal black bar representing the length of the standard duration and a horizontal red bar representing the length of the reproduced duration (see figure 2.2). This trial by trial feedback indicated whether the reproduction on that trial was shorter or longer than the standard. For the last four runs of each block, average feedback performance was given at the end of the run. The feedback screen was identical to that for the trial by trial feedback, except that the red bar represented the length of the average reproduced value over the run rather than the value from a single trial. The length of the black bar on the feedback screen was the same, regardless of the length of the standard duration represented. Therefore, changes in the length of the red bar represented proportional, rather than absolute changes in the length of participants' reproductions.

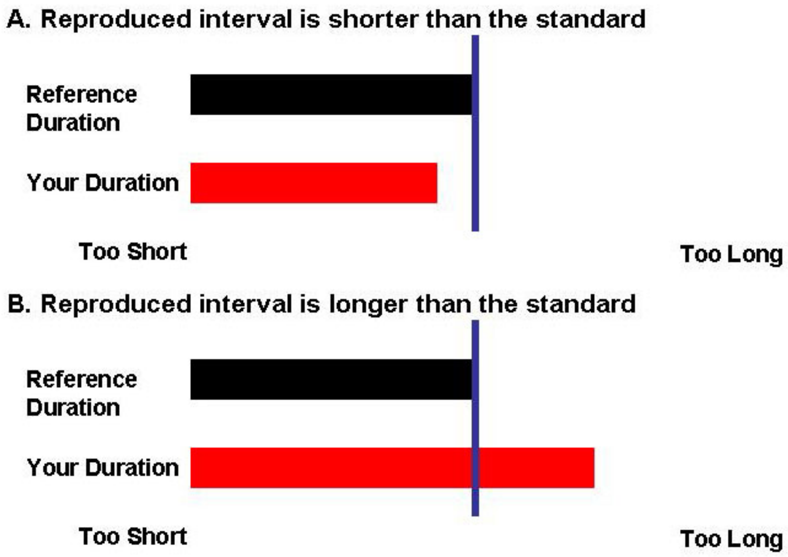


Figure 2.2. Feedback screens for temporal reproduction.
The black bar represents the reference, or standard duration and the red bar indicates the length of the participant's duration. The vertical line is the cutoff between a reproduction that was too short or too long. Part A shows feedback for a reproduction that was too short. Part B shows feedback for a reproduction that was too long.

Once they completed the study, participants filled out a final survey which assessed whether they used any particular strategies during the temporal reproduction task. The motivation for this assessment was to identify individuals who failed to comply with the instructions not to move or count. One individual reported using a counting strategy and was excluded from further analyses.

Data analysis

For the SRT data, trials where individuals responded prior to the tone or where their reaction times (RT) fell above 800 ms or below 100 ms were repeated. For each participant's data set, we used a continuous trimming procedure where we excluded trials falling 2.5 standard deviations above or below their mean RT.

Trials from the first run in each block of temporal reproduction were excluded from further analysis, as they were meant to serve as practice to help individuals develop a stable representation of the standard duration being presented in that block. For the test runs, trials where individuals responded prior to the cue were excluded from analysis. Two variables were of interest for the remaining trials: reproduced duration and latency to first tap (the time it took individuals to make their first reproduction tap). A trimming procedure was used on these variables to exclude trials where values fell 2.5 standard deviations above or below the individual's overall mean. From the remaining data, we assessed a number of additional performance measures, including accuracy index (ratio of reproduced duration to standard duration), coefficient of variation (CV), or the standard deviation of reproductions divided by the mean reproduced value. The CV is considered a measure of temporal sensitivity, with lower values marking less noise or a better ability to discriminate or reproduce a particular duration with consistency (Gibbon et al., 1997). The accuracy index is a ratio score which allows one to examine whether individuals tend to under-reproduce or over-reproduce the standards. The closer the ratio is to one, the more accurate the reproduction. Values greater than 1 indicate reproductions that are longer than the standard and values less than 1 indicate reproductions that are shorter (Baudouin, Vanneste, Pouthas, & Isingrini, 2006). We examined latency to first tap to determine whether it changed with changes in standard duration length. Modulation of this measure due to changing length of the standards would indicate that access time to memory representations increases with increased standard length or that individuals use some form of rehearsal strategy during the delay leading up to the first tap.

In addition, Weber slope analysis (Ivry & Hazeltine, 1995; Spencer & Zelaznik, 2003) was used as a tool to distinguish duration-dependent, or “clock” variance from variance due to peripheral factors, such as motor variability. The generalized form of Weber’s law, which plots variance on the ordinate and reproduced durations squared on the abscissa has been used for this purpose in previous studies. The slope of the function represents duration-dependent variance while the intercept represents peripheral variance. To determine whether clock variance for short and long durations in this task was equivalent, we plotted each individual’s data according to the generalized form of Weber’s law and then examined where individuals showed the most pronounced break in their function. The latter point was determined by fitting the best independent bi-linear function to each participant’s Weber function. For each portion of the bilinear fit, we then calculated the Weber fraction (the square root of the linear slope), which serves as an estimate of the rate of change in variance with changes in duration. We compared the Weber fractions across the breakpoint to determine whether the mechanisms used for timing across the breaks are the same or different.

Repeated measures (RM) analysis of variance (ANOVA) tests with standard duration (5) and run (8) as within-subjects variables were used to examine CV, accuracy index and tap latency performance. The Huynh-Feldt correction for degrees of freedom was used in cases where the Huynh-Feldt epsilon was less than .75, indicating that the sphericity assumption was violated. In cases where main effects of duration or run were found, we assessed whether linear or quadratic trends explained the data. Main effects were also explored using post-hoc t-tests. All post-hoc tests and correlations were assessed with Bonferroni-corrected $\alpha = .05$, two-tailed unless otherwise noted.

Results

SRT

Two sessions of SRT were completed for this study. A paired samples t-test revealed no effect of session on RT performance. Thus, the data reported here are the average scores collapsed across session. Mean RT across all participants was 219.95 (± 29.46) ms.

Temporal reproduction

Accuracy index. A RM ANOVA revealed no significant interaction, but main effects of run, $F(7, 105) = 3.00$, $p < .01$ and duration, $F(2.88, 43.16) = 5.49$, $p < .01$. No significant linear or quadratic trends were found for the run effect. Tests of within-subjects contrasts on duration revealed a significant linear trend, $F(1, 15) = 7.31$, $p < .05$, due to a general decrease in the accuracy index with increasing standard duration length. Figure 2.3 shows the accuracy index for each duration collapsed across runs and participants.

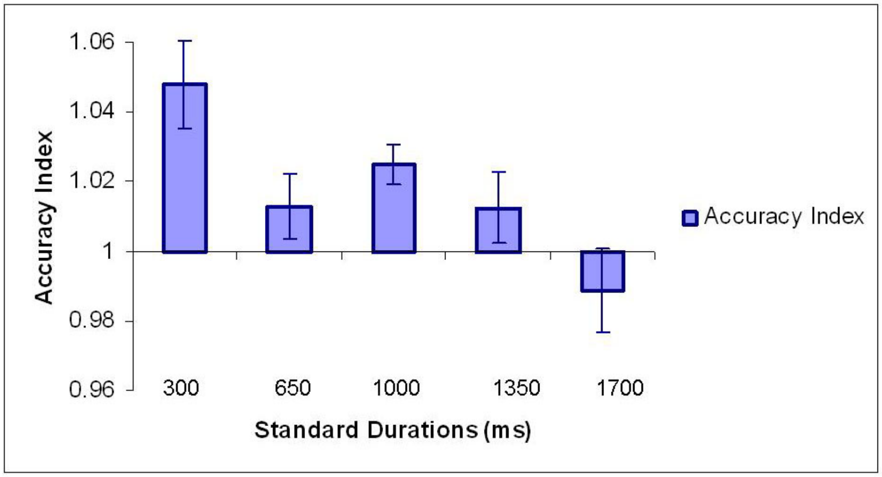


Figure 2.3. Mean Accuracy Index for each standard duration.
The abscissa crosses the ordinate at the point which represents perfect accuracy. Values greater than 1 indicate over-reproductions, while values less than 1 indicate under-reproductions. Error bars are mean ± 1 standard error.

As can be seen in the figure, participants tended to overshoot their reproductions for the shortest durations and undershoot their reproductions for the longest duration. However, the range of the values on the ordinate is greatly compressed, indicating that, on the whole, reproductions were fairly accurate.

Sensitivity. A RM ANOVA on CV revealed no run by duration interaction, but main effects of both duration, F (2.56, 38.40) = 3.14, $p < .05$, and run, F(5.02, 75.23) = 2.46, $p < .05$. Neither a linear nor a quadratic trend was found for the run effect. However, for duration, we found a significant quadratic trend, F(1, 15) = 17.99, $p < .01$, with the minimum value of the function, M = .08, found at the 1000 ms standard. Figure 2.4 shows the mean CV for each duration collapsed across participants.

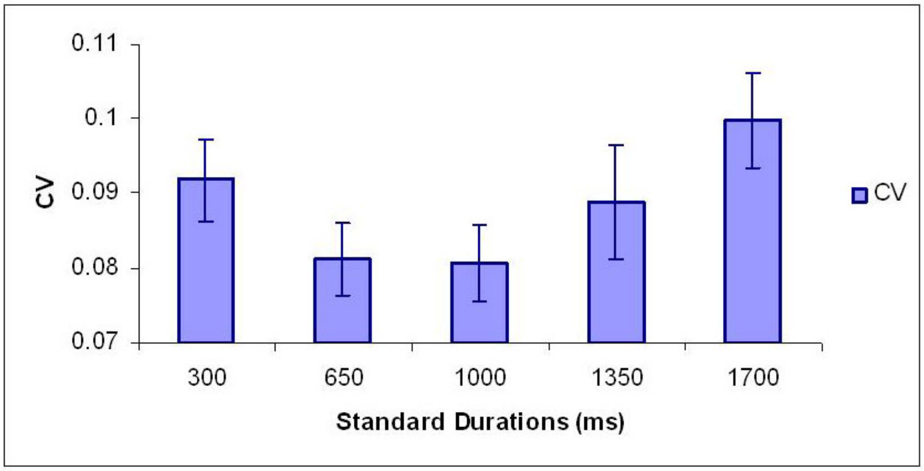


Figure 2.4. Mean CV for each standard.
Error bars represent the mean ± 1 standard error.

Correlations between CV values were conducted to examine the relationship across CV scores. If a single timer operates across all durations, significant relationships should be seen between all CV values. This was not observed; rather significant correlations were only found between 650 ms and 1000 ms, r = .662, and 1350 ms and 1700 ms, r = .885, with corrected α = .05. This pattern suggests different timing mechanisms may be engaged for shorter versus longer durations.

We also examined the Weber functions for each participant. Figure 2.5 illustrates the Weber plot averaged across all individuals.

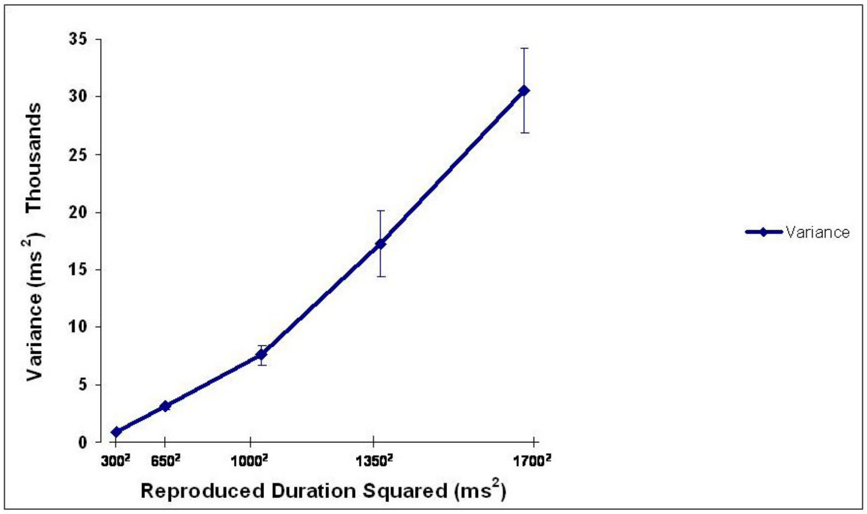


Figure 2.5. Weber plot averaged across all participants.
Error bars represent the mean variance ± 1 standard error.

Independent bilinear functions fit to each person's Weber function were used to determine each individual's ideal breakpoint. Over all participants, the mean breakpoint was 956.25 ms. This parallels the finding of the minimum CV at 1000 ms. Figure 2.6 shows the distribution of breakpoints across all individuals in this study.

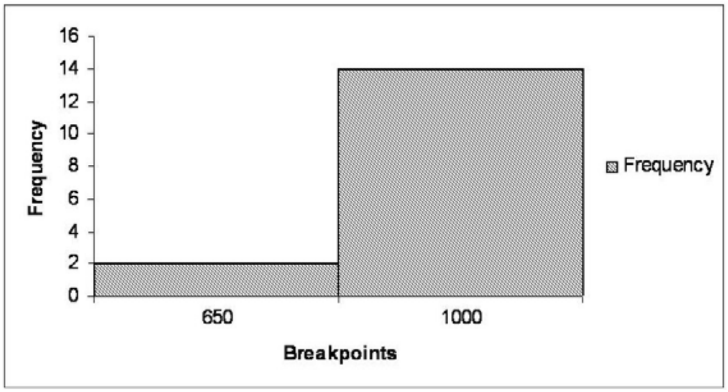


Figure 2.6. Breakpoint distribution across all participants.

A paired-samples t-test comparing the Weber fractions for the shortest and the longest durations across the ideal breakpoints revealed a significant difference, $t(16) = -2.93$, $p < .05$. This discrepancy in the Weber fractions as well as the main effect of duration on the CV values argues against the workings of a single scalar mechanism across durations within this task.

Relationship between sensitivity and SRT. After correction for multiple comparisons, correlations investigating the relationship between SRT and CV scores revealed a significant relationship only between SRT and the 1000 ms CV, r = .738, p < .05, Bonferroni-corrected. Correlations were also assessed between SRT and the Weber fractions on either side of the ideal breakpoint. A trend towards a significant relationship was found between SRT and the Weber fraction determined using the “short” duration portion of the ideal bilinear function, r = .550, p =.054.

Latency to first tap. A RM ANOVA on the latency to the first reproduction tap showed no run x duration interaction but main effects of both run, F(1.65, 24.82) = 6.30, p < .01, and duration, F(1.36, 20.42) = 31.56, p < .001. For the run effect, there was a significant linear trend, F(1, 15) = 7.23, p < .05, indicating a tendency for tap latency to decrease over time, with practice. Significant linear, F(1, 15) = 37.65, p < .001 and quadratic, F(1, 15) = 4.67, p < .05, contrasts explained the duration data. As seen in figure 2.7, tap latency increased as the duration to be timed increased in value. Tap latency was not equivalent to the standard duration length in most cases, however, it is important to note that there was a delay prior to the cue to tap which could have influenced latency values.

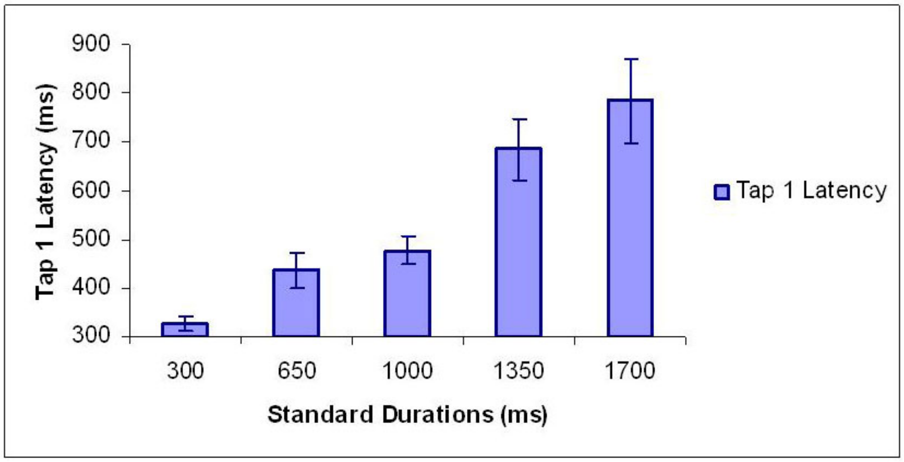


Figure 2.7. Latency to first tap averaged across runs and participants. Error bars represent the mean ± 1 standard error.

Discussion

The purpose of this study was to determine whether the scalar property holds across a number of durations spanning the milliseconds and seconds ranges. We found that, though individuals tended to over-reproduce short durations and under-reproduce long durations, they were generally accurate in their reproductions. Findings of non-constant CVs as well as different Weber fractions across the ideal breakpoint in the Weber function argue against a single scalar timer operating across durations in this task. The fact that the mean ideal breakpoint was close to 1 second in this study supports the argument by Lewis and Miall (2003b; 2003c; 2006b) that this duration marks a transition between timing systems. Moreover, the finding of correlations between the 650 ms and 1000 ms CV values suggests that the processes responsible for timing these two durations are highly related. The same is true of the 1350 and 1700 ms durations. However, we did not find significant correlations between any of the short and long durations. Again, this points to different mechanisms of timing for durations less than versus greater than 1 second. The significant correlation between SRT and the short Weber fraction implicates basic sensorimotor processes in timing durations on the order of milliseconds. However, the more fine-grained investigation of correlations between SRT and CV scores revealed that the only significant relationship existed between SRT and the CV for the 1000 ms duration. If the sensorimotor system is engaged when timing in the milliseconds range, one would expect correlations between SRT and the 300 ms and 650 ms CVs as well. Thus, it may be that the 1000 ms duration is unique and is timed with much greater sensitivity than the neighboring durations used in this study.

The proposal that the 1000 ms duration marks a point of maximal sensitivity is more consistent with an oscillator-based timer, rather than the interval timer proposed in the information processing model of scalar timing theory. This is in line with timing theories which postulate the involvement of one or more oscillators, which emit periodic signals and have different mean periods, for timing (Church & Broadbent, 1990). Points of maximal sensitivity can be found for durations whose values match the mean periods of the oscillators (Crystal, 1999, 2001, 2003). Several of the timing theories that hinge on the operation of internal oscillators still predict scalar variability across most durations; nonlinearities simply appear at durations that match or are multiplicative values of the periods of the component oscillators (Church & Broadbent, 1990; Matell & Meck, 2004).

However, it is also possible that the pattern of decreased sensitivity for the two most extreme durations could be explained by an anchor effect. For example, participants may have used a different strategy for reproducing the shortest and the longest standards than for reproducing the intermediate standards, especially in the second block set. Instead of trying to create an accurate reproduction for the shortest standard they may have reproduced a value they categorically deemed short. Likewise, they may have used a categorical process to determine the length of reproductions for the very longest duration in the set. Intermediate values would have had to be timed with a different, more accurate strategy, since these values would not lend as easily to a simple “short” versus “long” categorization. This anchor strategy could explain the quadratic trend in sensitivity across durations, marked by greater CVs for the extreme durations and the greatest sensitivity for the 1000 ms duration. Thus, for later versions of reproduction, we included additional durations, including two at the extreme points of the set which were objectively close to the endpoint durations used in this study to force participants to actively encode each standard rather than using a categorical strategy to create reproductions. Given findings from perceptual studies in which individuals tend to show greater sensitivity when asked to make judgments between hard to discriminate durations (Ferrara, Lejeune, & Wearden, 1997; Penney, Allan, Meck, & Gibbon, 1998), it seems reasonable that including additional values at the extreme points of our reproduction task may encourage participants to form more accurate representations of the durations at these extremes in order to make accurate reproductions. An additional standard was added to the intermediate set of durations in an attempt to more clearly determine the value of the possible ideal breakpoint in these later studies. Additionally, each standard was only presented once to prevent individuals from using information about the other standards for their reproductions.

A further finding from the current study was that the latency to make the first reproduction tap increased as the standard duration to be timed increased. It is particularly interesting that this pattern was seen despite the fact that individuals were given many trials over which to memorize each standard duration and that standards were presented in a blocked, as opposed to interleaved fashion. It is possible that individuals rehearsed the standard on every trial before reproducing it. However, the fact that the latency values were not always equivalent to the standard duration values, especially for longer durations, calls this into question. Another possibility is that the processes involved in accessing the memory representation of a standard duration in working memory and translating it into a motor program with the appropriate temporal properties are time sensitive. In particular, motor preparatory processes may take longer when having to reproduce longer durations. Accessing a memory representation of a longer standard may also take more time, due to the greater spread in the distribution of previous examples of these durations in memory. One way to distinguish whether these latency increases were associated with memory access or translation into a motor program is to compare tap 1 latency for temporal reproduction to response latency in a task that requires judgments about varying durations but no translation of standard durations into a motor program for response. The next two studies incorporate a task with these properties, namely, temporal discrimination. If increases in tap 1 latency are due to the translation of durations into motor representations, then we should not see latency increases with increasing standard duration lengths in the discrimination task. However, if these latency increases are due to memory processes, then latency increases should be found in this task.

CHAPTER III:

Between Subjects Study

Objective

This study compared timing performance for temporal reproduction and discrimination in a parallel task format across several hundred milliseconds to just under two seconds in length to determine whether a common scalar clock controls timing across these durations for both perceptual and motor tasks. For temporal reproduction, individuals reproduce a given duration with two finger taps. This requires that individuals transform their representation of the standard duration into a motor program. However, temporal discrimination does not make the same demands. Rather, individuals merely have to compare their memory representation of the standard to their memory representation of the given comparison duration and then make a judgment about their relative lengths. If a single clock is responsible for timing across durations, we should see similar patterns of sensitivity (as measured by CV and Weber fractions) across all durations; a single clock across tasks would predict similar CVs and Weber fractions for temporal reproduction and discrimination. In this study we also asked participants to complete a simple reaction time task to investigate whether individual differences on this simple sensorimotor processing measure explain differences in performance on temporal reproduction and discrimination.

Method

Participants

Twenty-nine (16 females, Age = 20.41 ± 1.72 years) college-aged participants completed the temporal reproduction task. Four of these individuals were excluded from analysis because they reported using either a counting or movement strategy to remember standard durations during the task. Nine (7 females, Age = 22.78 ± 3.63 years) college-aged participants completed temporal discrimination. Data from eight of these nine participants are also included in the within-subjects study reported in experiment 3. For the current study, data were taken from individuals who completed temporal discrimination prior to temporal reproduction in the later study. All participants were right-handed, as determined by the Edinburgh Handedness Inventory (Oldfield, 1971) and reported no hearing problems. The individuals who completed the reproduction task received course credit for their participation in the study. Individuals in the discrimination task were paid for their participation. All participants gave informed consent as approved by the University of Michigan Institutional Review Board and completed a health history and activity level questionnaire.

Procedure

The timing and SRT tasks were implemented using E-Prime software. Tones were presented binaurally via Koss UR-29 headphones.

Simple reaction time (SRT). Structure of the SRT task was identical to that reported in experiment 1. The temporal reproduction group completed two SRT blocks, one at the beginning of the experiment and one after the first four blocks of reproduction. The discrimination group, however, completed an SRT block prior to each block of the discrimination task, resulting in eight total blocks of SRT.

Temporal reproduction. Participants completed temporal reproduction with eight standard durations including 270, 300, 650, 1000, 1175, 1350, 1700, and 1870 ms. The most extreme standard durations were included to make the very shortest and longest durations harder to discriminate. These new endpoints were created by subtracting (for the shortest duration in the set) or adding (for the longest duration of the set) 10% of the value of the previous endpoint duration. The goal was to prevent an anchor effect on measures of sensitivity due to individuals using a different strategy (e.g. categorization) for judging the extreme durations as opposed to the intermediate durations. Each standard was presented within a single block of 7 runs of 12 trials each. As with the first reproduction task, the first run served as practice to familiarize the participants with the relevant standard duration and was excluded from further analysis. This also helped work against possible memory mixing between different durations. However, unlike the previous study, participants were only asked to complete temporal reproductions for a specified duration within a single block; duration blocks were never repeated. All of the blocks were completed within a single 3 hour testing session. Individuals received feedback at the end of each trial for the first run of each block. For the final 6 runs, feedback was given at the end of the run. The feedback screens were identical to those used for the reproduction study described in experiment 1 (See figure 2.2). Again, participants were instructed not to count during the task or move other than when reproducing the durations. At the completion of each duration block, participants were asked to stand and stretch to combat fatigue. Participants were given a longer break after completion of the first 4 duration blocks; they completed a block of the SRT task during this break. Trial structure was identical to that reported in experiment 1 (see figure 2.1).

Temporal discrimination. For this task, participants were asked to make a judgment about whether a comparison duration was shorter or longer than a given standard duration, typical of a two-alternative forced choice procedure (2AFC). Figure 3.1 shows the structure of each trial on this task.

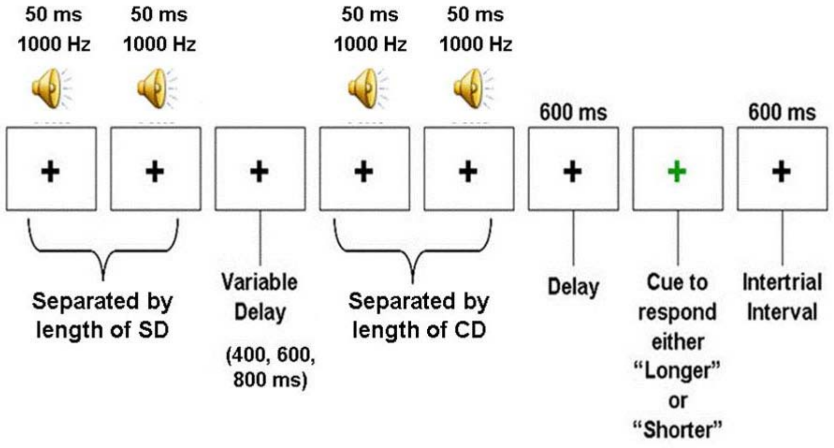


Figure 3.1. Schematic of the temporal discrimination task.
SD = Standard Duration, CD = Comparison Duration

At the start of the task, participants focused on a fixation cross in the center of a computer screen. They then heard two 50 ms 1000 Hz tones separated by the standard duration. After a variable delay of 400, 600, or 800 ms, they heard another pair of tones separated by the relevant comparison duration. After 600 ms, the fixation turned green, cueing the participant to respond either “shorter” or “longer” with a button press on the keyboard. The overall task design was derived from the psychophysical technique known as the method of constant stimuli, where a set number of comparison values are repeatedly presented in conjunction with a specific standard (Grondin & Rammsayer, 2003; Morgan, Watamaniuk, & McKee, 2000). Six comparison durations were presented for each standard, including three that were shorter and three that were longer than the standard. The comparison durations were values that were ± 40%, ± 15%, and ± 6% of the length of the standard durations. These percentages were based on reports of similar comparison values used in previous studies (Grondin, 2005; Grondin et al., 2004; Grondin, Roussel, Gamache, Roy, & Ouellet, 2005) and on pilot data we collected. Cumulative responses to the comparison durations were used to construct psychometric functions where probability of responding “long” was plotted on the ordinate and comparison duration values were plotted on the abscissa. Participants in this task were given the same 8 standard durations used in the reproduction task. For each standard, participants made judgments about 3 comparison durations that were shorter and 3 that were longer than the standard. Multiple repetitions of each comparison were necessary to construct stable 6 point psychometric functions. Participants completed 21 runs of 18 trials each; the first run served as practice and was excluded from analysis. As with the reproduction task, feedback was given at the end of each trial during the practice run and at the end of each run for the remaining 20 runs. Figure 3.2 illustrates the feedback given for each circumstance.

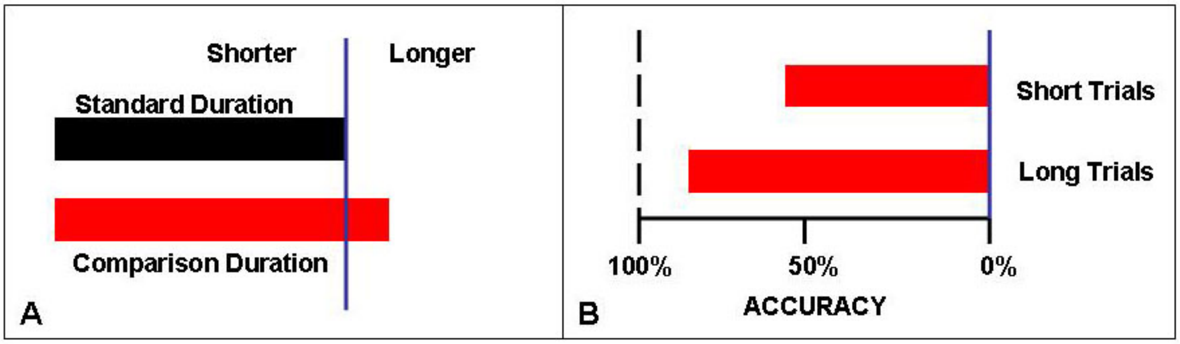


Figure 3.2. Examples of feedback used for the discrimination task.
Panel A shows the type of feedback individuals received at the end of each trial during the practice run. The given example shows a comparison duration that was longer than the standard. Panel B shows the type of feedback given at the end of one of the test runs. Participants were given their accuracy for trials where the comparison was shorter than the standard and for trials where the comparison was longer than the standard.

Each comparison duration was presented 3 times per run, totaling 60 repetitions across all 20 test runs. Due to the large number of trials needed (360) for each standard duration, this experiment was divided into 4 different testing sessions which were completed on different days; two duration blocks were completed each day with a SRT task preceding each block. Order of blocks was pseudo-randomized so that participants were never presented with adjacent durations in the list (e.g. they would never receive 270 ms and 300 ms as the standards on a single day). This format was adopted to prevent noise associated with presenting participants with standard durations whose memory distributions overlapped. Between each block, participants were asked to take at least a five minute break to prevent fatigue.

Data analysis

In the SRT task, trials were excluded in the same fashion as in the first reproduction experiment. Once again, RT values which fell above 800 ms or below 100 ms were excluded; we then excluded RTs which fell 2.5 standard deviations above or below the participant's mean.

For temporal reproduction we first excluded trials where individuals responded before they were given the response cue, and then examined reproduced duration and latency to first tap. For the reproduced duration data, we excluded trials where the reproduced value fell 2.5 standard deviations above or below the individual's mean across runs. The same performance measures as reported in the first reproduction experiment were then assessed, including accuracy index, CV, and Weber fractions (Ivry & Hazeltine, 1995). For latency to first tap, we determined the median value for each run and then calculated an average across these values. We used the median for this task in order to mirror the procedures used to calculate the latency measure for temporal discrimination. Individuals were quite variable in their latencies during the discrimination task and we felt that use of the median as a measure of central tendency was a more appropriate description of the data than calculation of means after trimming. For the examination of Weber fractions, we determined the ideal breakpoints by fitting the best independent bi-linear function to each participant's Weber function. We then calculated the Weber fraction on either side of the break and compared these values to determine whether the mechanisms used for timing across the breaks are the same. Planned comparisons were conducted to compare the minimum CV point against the CV scores for the two most extreme standard durations.

In temporal discrimination, performance measures were calculated across the last 20 runs of the task. The two critical dependent variables included the point of subjective equality (PSE) or threshold (μ) and the standard deviation (σ). PSE is the duration which individuals equivalently judge as either shorter or longer than the standard duration. The standard deviation is derived from the inverse of the slope of the psychometric function at the PSE. The probit transform, which assumes a cumulative normal distribution for the form of the psychometric function, was used to determine the threshold and slope parameters. For this method, we transformed the probabilities obtained at each comparison duration into Z-scores using the inverse cumulative normal distribution. We then performed a linear regression across these points and determined the slope (c_1) and intercept (c_0) of the function. The threshold was derived using the equation, $\mu = -\frac{c_0}{c_1}$, while the standard deviation was derived as follows, $\sigma = \frac{1}{c_1}$ (Treutwein, 1995). The resulting PSE and standard deviation values were used to calculate variance and PSE squared which were used to construct Weber functions for each participant. As with the reproduction task, variance was plotted on the ordinate and PSE squared was included on the abscissa. Accuracy index and CV scores were calculated using the PSE and standard deviation values derived from the psychometric functions. Latency to response was also investigated to see if there was a relationship between this variable and the length of the standard duration. For discrimination, latency values varied widely, therefore, in order to avoid using a measure of central tendency sensitive to extreme scores, we obtained the median instead of the mean per run. We then calculated the mean of the median scores across runs within each task. Because the two tasks involved different numbers of runs, we were not able to assess the effect of run for tap latency when conducting between-task comparisons. We were unable to examine run effects for the other dependent variables for temporal discrimination, as well, since these measures had to be calculated from the cumulative data across all trials.

Repeated measures ANOVAs with duration (8) as a within-subjects factor and task (2) as a between-subjects factor were used to assess performance as measured by CV, accuracy index, and tap latency scores. Main effects of duration were examined with linear and quadratic contrasts. In cases where the Huynh-Feldt epsilon was less than .75, we used the Huynh-Feldt correction for degrees of freedom to combat sphericity violations. When significant task x duration interactions were found, we also conducted follow-up RM ANOVAS within each task to clarify the pattern of simple effects.

Results

Simple RT

A paired samples t-test revealed no effect of session (2) on RT performance for individuals who completed the reproduction task. Mean RT for this task was 206.64 (± 17.84) ms. Individuals who completed the temporal discrimination task performed several more sessions of the SRT task. Mean RT for discrimination was 189.66 (± 22.65) ms. A RM ANOVA using session (8) as a within-subjects factor revealed a main effect of session, $F(4.42, 35.38) = 3.43$, $p < .05$. A significant linear trend fit the data, $F(1, 8) = 5.68$, $p < .05$. This trend was due to a practice effect, with individuals showing an improvement in SRT over time. To confirm that individuals who completed the tasks did not differ in their RT performance, we conducted an independent samples t-test comparing the total SRT from the reproduction study to the mean SRT across day 1 ($M = 200.34 \pm 29.56$) for individuals from the discrimination study (both involved two sessions of SRT). There was no task difference for RT performance.

Accuracy Index

A RM ANOVA on the accuracy index revealed no duration x task interaction and no main effect of task, but a significant main effect of duration, $F(7, 224) = 3.47$, $p < .01$. A linear contrast explained the duration effect, $F(1, 32) = 10.42$, $p < .01$. Figure 3.3 indicates that while individuals tended to over-reproduce and over-estimate durations less than 1175 ms, they showed the opposite pattern for longer durations. However, it is important to note that the accuracy range is, again, rather restricted, indicating high reproduction accuracy, overall. Additionally, individuals reproduced and discriminated the 650 ms and 1175 ms duration with the greatest accuracy.

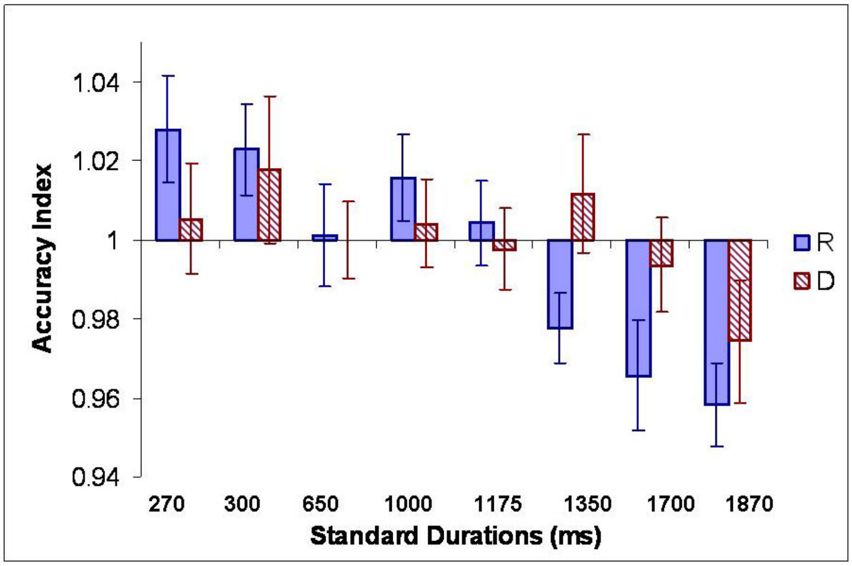


Figure 3.3. Mean accuracy index for each task.
Temporal reproduction (R) is shown in blue, while discrimination (D) is represented with the red dashed bars. The abscissa crosses the ordinate at 1, the point which represents perfect accuracy. Values greater than 1 indicate over-reproductions, while values less than 1 indicate under-reproductions. Error bars are mean ± 1 standard error.

Sensitivity

CV: Between task comparisons. A RM ANOVA on CV with duration (8) as the within-subjects factor and task (2) as the between subjects factor led to a significant duration x task interaction, F(3.18, 101.79) = 5.72, p < .01 as well main effects of duration, F(3.18, 101.79) = 7.50, p < .001 and task, F(1, 32) = 37.63, p < .001. Significant quadratic, F(1, 32) = 10.79, p < .01 and linear, F(1, 32) = 16.67, p < .001, trends fit the data for the duration effect. As figure 3.4 indicates, individuals show less timing sensitivity in the discrimination task as compared to the reproduction task.

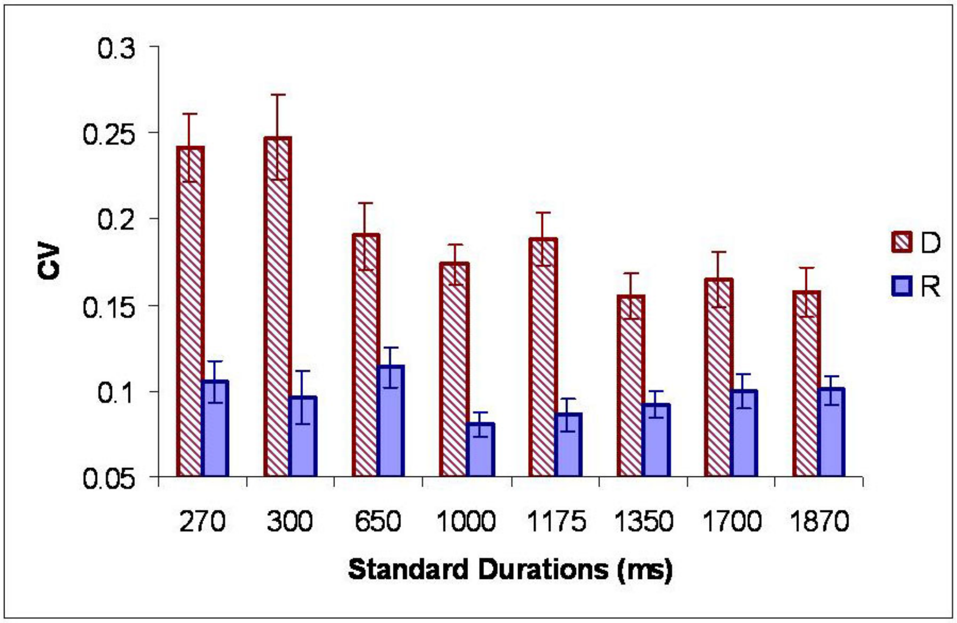


Figure 3.4. Mean CV across durations for temporal reproduction (R) and discrimination (D). Reproduction (R) data are shown in blue, while discrimination (D) is represented with the red dashed bars. Error bars represent the mean ± 1 standard error.

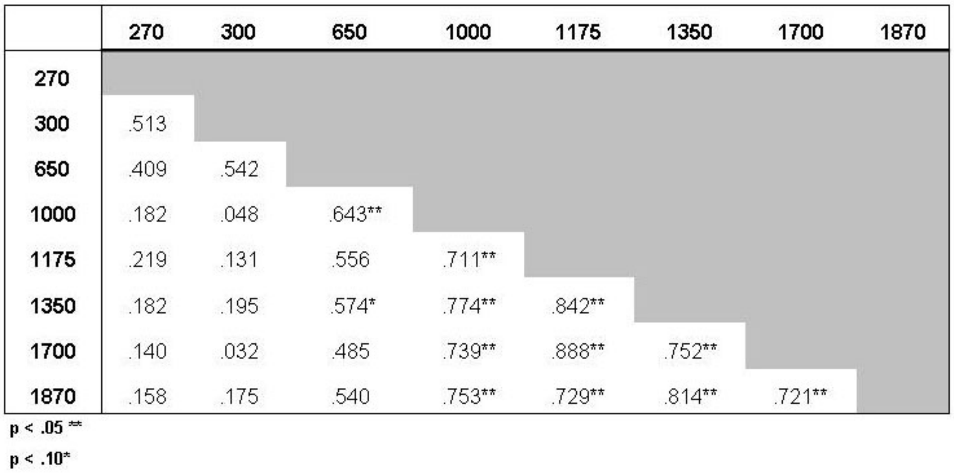
Given that there was no task difference in mean accuracy, the task effect on CV must be driven by larger standard deviation estimates for temporal discrimination as opposed to reproduction. Figure 3.4 also shows that while CVs steadily decrease across increasing standards for discrimination, they decrease and then increase for reproduction. Since we found a significant interaction, we explored simple effects.

CV Simple Effects: Temporal reproduction. A RM ANOVA on CV using duration (8) as a within-subjects factor revealed a main effect of duration, F(4.39, 105.33) = 3.52, p < .01. We also investigated whether there was a significant quadratic contrast for the duration effect, given the findings from the first reproduction study, and we conducted planned contrasts between the minimum point of the function and the two most extreme durations. The quadratic trend was a significant fit to the data, F(1, 24) = 7.44, p < .05. The minimum point of this function (M = .08) was found at the 1000 ms duration. One-tailed t-tests revealed significant differences between the 1000 ms duration and the 270 ms duration, t(24) = -3.07, p < .01, as well as the 1870 ms duration, t(24) = -3.64, p < .001.

CV Simple Effects: Temporal discrimination. A RM ANOVA revealed a main effect of duration, F(2.34, 18.71) = 3.52, p < .05, with a significant linear contrast fitting these data, F(1, 8) = 8.94, p < .05. We performed a post-hoc contrast comparing the CV scores for the most extreme standards and discovered a significant difference, t(8) = 2.87, p < .05. Though the pattern of CV values across standard durations is linear for this task, the values are not constant across durations, as would be predicted by scalar timing theory.

CV: Temporal Reproduction Correlations. We examined correlations between the CV scores within the reproduction task. Presence of a single scalar timer would suggest positive correlations across all durations. If different timers operate across short versus long durations, CVs for short durations should correlate with one another and CVs for long durations should correlate with one another, along with no, or possibly, negative correlations across duration sets. Table 3.1 shows the Pearson correlations for temporal reproduction; significant correlations were found between all standard durations larger than 650 ms; implicating a common timing process for long durations.

Table 3.1. Correlations between temporal reproduction CVs.



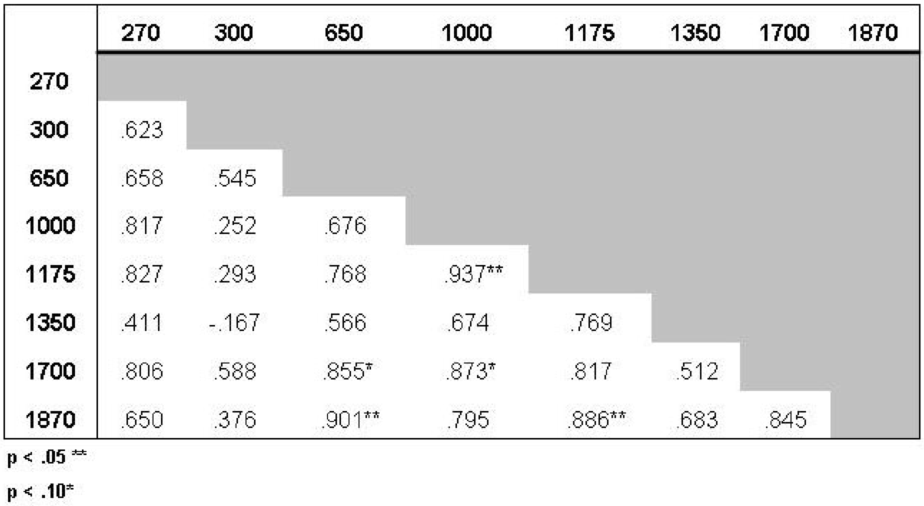
	270	300	650	1000	1175	1350	1700	1870
270								
300	.513							
650	.409	.542						
1000	.182	.048	.643**					
1175	.219	.131	.556	.711**				
1350	.182	.195	.574*	.774**	.842**			
1700	.140	.032	.485	.739**	.888**	.752**		
1870	.158	.175	.540	.753**	.729**	.814**	.721**	

p < .05 **

p < .10*

CV: Temporal Discrimination Correlations. Correlations between the CV scores were also examined within the discrimination task. Table 3.2 contains the Pearson correlations for this task; scattered correlations, typically between longer durations, were seen, but no definitive pattern emerged to clarify the nature of the underlying clock or clocks.

Table 3.2. Correlations between temporal discrimination CVs



	270	300	650	1000	1175	1350	1700	1870
270								
300	.623							
650	.658	.545						
1000	.817	.252	.676					
1175	.827	.293	.768	.937**				
1350	.411	-.167	.566	.674	.769			
1700	.806	.588	.855*	.873*	.817	.512		
1870	.650	.376	.901**	.795	.886**	.683	.845	

p < .05 **

p < .10*

Weber functions: Between task comparisons. We examined the Weber functions for each participant and determined each individual's ideal breakpoint for each task. The mean breakpoint for temporal reproduction was 1252.00 ± 92.23 ms, while the breakpoint for discrimination was 1252.78 ± 160.39 ms. Figure 3.5 shows the breakpoint distribution for each task.

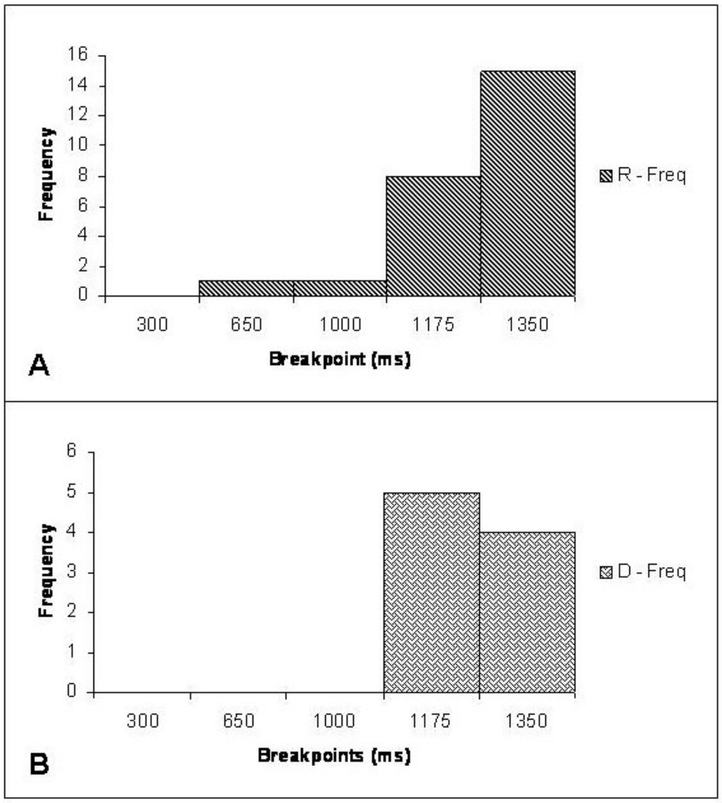


Figure 3.5. Distribution of breakpoints for each task.
Panel A shows temporal reproduction. Panel B shows temporal discrimination.

One problem with the calculation of Weber fractions in this study was that some individuals showed negative slopes for the portion of the bilinear function which spanned the right side of the breakpoint (long duration set). This violates the assumptions of scalar expectancy theory, so individuals who showed this pattern were eliminated from the analysis of slopes across the breakpoint. Seven participants were dropped from the reproduction group, and four participants were dropped from the discrimination group because of this problem. No negative slopes were found across the short duration set. Calculation of the mean Weber fractions across the remaining participants revealed the following means: M = .084 ± .030 across short durations for reproduction, M = .185 ± .128 across long durations for reproduction, M = .160 ± .066 across short durations for discrimination, and M = .137 ± .054 across long durations for discrimination. A RM ANOVA using duration set (short vs. long) as a within-subjects factor and task (reproduction vs. discrimination) as a between-subjects factor revealed no main effects of duration set or task, but a trend towards a duration set x task interaction, $F(1, 21) = 3.95$, $p = .06$. Given the mean values for the Weber fractions, this interaction was driven by different patterns of change in the steepness of the slopes across duration sets; for reproduction, the slope across the long duration set was steeper than that for the short duration set, while the opposite was true for discrimination. Post-hoc paired t-tests within each individual task showed a significant difference between duration set for temporal reproduction, $t(17) = -3.31$, $p < .01$, but no difference for temporal discrimination. A post-hoc independent t-test was also conducted to compare the two tasks on the Weber fractions across the short duration set alone, since this did not require eliminating any participants and could reveal whether there were any task differences strictly for short durations. We found a significant task difference, $t(9.21) = -3.35$, $p < .01$. Figure 3.6 shows the Weber functions averaged across participants for each task.

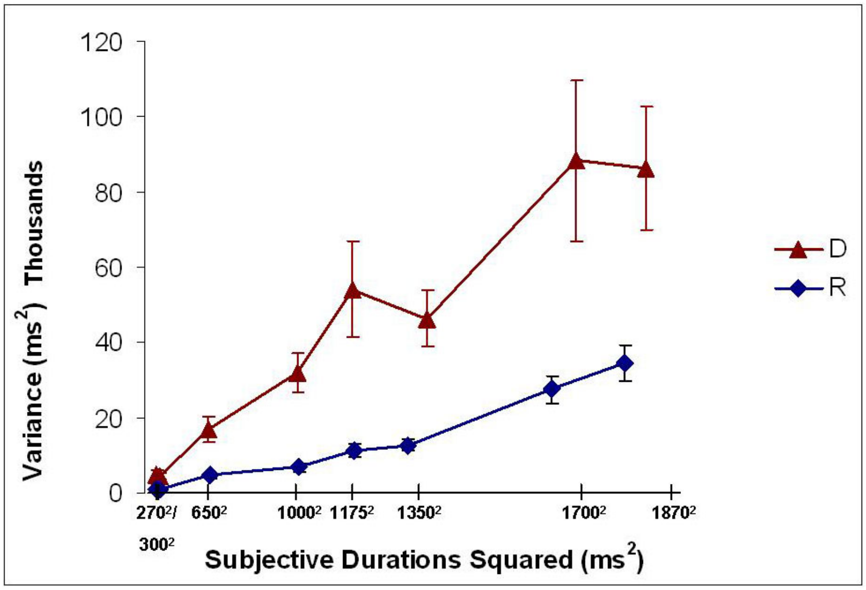


Figure 3.6. Weber functions for both tasks averaged across all participants. The blue diamonds represent data for temporal reproduction and the red triangles represent temporal discrimination. Error bars represent the mean ± 1 standard error.

Relationship between SRT and sensitivity: For temporal reproduction, there were no significant correlations between SRT and any of the CV values, nor were there correlations between the Weber fractions and SRT. Participants who completed the discrimination task, on the other hand, demonstrated significant positive correlations between SRT and the CV for the 650 ms duration, r = .835, as well as the CV for the 1870 ms duration, r = .814, at Bonferroni-corrected α = .05, two-tailed. These positive correlations suggest that individuals with longer RTs show less sensitivity when trying to discriminate 650 and 1870 ms durations. When we examined the correlations between Weber fractions for short and long duration sets with SRT, we found no significant relationships. These findings do little to clarify the nature of the timers responsible for temporal reproduction and discrimination of durations spanning milliseconds and seconds.

Latency to first tap

Between task comparisons. Two individuals were dropped from the repeated measures analysis, because their tap latency for at least one of the standard durations was beyond 2.5 standard deviations around the mean. A RM ANOVA using duration (8) as a within-subjects variable and task (2) as a between-subjects variable revealed a significant task x duration interaction, F(2.93, 87.94) = 15.64, p < .001, as well as main effects of both duration, F(2.93, 87.94) = 18.49, p < .001, and task, F(1, 30) = 27.48, p < .001. A linear trend explained the duration effect, F(1, 30) = 37.73, p < .001. Figure 3.7 shows the tap latencies across durations for the two tasks. It is clear that the task main effect is driven by longer tap latencies for temporal reproduction as compared to discrimination. Moreover, while discrimination latencies were relatively constant across durations, they increased for temporal reproduction. This pattern parallels that reported in the reproduction study from experiment 1.

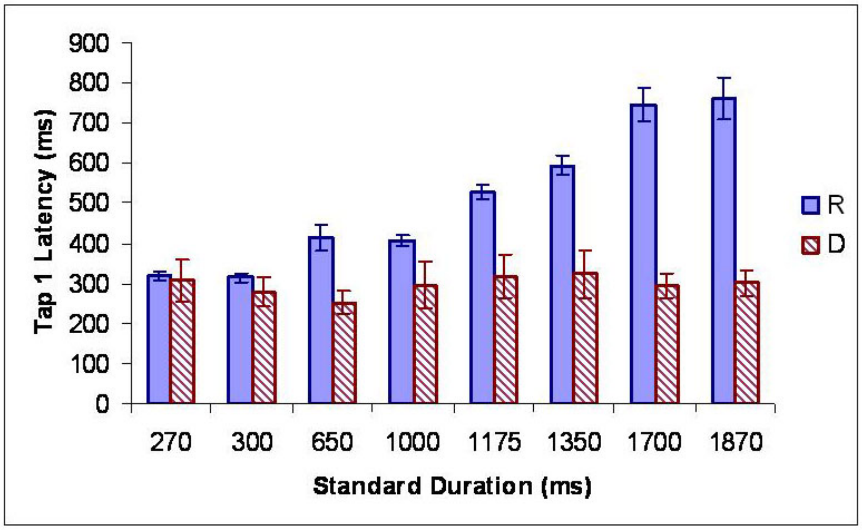


Figure 3.7. Latency to first tap averaged across runs and participants. Temporal reproduction (R) is shown in solid blue, while discrimination (D) is represented with the red dashed bars. Error bars represent the mean ± 1 standard error.

Latency to first tap simple effects: Temporal reproduction. A RM ANOVA with duration (8) as the within-subjects factor revealed a significant main effect, F(2.27, 49.96) = 51.04, p < .001, which was well explained by a linear trend, F(1, 22) = 93.54, p < .001. A post-hoc t-test comparing the latencies for the 270 ms and 1870 ms durations confirmed a significant difference, t(24) = -9.61, p < .001, suggesting that latency significantly increased across durations.

Latency to first tap simple effects: Temporal discrimination. A RM ANOVA with duration (8) as the within-subject factor did not reveal a significant duration main effect, confirming the relatively constant response latency across standard durations for temporal discrimination.

Discussion

This study investigated whether a common timer operates across similarly structured motor and perceptual timing tasks as well as across durations when task conditions are designed to prevent anchor effects on timing performance. Findings from the reproduction task largely replicated what we found in experiment 1. In particular, patterns of over-reproduction for short durations and under-reproduction for long durations held for the accuracy index as did the linear increase in tap latency across increasing standard durations. Also, a quadratic function explained the effect of duration on CV, with the minimum value, again, at the 1000 ms standard. Correlations amongst CV values for reproduction in the current study suggested that a common timer operates for long durations. While the correlations from experiment 1 suggested engagement of a common mechanism for timing short durations, as well, the current findings do not replicate this. However, size of some of the Pearson correlation coefficients between short durations in the current study suggest that, with more power, evidence for a common timer may have emerged. The Weber function breakpoint in the current study was larger than the breakpoint found in experiment 1, but the significant difference between short and long Weber fractions, suggestive of different timers across the two duration sets, was replicated. In contrast to experiment 1, there was no relationship between SRT and reproduction timing performance. Overall, these data argue against a single scalar timer across durations for temporal reproduction.

Though there were fewer participants in the discrimination group than the reproduction group due to the more intensive testing requirements, interesting patterns emerged in the data. Discrimination participants showed over-estimation for short durations and under-estimation for long durations in the accuracy index that were of a similar magnitude as those seen for the reproduction group. However, this group exhibited constant tap latencies with increasing standard duration length, in contrast to the increasing latencies seen for temporal reproduction. We also found an effect of duration on CV in this group, however, the pattern of change was best described by a linear as opposed to a quadratic contrast. In particular, CVs tended to decrease across short durations and then stabilize. Moreover, larger CVs for this task than for temporal reproduction indicate poorer sensitivity, due, possibly, to the operation of task-specific timers.

Scattered CV correlations were seen between standard durations of 650 ms and longer for temporal discrimination, providing some evidence that a common timer may operate across long durations. However, the pattern of significant correlations was not as pronounced as that for temporal reproduction. It is important to note that, large Pearson correlation coefficients for all of the non-significant comparisons suggested that, with more power, we might see significant correlations between CVs for all durations, indicative of a single timer. The discrimination task Weber function breakpoint was nearly equivalent to that seen for reproduction in this study, but comparison of the Weber fractions across the short and long duration sets within this task did not reveal a significant difference. This is in opposition to the significant duration set difference found for temporal reproduction. However, nearly half of the discrimination participants were not included in this analysis because they showed negative slopes across the long duration set. This finding, alone, counters the predictions of scalar expectancy theory, as it suggests that the excluded participants did not show increases in variance with corresponding increases in duration for the longer standards used in the study. A comparison of the Weber fractions across the short duration set for temporal reproduction and discrimination revealed a significant task difference, driven by a larger Weber fraction for discrimination. Finally, there were significant relationships between SRT and CV values for the 650 ms and 1870 ms durations.

The accuracy index findings from both temporal reproduction and discrimination fit with data from previous studies which have shown that humans tend to show close to a 1:1 relationship between objective and perceived time across a number of tasks, including temporal reproduction and production (Baudouin et al., 2006; Wearden, 1991a; Wearden & Helfrich, 2003), bisection (Wearden et al., 1997) and continuous tapping tasks (Collyer et al., 1992). This pattern of results also supports the prediction of mean accuracy as outlined for SET.

Sensitivity (CV) changes across standard durations were different for the two tasks in this study. It is important to note that we found a quadratic trend with reproduction, despite inclusion of additional values at the extreme ends of the duration set to prevent anchor effects. Other researchers have found a similar U-shaped function with CVs for both production and categorization timing tasks in pigeons using durations of 500 ms up to 64 s (Bizo et al., 2006) and rats using durations of several seconds in length (Crystal, 2001), despite many reports of constant CV's across a wide range of durations (Malapani & Fairhurst, 2002; Rakitin et al., 1998; Wearden, 1991a; Wearden & Bray, 2001). Patterns of CV values similar to what we found in our discrimination task--increased CV for very short durations accompanied by a decrease and stabilization across the larger durations--have been found by other researchers who asked people to perform a discrimination task with standard durations ranging from 0 ms to 5 s (Fetterman & Killeen, 1992). The differences in the pattern of CV changes across durations for the tasks hint that the mechanism(s) responsible for timing in the two tasks may operate differently across millisecond and second durations.

Though individuals showed less timing sensitivity in temporal discrimination than in temporal reproduction, they exhibited similar patterns of accuracy. Thus, the larger CVs for the discrimination task were driven by greater variability estimates in temporal discrimination. This finding is in line with Ivry & Hazeltine's (1995) work showing that perceptual timing tasks led to greater variance estimates than those for temporal reproduction. It is possible that greater variance for the perceptual tasks is contributed by processes engaged during the decision stage of SET. Our estimates of the Weber fractions for both the perceptual and motor tasks, however, were much larger than those obtained by these researchers, whose Weber fractions tended to hover between .02 and .05 (Ivry & Hazeltine, 1995). One reason for this might be that Weber fractions in the previous study were obtained over a restricted set of durations that ranged in value from 325 ms to 550 ms, which were likely harder to discriminate from one another than the durations incorporated in our study (Ferrara et al., 1997; Penney et al., 1998).

Correlations amongst CV values suggested that, for temporal reproduction, individuals engaged similar mechanisms to time the longer durations. Correlation patterns were less clear for discrimination. The paucity of correlations in the discrimination task could be a problem with power, due to a small sample size. However, the lack of correlations amongst the short durations for temporal reproduction is somewhat difficult to reconcile. One possibility is that the total range of durations that were tested in our study actually spanned several timescales and that the durations we chose to represent the milliseconds range spanned more than one of these scales (Fetterman & Killeen, 1992; Michon, 1985). If this were the case, we might expect to see a great deal of variability in ideal breakpoints, with some breakpoints located near the shortest durations. However, our breakpoint findings revealed no individuals whose ideal break was present at the 300 ms standard.

Breakpoints in the Weber functions for each task were similar, though these estimates were larger than the breakpoint estimate from the reproduction task discussed in experiment 1. Interestingly, the minimum point of the quadratic function fit to the CV data in the current reproduction task was located at 1000 ms, in line with the 1000 ms transition proposed by Lewis and Miall (2003b), but less than the value of the breakpoint obtained by fitting the independent bilinear function to the reproduction data (M = 1252.00). However, inspection of the reproduction CV values near the breakpoint suggests that they may not differ significantly from the 1000 ms CV. Thus, there appears to be a range of increased sensitivity within which the breakpoint in the Weber function is found. The inclusion of additional durations in this study allowed us to determine the breakpoint with more precision than in experiment 1.

Unlike the first study, there was no relationship between SRT and reproduction CVs. However, we did see a relationship between this measure and the 650 ms and 1870 ms durations for the discrimination task. This finding argues against a specialized role for sensorimotor processes for the range of short durations or, more specifically, the 1000 ms minimum CV for reproduction.

Thus, the combined results from our first two studies leave the role of sensorimotor processes in motor and perceptual timing unclear.

As with our first reproduction study, latency to make the first reproduction tap increased as a function of increasing standard duration. However, tap latency for discrimination remained relatively constant. This incongruity can be explained by differences associated with motor preparatory processes for each task. For reproduction, making the appropriate response requires accessing the memory representation of a standard duration either in working or reference memory and translating it into a motor program. The tap latency results suggest that the length of time to prepare a response in this task is proportional to the changes in length of the standard duration being reproduced. In particular, motor preparatory processes may take longer for longer durations. In contrast, motor preparatory processes for temporal discrimination merely require preparing a single response with the appropriate finger; the finger used corresponds to the decision that was made about the comparison duration in relation to the standard, in this case “shorter” vs. “longer.” Constant latencies in the discrimination task reflect the amount of time needed to prepare a single finger-press response.

Despite some minor inconsistencies with the findings from our first reproduction study, and problems fully investigating the Weber fractions for long duration sets, it is clear that there is evidence for different timing mechanisms across short and long durations within temporal reproduction, which mirrors the findings from experiment 1. Moreover, there may be different mechanisms for timing across tasks. This task difference seems especially relevant for timing across milliseconds-length durations. However, the two tasks used in this study differed in methodology which may have contributed to the task differences observed. In particular, the discrimination task involved many more trials per standard duration than reproduction. Discrimination also involved more testing sessions. To confirm that the task effects we found were truly indicative of the engagement of separate processes and not merely a consequence of these experimental differences and the simple fact that different participants completed each task, we decided to examine performance on these two tasks within the same set of individuals. This also allowed us to examine individual differences to determine whether people demonstrate similar patterns of timing sensitivity across the two tasks.

CHAPTER IV:

Within Subjects Study

Objective

The purpose of this within-subjects study was to examine whether a single scalar timer is responsible for timing across millisecond and second durations and across perceptual and motor tasks with a parallel task structure. In particular, this study was designed to confirm that the task differences found in the between-subjects study reported in experiment 2 were not simply due to design differences between tasks, such as the number of trials or testing sessions involved or the fact that different participants completed each task. In addition, the current design allowed for individual differences in timing performance to be examined, in particular, whether individuals show similar patterns of temporal sensitivity across the motor and perceptual tasks. If individuals show inter-task correlations for CVs, this will support the engagement of similar processes for timing in motor and perceptual tasks.

Method

Participants

Sixteen (12 females, Age = 21 ± 3.40 years) college-aged participants completed both temporal reproduction and discrimination. All participants were right-handed, as determined by the Edinburgh Handedness Inventory (Oldfield, 1971) and reported no hearing problems. Individuals were paid for their participation and gave informed consent as approved by the University of Michigan Institutional Review Board. They also completed a health history and activity level questionnaire on the first testing day.

Procedure

Participants performed temporal reproduction and discrimination using the same 8 standard durations as mentioned in experiment 2 (270, 300, 650, 1000, 1175, 1350, 1700, and 1870 ms). They also completed blocks of a simple RT task. All programs were created and presented using E-Prime software, and tones were presented via Koss UR-29 headphones. The entire study was completed over the course of eight different testing sessions on different days. Each task was completed across a block of four days. All sessions for one of the tasks were completed before any of the sessions were completed for the other task. Task order was counterbalanced. Two standard duration blocks were completed each day. Within each task, each standard was presented within a single block of 21 runs of 18 trials each. For both tasks, the first run served as practice to familiarize participants with the relevant standard duration and was excluded from further analysis. Again, feedback was given at the end of each trial in the practice run and at each run's end for the remaining runs (see figures 2.2 and 3.2). The individual trial structure for each task was identical to that reported in chapters 2 and 3 (see figures 2.1 and 3.1). Participants were told not to count or move during the tasks and were asked to stand and stretch to combat fatigue in the middle and at the end of each duration block. A block of the simple RT task was completed prior to the presentation of each duration block on each testing day, resulting in 16 simple RT blocks across the entire study. After the first duration block on each day, participants were asked to take at least a five minute break so that they could rest prior to completing the second half of the testing session. At the end of each testing session participants completed a final survey to determine whether they used explicit counting or movement strategies during either task. There were no reports of such strategy use, so all participants were retained for analysis.

Data analysis

The dependent variables (CV, accuracy index, latency to first tap, and Weber fractions) for each task were calculated using the same procedures as reported in experiment 2. In addition, we investigated both within and between task correlations on CV scores to determine whether, within individuals, temporal sensitivity was related across durations and across tasks. The calculation of the critical dependent variables for the discrimination task were dependent on estimates derived from cumulative responses, thus, we were unable to assess the effect of run on performance for this task and for comparisons between temporal reproduction and discrimination.

Results

Simple RT

As a precaution, we included timing task as a within-subjects factor in an ANOVA to confirm that SRT was not differentially affected when paired with each task. The RM ANOVA with task (2) and session (16) as the within-subjects factors revealed no interaction of task with session and no main effect of task. There was, however, a main effect of session, F(3.17, 44.39) = 3.83, p < .05, which was explained by a significant linear contrast, F(1, 14) = 5.32, p < .05. The linear trend was marked by a general decrease in SRT across testing sessions. The mean RT obtained across the days when individuals performed the reproduction task was M = 189.58 ± 24.30 and across the days when they performed the discrimination task was M = 188.10 ± 19.63.

Accuracy index

Between-task comparisons. Four participants were excluded from the repeated measures analysis, because at least one of their ratio error scores fell outside the range of their mean ± 2.5 standard deviations. A RM ANOVA on the accuracy index revealed no duration by task interaction and no main effect of task, but a significant main effect of duration, F(7, 77) = 4.24, p < .01. A linear contrast explained the duration effect, F(1, 11) = 11.44, p < .01. Figure 4.1 shows the data from the two tasks. As found previously, both tasks indicate that while individuals tend to overestimate and over-reproduce short durations, they underestimate and under-reproduce long durations. For the reproduction task, individuals were most accurate for the 1175 ms and 1700 ms durations, while individuals were most accurate for the discrimination duration for the 1000 ms duration.

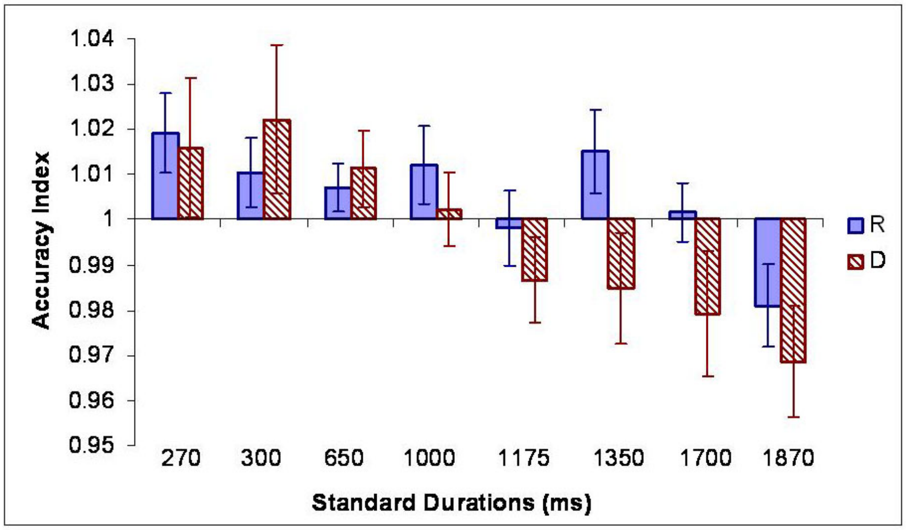


Figure 4.1. Mean accuracy index for each task.
Temporal reproduction is represented in solid blue; temporal discrimination is represented with the red dashed bars. The abscissa crosses the ordinate at 1, the point which represents perfect accuracy. Values greater than 1 indicate over-reproductions, while values less than 1 indicate under-reproductions. Error bars are mean ± 1 standard error.

Sensitivity

CV: Between task comparisons. A RM ANOVA on CV with duration (8) and task (2) as within-subjects factors was conducted on these data. Data from 3 participants was excluded from this analysis because their CV values for at least one of the standard durations fell outside the range of ± 2.5 standard deviations around the group mean. This analysis revealed no significant interaction between task and duration. However, there were main effects of both task, F(1, 12) = 66.14, $p < .001$, and duration, F(7, 84) = 3.10, $p < .01$. A significant quadratic trend explained the pattern of data across durations, F(1, 12) = 17.59, $p < .01$. The minimum value of this function (M = .13) was at the 1000 ms standard duration. Figure 4.2 shows the CV data for these two tasks. It is clear that the task main effect is driven by larger CVs for temporal discrimination.

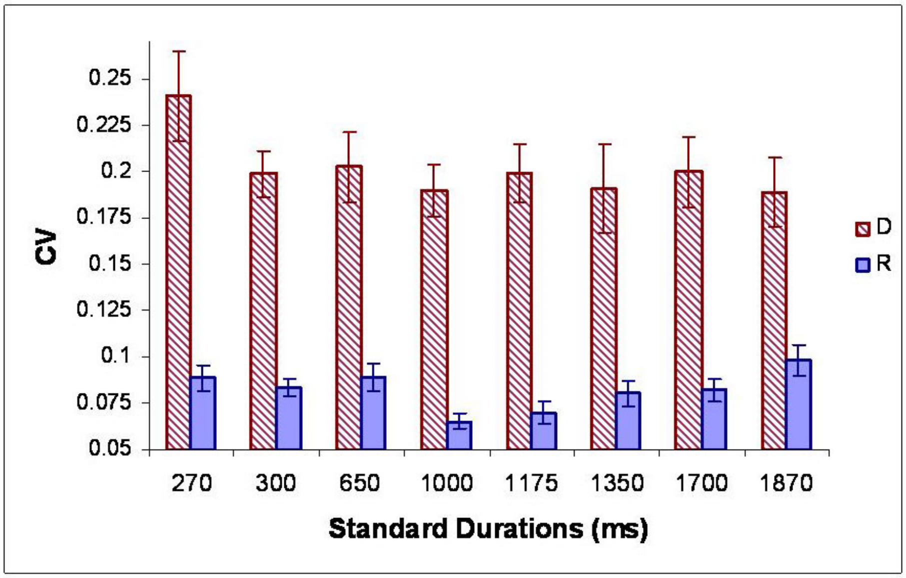
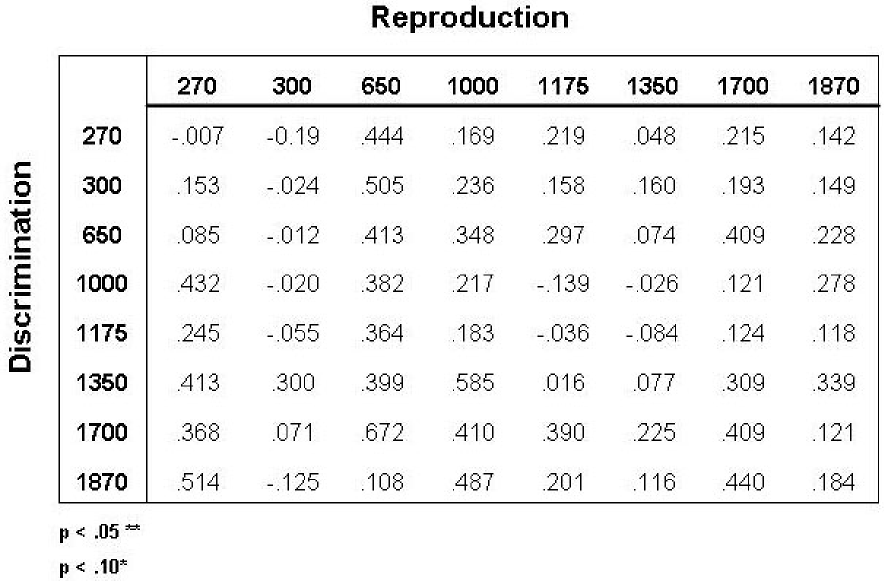


Figure 4.2. CV data from the two timing tasks.
Temporal reproduction (R) is represented in solid blue; temporal discrimination (D) is represented with the red dashed bars. Average CV scores collapsed across task are shown by the dotted line. Error bars represent the mean ± 1 standard error.

CV: Between-Task Correlations. No significant correlations were found between any of the CV values for the two tasks, even for cases where the standard durations matched. This suggests that the two tasks do not engage similar timing mechanisms. However, again, there are some instances where the Pearson correlation coefficients are large enough that they might achieve significance with more statistical power. In particular, several of the between-task correlations for the 650 ms, 1000 ms, and 1700 ms standards appear large enough to warrant additional investigation.

Table 4.1. Correlations between CVs across tasks



Reproduction

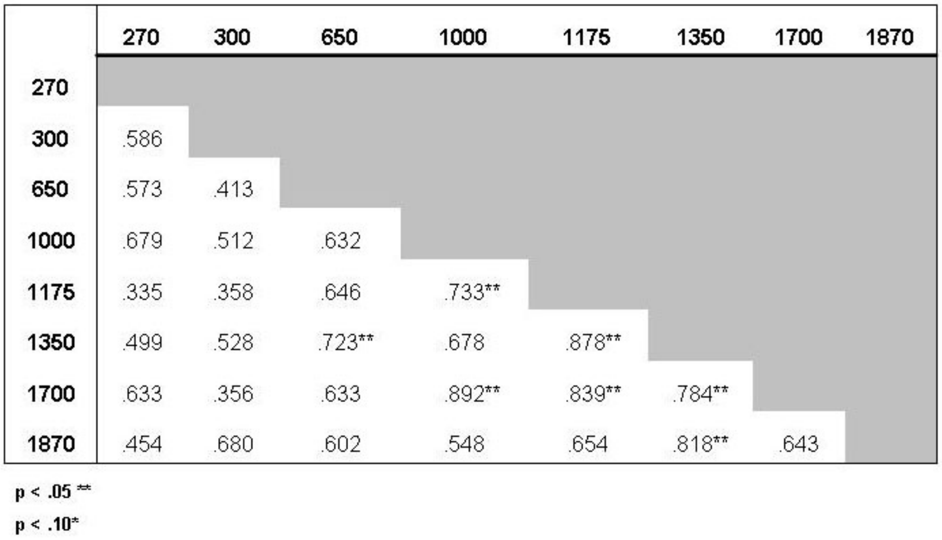
Discrimination	270	300	650	1000	1175	1350	1700	1870
270	-.007	-0.19	.444	.169	.219	.048	.215	.142
300	.153	-.024	.505	.236	.158	.160	.193	.149
650	.085	-.012	.413	.348	.297	.074	.409	.228
1000	.432	-.020	.382	.217	-.139	-.026	.121	.278
1175	.245	-.055	.364	.183	-.036	-.084	.124	.118
1350	.413	.300	.399	.585	.016	.077	.309	.339
1700	.368	.071	.672	.410	.390	.225	.409	.121
1870	.514	-.125	.108	.487	.201	.116	.440	.184

$p < .05$ **

$p < .10$*

CV: Temporal Reproduction Correlations. We examined correlations between CV scores within the reproduction task and found several significant correlations amongst longer durations, as demonstrated in Table 4.2. Though Pearson correlation coefficients between many of the other durations were reasonably large, they did not reach significance. These findings mirror those for the reproduction task in experiment 2.

Table 4.2. Correlations between temporal reproduction CVs



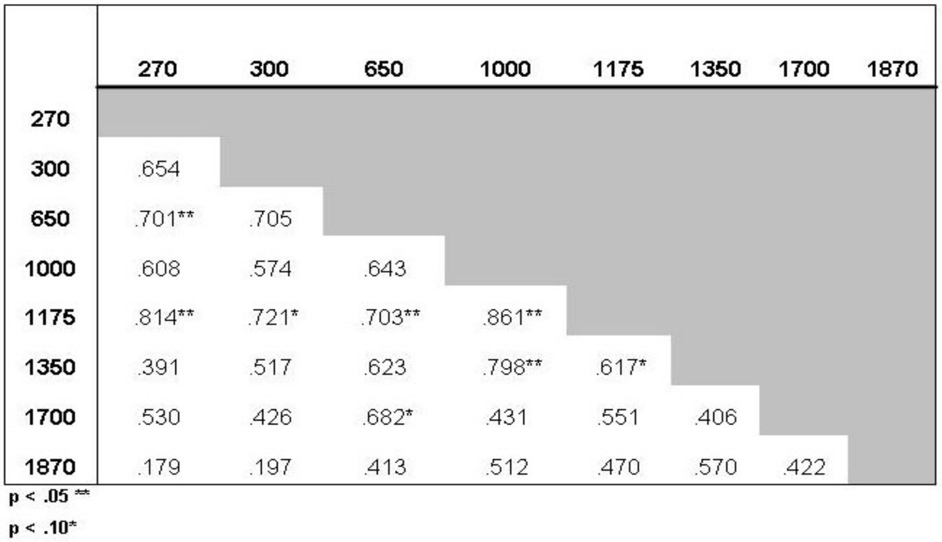
	270	300	650	1000	1175	1350	1700	1870
270								
300	.586							
650	.573	.413						
1000	.679	.512	.632					
1175	.335	.358	.646	.733**				
1350	.499	.528	.723**	.678	.878**			
1700	.633	.356	.633	.892**	.839**	.784**		
1870	.454	.680	.602	.548	.654	.818**	.643	

p < .05 **
p < .10*

CV: Temporal Discrimination Correlations.

Correlations between CVs within the temporal discrimination task revealed significant correlations between the CV for the 1175 ms duration and all of the shorter durations. There were also significant correlations between the 1000 ms and 1350 ms CVs as well as between the 270 ms and 650 ms CVs. Though they did not reach significance, there is some evidence that other correlations might reach significant with greater power, including many of the CVs for durations in the milliseconds range.

Table 4.3. Correlations between temporal discrimination CVs



	270	300	650	1000	1175	1350	1700	1870
270								
300	.654							
650	.701**	.705						
1000	.608	.574	.643					
1175	.814**	.721*	.703**	.861**				
1350	.391	.517	.623	.798**	.617*			
1700	.530	.426	.682*	.431	.551	.406		
1870	.179	.197	.413	.512	.470	.570	.422	

p < .05 **

p < .10*

Weber functions: Between task comparisons.

We determined each individual’s ideal breakpoint for each task by fitting independent bilinear functions to their Weber plots for the two tasks. This analysis revealed a mean breakpoint for temporal reproduction at M = 1251.56 ± 47.84, and for temporal discrimination at M = 1284.38 ± 21.88. Figure 4.3 shows the distribution of breakpoints across participants for each of the tasks.

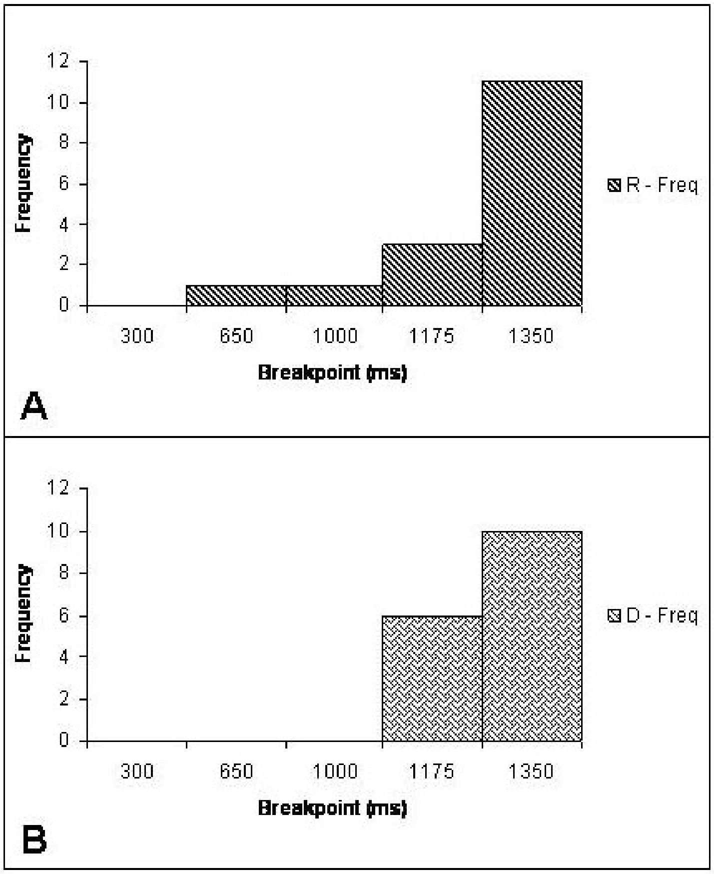


Figure 4.3. Distribution of breakpoints for each task.
Panel A shows temporal reproduction. Panel B shows temporal discrimination.

We used a RM ANOVA using task (2) and duration set (2) to examine the Weber fractions obtained across each side of the breakpoint. However, half of our study participants showed negative slopes across the long duration set for at least one of the timing tasks. This pattern runs counter to the predictions of proportionally increasing variance with increasing standard duration length predicted by scalar expectancy theory. None of the slopes across the short duration set were negative. Individuals with negative Weber fractions were excluded from the repeated measures analysis, leaving only 8 participants. With this small number of participants, we found no significant task x duration set interaction, nor were there significant main effects of either task or duration set.

Figure 4.4 shows the observed Weber plots on either side of the ideal breakpoint for 5 representative participants within each task. It is important to note that the y-axis scale is different for the two tasks, with the discrimination task showing much larger variance estimates than the reproduction task.

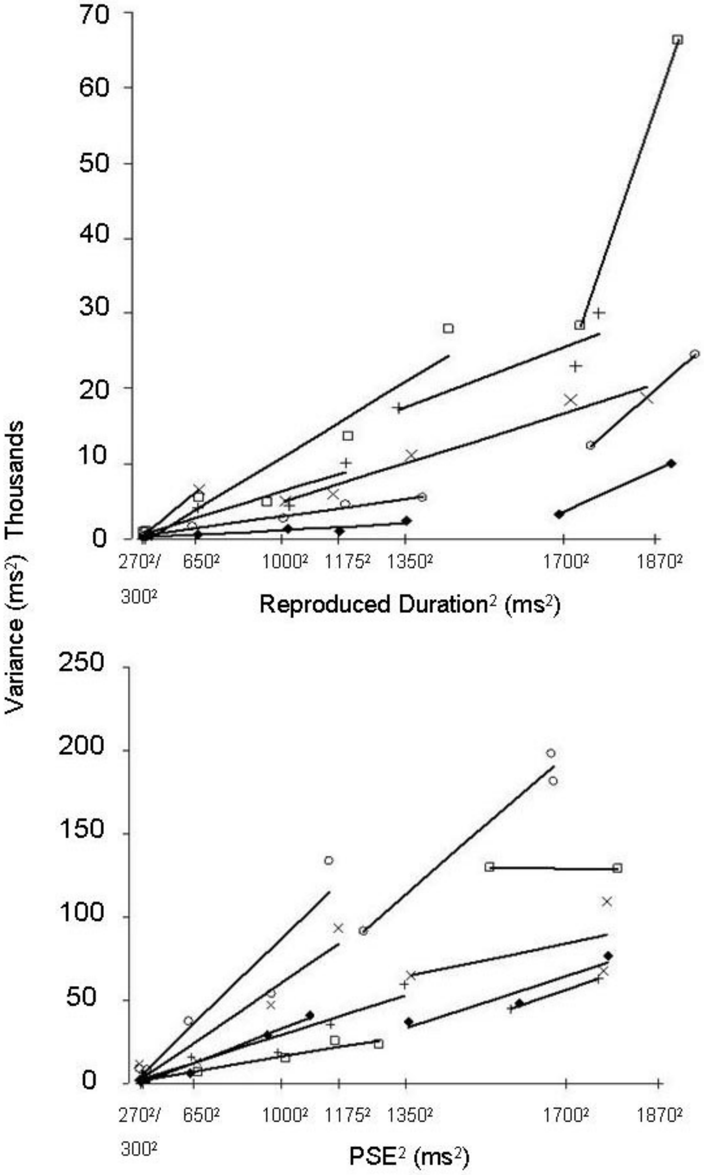


Figure 4.4. Weber functions on either side of the ideal breakpoint for five participants in temporal reproduction (A) and discrimination (B).
Error bars represent the mean ± 1 standard error.

Given that the most common breakpoint (last point of the first fitted line) for participants in both tasks was 1350 ms, leaving the 1700 and 1870 ms standards as the points constituting the long duration set for many participants, we became concerned that the negative Weber slopes for the long durations were a consequence of our methods to eliminate anchor effects. Specifically, individuals were expected to have trouble psychologically distinguishing 1700 ms from 1870 ms due to memory distributions that greatly overlap and may have similar spreads. This could easily have led to similar variance estimates for these two standards which would have affected not only the determination of the appropriate breakpoint but may also have led to negative slopes across these durations. In order to examine this possibility, we created truncated versions of each individual's Weber function for each task, eliminating the data from the most extreme standards. We then fitted new independent bilinear fits to these functions to obtain new breakpoint estimates and Weber fractions for each participant. The breakpoints for each task were M = 1065.63 ± 52.68 for reproduction and M = 1142.19 ± 32.81 for discrimination. Figure 4.5 shows the distribution of ideal breakpoints from the truncated data.

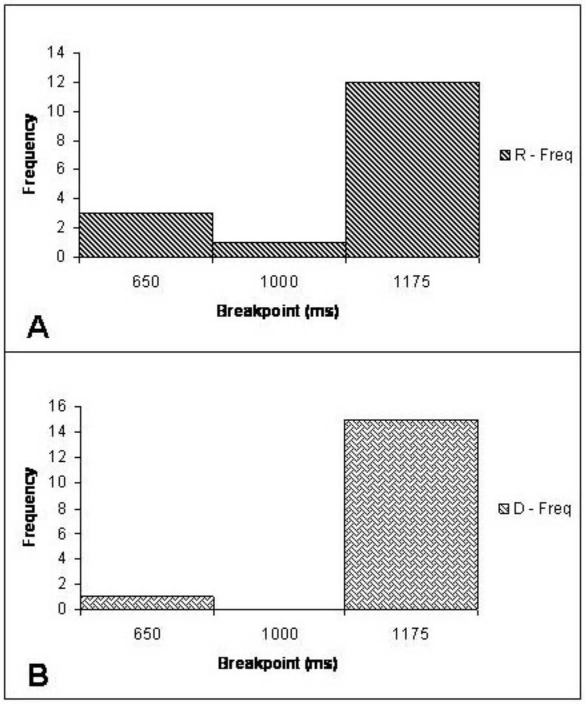


Figure 4.5. Distribution of breakpoints for each task using the truncated set of durations. Panel A shows temporal reproduction. Panel B shows temporal discrimination.

For this analysis, 5 participants were dropped due to negative slopes, and negative slopes only occurred for the long duration set within the discrimination task. A RM ANOVA with task (2) and duration set (2) as the within-subjects factors showed no significant interaction, but a main effect of task, F(1, 10) = 105.10, p < .001 and a trend towards a main effect of duration set, F(1, 10) = 4.40, p = .06. The main effect of task was due to larger Weber fractions overall in the discrimination as compared to the reproduction task, while the trend towards the main effect of duration was driven by larger Weber fractions for the long as opposed to short duration set for each task (reproduction short set, M = .07 ± .04; reproduction long set, M = .08 ± .04; discrimination short set, M = .20 ± .07; discrimination long set, M = .29 ± .12). In an effort to examine whether a duration set effect was present for reproduction when the truncated data from all participants were included, we conducted a paired t-test across duration set. However, we found no significant difference between the short and long Weber fractions.

Relationship between SRT and sensitivity: For temporal reproduction, there were no significant correlations between SRT and any of the CV values after Bonferroni correction. However, interestingly, there was a significant correlation between SRT and the long duration set Weber fraction from the full Weber plots, r = .616. For temporal discrimination, there was a significant relationship between the 650 ms CV and SRT, r = .658 as well as between SRT and the short duration set Weber fraction from the truncated Weber functions, r = .542. The positive correlation between the CV for the 650 ms standard for discrimination replicates a finding from experiment 2 and suggests that individuals with longer SRTs have less sensitivity when trying to discriminate the 650 duration; the correlation with the truncated short duration set Weber fraction implies a similar relationship for durations shorter than the mean discrimination breakpoint (1142.19 ms). Additionally, there was a correlation between the reproduction long duration set Weber fraction and SRT, which implies a role for sensorimotor processes during reproduction of durations longer than 1065.63 ms. However, this is in contrast to the absence of such a relationship in experiment 2 and the trend towards a relationship with the short duration set Weber fraction found for reproduction in experiment 1.

Latency to first tap

Three individuals were dropped from the repeated measures analysis examining tap 1 latency, because their latency for at least one of the standard durations fell beyond 2.5 standard deviations above or below the group mean. The RM ANOVA with task (2) and duration (8) as within-subjects variables revealed a significant task x duration interaction, F(3.43, 41.11) = 18.07, p < .001. There were also significant main effects of task, F(1, 12) = 78.13, p < .001 and duration, F(3.62, 43.43) = 22.17, p < .001. A linear trend explained the duration effect, F(1, 12) = 50.25, p < .001. The task main effect was driven by generally larger latencies for temporal reproduction than for discrimination. Figure 4.5 shows the tap 1 latency values for each task.

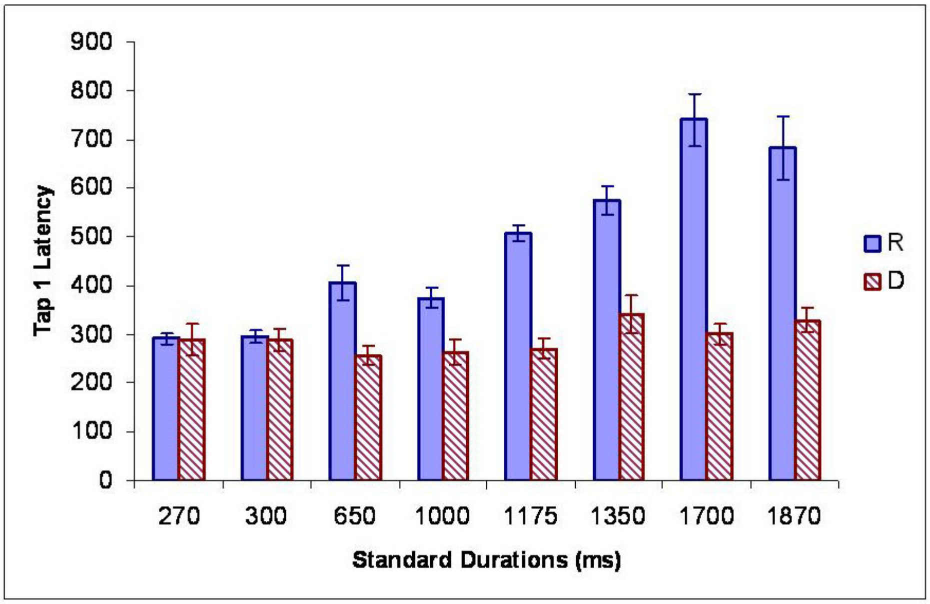


Figure 4.6. Response latency values for each timing task.
Temporal reproduction (R) is represented in solid blue; temporal discrimination (D) is represented with the red dashed bars. Error bars represent the mean ± 1 standard error.

In order to examine simple effects, we conducted RM ANOVAs within each task, using duration (8) as a within-subjects factor. For temporal reproduction, we found a significant main effect of duration, F(2.29, 29.82) = 30.79, p < .001, with a significant linear contrast fitting the data, F(1, 13) = 58.72, p < .001. For temporal discrimination, there was no significant main effect of duration. These results seamlessly replicate the findings from experiment 2.

Discussion

This study investigated whether a common timer operates across millisecond and second durations as well as similarly structured motor and perceptual timing tasks when the same set of participants perform each task. Data from the accuracy index and tap latency measures perfectly replicated the findings from experiment 2. Again, individuals demonstrated over-reproduction and over-estimation of the shortest durations accompanied by under-reproduction and under-estimation of the longest durations. Also, tap latency increased with increasing duration for reproduction, but remained constant for discrimination.

In contrast to experiment 2, we did not find an interaction of task and duration for the CV measure. However, the main effect of task was replicated, as was the main effect of duration, supporting the overall conclusion that a single scalar timer does not operate across durations and may not serve both timing tasks. A quadratic fit explained the overall CV data with a minimum value at the 1000 ms standard, similar to the reproduction task findings from experiments 1 and 2. Significant CV correlations between long standard durations in the reproduction task mirrored the pattern of correlations for this task seen in experiment 2. CV correlations for discrimination were unlike what we found in that experiment, however. In experiment 2, scattered correlations hinted at a common timer for long durations in discrimination, but the current study revealed correlations between the 1175 ms CV and the CVs for all of the shorter standard durations, as well as additional correlations between standards in the middle of the duration set. Unfortunately, this pattern does not provide a clear picture of the properties of the internal clock operating for temporal discrimination. Inter-task CV correlations revealed no significant relationships, further supporting task-specific clocks across all durations.

Analysis of the Weber fractions using the full set of standard durations led to breakpoint estimates that were close in value to those obtained in experiment 2. However, unlike experiment 2, there were no significant interactions or main effects for Weber fractions using this data set. Intriguingly, half of the participants were eliminated from this analysis due to negative slopes across the long duration set; this was also a problem in experiment 2. The presence of negative slopes argues against the scalar expectancy theory's prediction of increasing variance with increasing duration. To confirm that these negative slopes were not a consequence of the endpoint durations chosen to eliminate anchor effects, we performed a Weber slope analysis using a truncated data set. The new breakpoint estimates were a little larger than 1000 ms for both tasks. Despite this change, there were still 5 participants who had to be eliminated due to negative slopes across the long duration set for temporal discrimination. For the truncated data, there was no task by duration set interaction, in contrast to experiment 2, but there was a main effect of task and a trend towards a duration set main effect. These results support the notion of separate timers across tasks and, possibly, across durations. However, we performed a paired-t test within the reproduction task to examine the effect of duration set when all participants were included in the analysis. This led to the discrepant finding of no duration set difference for the Weber fractions in temporal reproduction. This is completely counter to the findings from experiments 1 and 2, where such a difference was present.

Investigation of the relationship between SRT and timing sensitivity measures for temporal reproduction revealed a significant correlation between SRT and the long duration set Weber fraction calculated using all of the standard durations. In experiment 2, we found no relationship between SRT and any CVs or Weber fractions for reproduction. Temporal discrimination revealed a significant relationship between SRT and the 650 ms CV, in accordance with experiment 2, as well as between SRT and the short Weber fraction from the truncated data set. This replication of the relationship between SRT and the 650 ms duration CV suggests a special role for sensorimotor processes in helping individuals discriminate 650 ms from comparison values. Whatever the involvement of sensorimotor processes, they do not seem to be engaged in the same fashion across tasks.

The fact that individuals' reproductions and PSE estimates in this study were generally close in value to the objective standard durations fits well with data from other researchers who, using a variety of timing tasks, found that mean subjective estimates of durations match their objective lengths (Baudouin et al., 2006; Collyer et al., 1992; Wearden, 1991a; Wearden & Helfrich, 2003; Wearden et al., 1997). In addition, our tap latency data support the notion that translating a duration into an executable motor program for reproduction involves a temporally-sensitive process related to the standard duration in question, though the temporal relationship between this process and the length of the standard is not necessarily one to one. This finding supports previous work by Vidal, Bonnet, and Macar (1991; 1992) who used a pre-cuing paradigm to determine whether duration of a required action can be programmed prior to initiation of the action. They found that RTs were longer prior to execution of a button press that had to be maintained for 2500 ms as opposed to one that had to be maintained for 700 ms. Their findings and ours indicate that action duration is programmed prior to motor execution. The task differences we found in this measure also support this position.

In terms of temporal sensitivity for the current experiment, we found no interactions between task and duration for the CV measures or between task and duration set for Weber fractions from either the full or truncated data set. This suggests that the manner in which sensitivity levels changed across increasing durations was similar for the two tasks, even though overall task estimates of sensitivity were different. This lack of an interaction for the CV estimates is at odds with what we found in experiment 2; it suggests that having the same set of participants complete both tasks when they involve parallel testing parameters removes some of the noise associated with a between-task investigation of internal clock properties. It is also likely that equating the number of trials across tasks equated other factors, such as fatigue and practice effects, which may have differentially contributed noise to the data from experiment 2. However, the task main effects for CV and the truncated Weber fractions, as well as the lack of intertask correlations combine to provide credence to the argument for task-specific timers.

In conjunction with the lack of interactions just mentioned, the main effect of duration for the CV measure as well as the trend for a duration set main effect for the truncated Weber fractions argue against a single scalar timer across durations. Moreover, the quadratic fit to the CV data implicates a mechanism which leads to increased timing sensitivity for durations in the realm of 1000 ms. This minimum value matches that of the temporal reproduction CV function in experiment 2, but, once again, does not match the breakpoints (reproduction: M = 1251.56 ms, discrimination: M = 1284. 38 ms) obtained when data from the full set of standards in this study were used to construct Weber functions. In fact, these breakpoints are closer to the region (> 1180 ms) in which counting becomes a useful strategy (Grondin et al., 1999). However, the breakpoints determined using the truncated data set are similar to the 1000 ms minimum (reproduction: M = 1065.63 ms, discrimination: M = 1142.19) which is also the proposed transition between timers suggested by Lewis and Miall (2003a; 2003b; 2003c; 2006b). It is important to note that the quadratic pattern of CV values is similar to data from other researchers who have argued for nonlinearities in timing when examining motor and perceptual performance in pigeons (Bizo et al., 2006) and rats (Crystal, 2001, 2003).

Evidence for different clocks across the two tasks comes from the lack of intertask CV correlations. Even given the task differences in motor preparation requirements and the possible differences in memory engagement, one would expect correlations to emerge if common timing components are shared across tasks. Little is revealed about the relationship between short and long durations by looking at the intra-task correlations. For example, while correlations between reproduction CVs suggest a common timer for long durations, discrimination CV correlations show a number of significant relationships between the 1175 ms CV and those of other standard durations. One question concerning these results is whether more power in the intra-task correlation analyses would lead to a more interpretable pattern of correlations. For instance, many of the non-significant intra-task comparisons for each task were marked by rather large Pearson correlation coefficients (See tables 4.2 and 4.3) In particular, for temporal reproduction, the addition of more participants might lead to evidence that a common clock operates across all durations.

Overall, our findings from the CV data, Weber fractions, and inter-task correlations in this study suggest that different mechanisms may operate across motor and perceptual timing tasks. Evidence against a single scalar clock across durations for the two tasks is also supported by the duration main effects for the CV and truncated Weber fraction data. One important question to address is whether, instead of different timing mechanisms, operation of a single non-scalar clock could lead to the current results. While the general lack of significant correlations between short and long duration CVs across the two tasks for this experiment argues against the notion of a single timer, further research needs to be conducted to evaluate the validity of this possibility.

CHAPTER V:

General Discussion and Conclusions

The main purpose of this dissertation was to investigate whether a scalar timing mechanism is ubiquitous across millisecond and second durations as well as across perceptual and motor tasks. We were particularly interested in testing the information-processing model of scalar expectancy theory (Gibbon et al., 1984), which has dominated the timing literature for the last several decades (Allan, 1998; Buhusi & Meck, 2005; Gibbon et al., 1997; Grondin, 2001). We designed perceptual and motor timing tasks with highly similar structures in order to equate as many of the underlying processing stages as possible and investigated performance across a broad range of durations spanning both milliseconds and seconds. Overall, we cast doubt on the view that a single scalar mechanism appropriately describes timing across tasks and durations. Instead, it appears that different timers may operate in perceptual and motor tasks, and that changes in temporal variance within a task may not increase linearly with increases in duration. While the results of our studies do not completely undercut SET, we have taken an important step towards creating a set of necessary conditions in which to evaluate the validity of this model for motor and perceptual timing across multiple timescales.

Timing across tasks

Of the few studies that have directly compared timing performance across tasks (Ivry & Hazeltine, 1995; Keele et al., 1985), performance has generally been assessed within a single timescale (e.g. milliseconds range). These studies have found evidence for a common scalar clock across motor and perceptual tasks based on the finding of equivalent Weber slopes across these tasks under conditions where tasks were manipulated to have a more parallel structure. It is important to note that in their first study, which included a comparison of continuation tapping with temporal discrimination without any manipulation of task structure, equivalent slopes were not found across tasks. Given that the structure of the perceptual and motor tasks used in the current set of studies were designed to equate perceptual and encoding requirements, we would have expected results that parallel those of Ivry and Hazeltine (1995), namely parallel slopes across tasks. However, our analyses of CV values and Weber fractions in experiments 2 and 3 counter this result. Instead, our findings suggest that people time with less sensitivity (higher CVs) for temporal discrimination than reproduction and that duration-dependent variance estimates are generally larger for temporal discrimination. Even if we ignore the Weber fractions obtained from the long duration side of the ideal breakpoint (due to issues with negative Weber slopes), task differences emerge between the Weber fractions for the short duration set. This finding is of importance to the timing literature, as it calls into question the oft-cited finding of no task difference in this range for motor and perceptual tasks (Ivry & Hazeltine, 1995; Keele et al., 1985). One important caveat is that, despite the attempt to structure the motor and perceptual tasks in the current study to be highly parallel, task requirements certainly differed at the motor preparation and response stages. While it is not clear that these differences would have affected the format of the memory representations formed at encoding, it is possible that these response differences may have led to some of the tasks differences that we observed, especially for the CV data.

The absence of significant correlations between CV values for the two timing tasks in experiment 3, despite involvement of the same study participants, argues against a common timer (Keele et al., 1985; Robertson et al., 1999). For example, the fact that there were no significant relationships between CV scores for the two tasks, even when they involved the same standard durations (e.g. 300 ms reproduction CV vs. 300 ms discrimination CV), suggests that the mechanisms that individuals used to time durations in the two tasks were unrelated. Though tasks differences in motor preparation and performance may have contributed noise to the CV data, we would still have expected individuals to show evidence of a between-task relationship between these values if they engaged a common timing process. The accuracy index measure revealed similar mean subjective estimates (denominator of the CV calculation) of durations for the two tasks, supporting the fact that the CV task differences were driven by greater variability (numerator of the CV calculation) during temporal discrimination than temporal reproduction. Thus, different internal clocks appear to be responsible for motor and perceptual timing; the perceptual timing mechanism appears more variable than the mechanism responsible for timing in motor tasks, despite the fact that both mechanisms lead to relatively good accuracy.

Differences in patterns of tap latency constitute one of the most distinguishing markers between the reproduction and discrimination tasks used in this group of studies. Increased latency across durations for the reproduction task but not the discrimination task are consistent with the finding by Vidal, Bonnet, and Macar (1991; 1992) that action duration is coded as part of a motor program and can be processed prior to motor execution. This feature of temporal reproduction is also consistent with Lewis and Miall's (2003b; 2003c; 2006b) theory that timing tasks which require replication of a duration via an action may be especially reliant on the motor system. It is possible that motor preparation processes contributed additional variability to performance in temporal reproduction due to the need to include duration as a dimension of the response. However, it is unclear whether this required feature of the response necessitates differential encoding and memory processes than those involved for temporal discrimination. Specifically, does the need to include duration as part of the response affect the quality of encoding and storage of duration representations, suggesting the possible involvement of different timing processes? Our lack of correlations between CVs for the two tasks as well as the differences found between Weber slopes, especially across short durations for the truncated data set in experiment 3, suggest that this may be the case. However, additional work using tasks which manipulate encoding, memory, and motor preparation requirements in timing is needed before definitive conclusions can be made.

On a different note, the task difference in tap latency might not be due strictly to differences in motor preparation processes, per se, but to consistent differences in strategies participants incorporated to perform each task. For example, for reproduction, participants may have tried to rehearse the given standard duration prior to response or to create a latency that was temporally congruous with the standard in order to create a form of rhythm that might help with their reproductions. Regardless of the source of task differences on this measure, it persisted across experiments, even when the same participants completed both tasks.

We used Weber slope analysis (Ivry & Hazeltine, 1995; Spencer & Zelaznik, 2003) as a means to garner separate variance estimates for duration-dependent (clock) as opposed to duration-independent sources. While another model (Wing & Kristofferson, 1973) allows for decomposition of variability into similar constituent components, it requires use of a repetitive tapping procedure that estimates duration-independent sources of variance from the correlation between successive responses and then determines duration-dependent variance indirectly by subtracting this other source of variance from total variance. However, this model does not provide a means for decomposing variability for during discrimination tasks. Weber slope analysis, on the other hand, allows estimates of duration-dependent and duration-independent components of variance to be determine for both motor and perceptual tasks and enables between-task comparison of these estimates. Our findings that the duration-dependent sources of variance for temporal reproduction and discrimination do, in fact, differ are consistent with the claim made by Lewis and Miall (2003b; 2003c; 2006b) that activated regions of cortex may dissociate when timing involves translation of a standard duration into an action as opposed to a simple comparison of duration representations in memory. These authors argue that motor regions of cortex may be specialized for timing in the first instance, while frontal regions of cortex are involved for the other. However if sensorimotor processes are engaged for timing in temporal reproduction, they do not appear to overlap with the processes involved in SRT performance; we did not see consistent correlations between this measure and CVs or Weber fractions in the reproduction task.

One important clarification is that, despite our evidence pointing to different timers across tasks, it is not necessarily the case that these different timers cannot each be consistent with SET. It is entirely possible for reproduction and discrimination to rely on different clocks which each have scalar properties. If these clocks are structured similarly to the one described by the information processing instantiation of scalar expectancy theory, then the task differences in CVs and Weber fractions may indicate broader distributions of stored representations of durations in memory for temporal discrimination, or perhaps a different threshold setting at the decision stage. Scalar expectancy theory postulates that individuals use a ratio rule at the decision stage which helps them decide whether a comparison duration or a duration being reproduced is similar to the standard. It is possible that individuals use different decision criteria for the two tasks (e.g. a more lax threshold for discrimination) which lead to more variable responses for discrimination. It is necessary to consider the pattern of results across durations within each task to more fully understand the nature of the timing mechanisms operating in each.

Timing across durations

Our studies suggest that a single scalar clock may not be responsible for timing across millisecond and second durations. Support for this was strongest for temporal reproduction which showed significant differences in sensitivity across standard durations for all three experiments. In fact, a quadratic, U-shaped function consistently described the pattern of CV values for all three versions of reproduction. Similar patterns have been found in recent motor and perceptual studies of timing using rats and pigeons (Bizo et al., 2006; Crystal, 2001, 2003), and indicates a deviation from the expected pattern of constant CVs across durations as predicted by SET. In our studies the minimum CV for reproduction always occurred at the 1000 ms duration, which is the point at which some researchers argue a transition occurs between timing mechanisms that are more automatic and reliant on the motor system and those which engage executive control processes (Lewis & Miall, 2003a, 2003b, 2003c, 2006b). The mean breakpoints from the Weber functions for experiment 1 (M = 956.25 ms) and the truncated data set for experiment 3 (M = 1065.63) were close in value to the 1000 ms standard. Though the breakpoints from experiment 2 and the full data set in experiment 3 were larger, they may have been a consequence of the standard durations chosen to prevent anchor effects. Significant differences between short and long duration set Weber fractions were found in chapters 2 and 3 for temporal reproduction; this pattern was less apparent in experiment 3 for the Weber truncated data set. Thus, while the CV data provide consistent evidence of nonlinear timing in temporal reproduction, findings from the Weber slope analysis are less clear. One reason for this is that fitting independent bilinear regressions to the data assumes the possibility of two separate scalar timers across a break. However, it may be that a single timer operates for temporal reproduction, but that it is not appropriately described by the information processing model of scalar expectancy theory. One alternative is a timer consisting of uses oscillators with specific periods instead of a pacemaker-accumulator device to time durations. With this type of timer, one would expect points of maximal sensitivity at durations that match the ideal periods of one or more of these oscillators (Church & Broadbent, 1990; Crystal, 1999, 2001; Matell & Meck, 2004). Our CV results suggest that temporal reproduction may involve an oscillator-based mechanism with at least one component oscillator whose period is close to 1000 ms in duration.

Correlations between CVs for reproduction in chapters 3 and 4 reveal significant relationships between many of the durations at the longer end of the standard duration set; this finding, alone, implies that a common mechanism times these long durations, but that the same mechanism is not responsible for shorter durations. We should note, however, that for both chapters 3 and 4, a number of other correlation coefficients that did not reach significance were still quite large; added power might reveal a pattern of correlations which would lead to different conclusions about the timing mechanism(s) involved in temporal reproduction, especially if the correlations between short and long duration CVs in experiment 3 were to reach significance. While we cannot make a definitive conclusion regarding the properties of the clock or clocks that are responsible for timing across durations within temporal reproduction, we can state that SET predictions do not account for increased sensitivity at certain durations, as seen with our data.

Temporal discrimination was also consistently marked by non-equivalent CVs across durations. In general, the pattern of CVs across standard durations in chapters 3 and 4 consisted of large CVs for the shortest standards followed by a sharp decrease and then stabilization from the 650 ms standard onward. Other researchers have found similar patterns of CV change where values increased for standards less than 250 ms in length, and they argue that these changes may be accounted for by the generalized form of Weber's law (Crystal, 1999; Fetterman & Killeen, 1992). However, our shortest standards are longer than the cutoff proposed by these studies. It is possible that the CV changes in our study may mark an additional transition between timescales for temporal discrimination that was not captured in the Weber slope analysis. Significant differences between short and long Weber fractions were only found for the truncated data set in experiment 3, where the mean ideal breakpoint was M = 1142.19, which is still reasonably close to the proposed 1000 ms transition between motor and cognitive timing proposed by Lewis and Miall (2003b; 2003c; 2006b). However, a number of study participants showed decreasing slopes across the long durations with this measure, which is in opposition to the predictions of scalar increases in standard deviation with increased durations in SET.

Even with use of the truncated data in experiment 3, five participants still exhibited negative slopes for the long portion of the data set within temporal discrimination. None of these participants reported using an explicit counting or movement strategy, however, it is possible that they may have used some other means of subdividing the standard and comparison durations in such a way that variability was reduced for longer durations. While a few of these individuals reported trying to associate the standard and comparison durations with the length of a word or words that they repeated in their heads, this specific strategy was not adopted by the remaining individuals in this group. Thus, it is not clear that the individuals who showed negative slopes were depending on the same kind of strategy to remember and make judgments about longer durations. Future studies should address whether some other factor, such as attention, may have differentially influenced the behavior of these participants for longer durations or whether this particular subgroup of participants relied on a different type of timer when discriminating longer durations than individuals who exhibited the expected increases in variance.

When we examined the correlations between CVs within the temporal discrimination task, we found relatively scattered correlations in experiment 2, and correlations between the intermediate standard durations and both shorter and longer standards in experiment 3. However, there were a number of Pearson correlation coefficients that were relatively large but did not reach significance in both of these data sets. Additional power could reveal a more consistent pattern of correlations, which would help clarify whether temporal discrimination of millisecond and second durations engages different timers. The differences in Weber slopes for the truncated data set in experiment 3 as well as the finding of negative slopes across the long duration set for about a third of the study participants suggests different timers across durations in this task; the mere presence of negative slopes in the Weber functions indicates a departure from the predictions of scalar expectancy theory. Given these somewhat discrepant findings, further investigation is necessary to clarify the properties of the internal clock(s) responsible for temporal discrimination.

Despite the occasional presence of negative Weber slopes across the long duration set in temporal reproduction and discrimination for experiments 2 and 3, neither task involved any negative slopes for the linear function fitted to the “short” portion of the duration set. This fits with the results of Ivry and Hazeltine (1995) who used Weber slope analysis to examine Weber fractions across tasks for durations spanning 325 to 550 ms. They found that the generalized form of Weber’s law was reasonable for explaining timing behavior in this range. Our findings from Weber slope analysis indicate that, within a task, SET may adequately explain increases in standard deviation values across durations within the milliseconds range, but it does not adequately account for the data we obtained when tasks span multiple timescales.

Implications for other models of timing

Our findings suggest a need for a more thorough investigation of scalar timing theory and to evaluate whether other models of timing are more appropriate for explaining the data we obtained. One model which has been proposed to explain nonlinearities similar to those that we found in our reproduction study replaces the pacemaker from the information processing model of scalar expectancy theory with multiple oscillators, each with a different period (Church & Broadbent, 1990; Crystal, 1999, 2001, 2003). This model can explain points of maximal sensitivity, such as the 1000 ms duration in our reproduction task, by postulating that one of the oscillators has a period close to that duration, and, therefore, times that duration with less variability than other durations. However, a problem with this model is that it is limited to timing durations whose lengths are shorter than the period of the longest oscillator in the set. Therefore, it may not be appropriate for investigating timing of durations many seconds or minutes in length. A more recent model which can get around this problem and which may still be able to accommodate findings of specific non-linearities is the striatal beat frequency (SBF) model (Matell & Meck, 2004). This model was developed in an effort to present a neurobiologically plausible model of timing which can account for behavioral and neuropharmacological findings in the timing literature. Specifically, this model proposes that striatal spiny neurons act as coincidence detectors which, at the time of reward or feedback, determine the current state of a set of cortical oscillators. For later trials, these striatal neurons compared the current state of activation of the cortical neurons to the pattern that was previously reinforced. This theory can accommodate our findings of maximal sensitivity at 1000 ms by assuming that the inherent period of one of the cortical oscillators is close to this value. Both this model and the multiple oscillator model (Church & Broadbent, 1990) would predict additional points of maximal sensitivity at the harmonics (i.e. twice the value, three times the value, etc.) of these ideal periods. Alternatively, the SBF model can explain increases sensitivity at 1000 ms, because durations that have been repeatedly reinforced would be timed with greater precision. One second is a salient unit of time for humans and is constantly reinforced through observation of timepieces. It is possible that increased sensitivity to 1000 ms in our reproduction tasks is a result of well-tuned coincidence detection of the pattern of oscillator activity representing this duration.

Relationship between timing and SRT

We investigated whether there was a relationship between SRT and timing performance in temporal reproduction and discrimination in order to clarify the role of sensorimotor processes for timing in these tasks. Several researchers have proposed a specialized role for sensorimotor processes when timing durations less than 500 ms (Michon, 1985) or 1000 ms (Lewis & Miall, 2003b, 2003c) in length or when timing in tasks that require translation of a standard duration into an action (Lewis & Miall, 2003b, 2003c). Studies have demonstrated that timing plays an important function in helping individuals make a decision about how to respond in a serial choice reaction time task (Grosjean, Rosenbaum, & Elsinger, 2001; Praamstra, Kourtis, Kwok, & Oostenveld, 2006).

This suggests that the processes involved in timing and reaction time may be inextricably linked and that SRT may serve as a marker of timing sensitivity under certain conditions. Moreover, the fact that dopamine agonists lead to increases in clock speed as well as faster RTs has led some researchers to suggest that RT and timing may be reliant on some of the same neural structures (MacDonald & Meek, 2004). The most consistent relationship that we found was between SRT and CV for the 650 ms standard in temporal discrimination. However, this was not strong enough evidence to support the claim that SRT plays a significant role in timing, at least not across the conditions expected.

Caveats

As mentioned previously, the motor and perceptual tasks used in this study were structured to equate perceptual and memory processes as closely as possible. In addition, standard durations were presented on every trial to facilitate veridical encoding of these durations and minimize the need for accessing representations from reference memory. However, it is possible that individuals may have drawn representations from reference memory in the service of temporal discrimination, but not temporal reproduction. Further motor preparation requirements differed between tasks, as supported by the findings of increasing tap latencies across increasing standard durations for reproduction but not discrimination. These differences may have contributed to our finding task differences between timing mechanisms in this study. However, we would have expected, even with these differences, to have found a relationship between CV scores for the two tasks if timing in both involves the same pacemaker, accumulator, and working memory processes. This was not the case. Furthermore, we would argue that our tasks were more parallel than those presented in the studies by Ivry and Hazeltine (1995) who managed to find evidence of a common timer in several experiments. Thus, likelihood of finding a common timer was in our favor.

One might question whether the task differences in temporal sensitivity could have resulted from differences in sustained attention. There is a posited role for attention in modulating the output of the pacemaker component of the information processing model of SET. It is possible that individuals may have had a harder time maintaining attentional focus during the discrimination task, which could have led to representations with missed pulses, ultimately leading to more variable duration representations in memory. One way to try to equate the attentional demands of the two tasks is to use the single stimulus technique for discrimination, which involves presenting participants with only a single probe or comparison duration on each trial (Grondin, 2005; Grondin & Helfrich, 2003; Grondin et al., 2005; Morgan et al., 2000). Participants are never presented with the standard to be timed. Instead, they develop an implicit representation of the length of the standard through trial by trial feedback. This design would ensure that individuals only have to pay attention to a single duration on each trial, however it might also lead to additional problems. For instance, since the reproduction task involves presenting the standard on every trial, it is likely that individuals never have to access long term memory in order to retrieve representations of the standard. In contrast, use of the single stimulus method for discrimination would be heavily reliant on drawing representations from long term memory. Thus, the two tasks might show patterns of performance that were the result of accessing different memory stores, which could bias towards finding task differences.

There is some question as to whether the negative Weber slopes that we found in chapters 3 and 4 are indicative of a switch between different timing mechanisms, or whether they may have resulted from some other factor. For example, counting is known to cause departures from scalar timing (Grondin et al., 1999; Hinton & Rao, 2004; Killeen & Weiss, 1987). Though we explicitly asked participants not to count during the task, it is possible that they still used this strategy, if only part of the time, when timing long durations. These individuals may not have reported using this strategy on their final surveys, because they knew that they were not supposed to have relied on this strategy. However, an experimenter was present in the room with the participants during the entire study to ensure that they did not count aloud or move during the task. One technique that could be attempted in future studies to prevent individuals from counting would be to use articulatory suppression. While this technique would prevent counting, it might lead to other problems, such as attentional changes and introduction of movement during encoding. Moreover, participants might still be able to use a subdividing strategy based on the words or sounds used for articulatory suppression.

Despite the fact that our motor and perceptual tasks involved a parallel design in order to minimize task differences, it is important to note that our tasks were structured so that individuals may not have had to access representations in long term memory; the standard duration was presented at the start of every trial, so it was readily available in working memory when individuals were cued to make their response. We used this design structure to ensure that our participants developed stable representations of the standard duration in both working and long term memory so that we could measure their ideal performance. However, most timing studies reported in the literature require individuals to access representations of the standard duration stored in long term memory in service of the given task (Rakitin et al., 1998; Wearden, 1991b, 1992; Wearden & Helfrich, 2003; Wearden et al., 1997). For example, these studies present individuals with a standard duration at the start of the task and then require them to either reproduce the standard or compare it to a probe duration for subsequent trials, without re-exposure to the standard. It is possible that evidence for departures from SET in our study may have resulted from the absence of transformation of accumulated pulses into reference memory representations in our tasks. However, evidence from other studies (Wearden & Bray, 2001) showing that scalar timing prevails even in episodic temporal generalization and bisection tasks where individuals do not have to access long-term memory representations minimizes this concern.

Contribution to the timing literature

This is the first study that we know of to systematically examine and compare the performance of human participants on a number of closely-spaced durations spanning milliseconds and seconds within motor and perceptual tasks designed with highly parallel structures. Of particular note is that our data question whether a single scalar timing mechanism times across tasks and durations. Instead, we found evidence for task-specific timers--a finding that is in direct contrast to studies often cited as evidence for a common inter-task timer (Ivry & Hazeltine, 1995; Keele et al., 1985). We also found departures from scalar timing in both temporal reproduction and discrimination, despite prior evidence that timing across this range is scalar (Grondin, 2001; Wearden, 1991a; Wearden & Bray, 2001). For temporal reproduction, the consistent quadratic trend in the CV data suggests that certain durations may be timed with greater sensitivity than others. The fact that negative Weber slopes were found across long, but not short duration sets for temporal discrimination implies that, while the generalized form of Weber's law may adequately describe performance in the milliseconds range on this task (Ivry & Hazeltine, 1995), it is not appropriate for explaining timing across durations spanning both milliseconds and seconds. These findings call for further study of the information-processing model of scalar expectancy theory as well as a thorough investigation of timing performance in the range of milliseconds to seconds under similar controlled conditions. In particular, studies should be extended to include testing of additional durations to clarify where critical timescale transitions actually take place and to determine whether other durations may represent points of maximal sensitivity. Also investigations should include timing tasks that are more reliant on reference memory in an effort to determine the validity of SET across a variety of task conditions which involve differential processing at memory and motor preparation stages of performance.

Future directions

An important goal for future studies is to determine whether the pattern of data we found for temporal reproduction is indicative of a shift between different timing mechanisms or may, instead, point to a single oscillator-based timer. For this purpose, it is critical to perform more systematic investigations of temporal reproduction performance which would include adding a number of additional standard durations, including multiples (e.g. 2000 ms, 3000 ms, etc.) of the 1000 ms point of maximal sensitivity from our experiments. If similar increases in sensitivity are found for these harmonic values, an oscillator clock would be implicated for timing in this task.

Also, the finding of negative Weber slopes was problematic for investigating duration-dependent sources of variance in our studies. It is possible that these negative slopes may have been a consequence of including end-point duration pairs that were difficult to distinguish from one another. While investigation of truncated data sets solved the problem, to some degree, these data cannot be viewed as equivalent to those we would have obtained without the similar end-point pairs. Thus, one important future avenue of research is to examine performance on both discrimination and reproduction in a new set of studies using standard durations that are reasonably discriminable. If negative slopes are still present, then this would lend further credence to the idea of a change in timing mechanisms between short and long durations.

In addition, it is important to continue systematic investigations of motor and perceptual timing across an even larger set of durations spanning tens of milliseconds to several seconds in length in an attempt to clarifying where functional breaks in timing performance occur. A number of timing researchers argue for two or more timescale shifts in this range (Buhusi & Meck, 2005; Buonomano & Karmarkar, 2002). However, it is not clear where the endpoints between these timescales are located. Mapping these transitions is an important step towards resolving the discrepancies in the literature regarding where functional breaks may occur but also towards the development of a clearer understanding of the nuances of human timing. Moreover, these investigations are important for localizing the precise timing deficits present in special populations, such as Parkinson’s disease patients, and may lead to the development of more targeted therapies and treatments to combat timing-related problems in these individuals.

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