



Dissecting the clock: Understanding the mechanisms of timing across tasks and temporal intervals

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ABSTRACT

Currently, it is unclear what model of timing best describes temporal processing across millisecond and second timescales in tasks with different response requirements. In the present set of experiments, we assessed whether the popular dedicated scalar model of timing accounts for performance across a restricted timescale surrounding the 1-second duration for different tasks. The first two experiments evaluate whether temporal variability scales proportionally with the timed duration within temporal reproduction. The third experiment compares timing across millisecond and second timescales using temporal reproduction and discrimination tasks designed with parallel structures. The data exhibit violations of the assumptions of a single scalar timekeeper across millisecond and second timescales within temporal reproduction; these violations are less apparent for temporal discrimination. The finding of differences across tasks suggests that task demands influence the mechanisms that are engaged for keeping time.

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1. Introduction

Timing is fundamental to many motor and cognitive processes. Temporally coordinated movements are required to perform actions, like swinging a golf club. Timing is also required for conditioned learning and the ability to represent sequential relationships between stimuli. Though many timescales are relevant for human behavior (Buhsu & Meck, 2005; Buonomano & Karmarkar, 2002), debate exists about the nature of the mechanism(s) for timing on the order of milliseconds and seconds.

One core contention is whether timing in this range occurs via a dedicated mechanism or is simply an emergent (intrinsic) product of neural activity during a particular task (Ivry & Schlerf, 2008). Some research implicates motor system specialization for timing milliseconds (Lewis & Miall, 2003b,c), because millisecond-level precision of muscle responses is needed to produce appropriate movements (Mauk & Buonomano, 2004). Intrinsic models of timing, such as state-dependent networks, may be especially suited for timing at this scale, while a dedicated process, such as a clock-counter model, may operate for seconds-length timing (Ivry & Schlerf, 2008; Mauk & Buonomano, 2004). However, a state-dependent network may only operate feasibly

over a restricted timescale up to a few hundred milliseconds (Spencer, Karmarkar, & Ivry, 2009). Proponents of a dedicated clock, likewise, disagree about the mechanisms involved, such as whether a pacemaker-accumulator device or a series of oscillators is responsible for timing. This leaves open the question of precisely what kind of mechanism times durations of a few hundred milliseconds and longer. If different timers operate for different timescales, where is the transition between timers? Moreover, do tasks with different response requirements depend on the same internal timing mechanism(s) (Ivry & Hazeltine, 1995; Keele, Pokorny, Corcos, & Ivry, 1985; Lewis & Miall, 2003b; Merchant, Zarco, & Prado, 2008)? Translating durations into motor programs for reproduction (motor timing), for instance, is rather different than simply comparing two durations represented in memory (perceptual timing).

1.1. Dedicated clock–scalar timing theory

Perhaps the most popular dedicated model of timing is the information processing instantiation of scalar expectancy theory (SET) (Gibbon, Church, & Meck, 1984). SET can explain timing performance regularities, such as the superimposition of normalized response rate distributions, in both humans and animals (Allan, 1998; Church, 2003; Gibbon, 1991; Grondin, 2001). Components of SET include a pacemaker that generates pulses at regular intervals and an attentionally-mediated switch (Fortin, 2003; Grondin & Rammsayer,

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2003; Meck, 1984; Meck & Benson, 2002). The switch closes at the onset of a relevant stimulus, allowing pulses to flow to an accumulator. At stimulus termination the switch opens and the representation of the accumulated pulses is transferred to working memory and, eventually, long-term memory. When a judgment must be made, individuals use a ratio rule to compare the representation of the duration currently in working memory with one pulled from long-term memory (Allan, 1998; Church, 1984, 2003; Gibbon et al., 1984).

In SET, scalar variance from memory and decision processes is thought to overwhelm all other sources of variability (Allan, 1998; Gibbon et al., 1984; Grondin, 2001). Thus, the relationship between timing variability and the target duration should follow Weber's law—standard deviation increases proportionally with increasing target duration. Specifically, the coefficient of variation (CV), or standard deviation divided by the mean target interval, should be constant across durations.

SET can account for human timing performance across a variety of tasks, including analogues to those used in the animal literature (Rakitin et al., 1998; Wearden, 1991a,b, 1992; Wearden, Edwards, Fakhri, & Percival, 1998; Wearden, Rogers, & Thomas, 1997), ones not requiring long-term memory access (Wearden & Bray, 2001), and tasks specially-developed for human research (e.g. temporal production, reproduction, and continuation tapping) (Ivry & Hazeltine, 1995; Keele et al., 1985; Wearden & McShane, 1988). Nevertheless, it remains unclear whether a single scalar mechanism accounts for human timing across milliseconds and seconds in both perceptual and motor tasks. This question remains unanswered by studies that test only a few durations within either the millisecond or the second range and others that confound task and timescale—typically, motor tasks examine milliseconds-length durations while perceptual tasks evaluate longer durations (Allan, 1998; Gibbon, Malapani, Dale, & Gallistel, 1997). Many within-subject comparisons across timescales usually test a single duration in each (Droit-Volet, 2002; Lavoie & Grondin, 2004; Rammsayer, 1999; Rammsayer & Lima, 1991), whereas similar comparisons across tasks have tested durations of 1 s and shorter (Ivry & Hazeltine, 1995; Keele et al., 1985; Merchant, Zarco, & Prado, 2008). A few widely-spaced durations in a single task are insufficient to accurately characterize the mechanics of timing. Instead, a larger duration set across timescales in multiple tasks must be used to evaluate potential transitions indicative of different timing mechanisms or other critical features of an internal clock (Collyer, Broadbent, & Church, 1992; Crystal, 1999, 2001, 2003; Crystal, Church & Broadbent, 1997; Rammsayer, 1999).

1.2. Transitions and nonlinearities across timescales

Researchers show little consensus about where proposed functional transitions on the temporal scale occur. Michon (1985) argued that 500 ms delineates automatic (<500 ms) versus cognitively-mediated (>500 ms) temporal processes, while Karmarkar and Buonomano (2007) identified this duration as the transition between a state-dependent (<500 ms) and a scalar timer (>500 ms). Others posit that 2–3 s marks the upper bound of the “psychological present” in which successively-presented stimuli are still perceived as part of the same group (Lavoie & Grondin, 2004; see Pöppel (2004) for a review). Finally, several neuroimaging experiments implicate a shift between motor and cognitive timing systems in the region of 1 s (Lewis & Miall, 2003a,b,c, 2006). Pharmacological studies and behavioral studies manipulating cognitive load and controlled attention further implicate executive processes in seconds-length timing (Brown, 1997; Fortin, 2003; Fortin & Breton, 1995; Fortin & Rousseau, 1998; Rammsayer, 1992, 1997, 1999, 2006); their involvement in timing milliseconds-length durations is less clear (Grondin & Rammsayer, 2003; Macar, Grondin & Casini, 1994; Rammsayer & Lima, 1991; Rammsayer & Ulrich, 2005).

More general departures from scalar variability have been observed across a wide range of durations. For example, a review by Gibbon et al. (1997) evaluated the CV data from a multitude of human and animal studies and identified patterns of increasing CV for

durations up to 100 ms, stable CVs from 100 ms to 1500 ms, and increasing CVs for durations 1500 ms and longer. However, these patterns were derived from visual observation of between-subject patterns, with few studies including tests of durations spanning multiple timescales within the same participants. Some animal studies have found durations that are timed with greater precision than their neighbors (Bizo, Chu, Sanabria, & Killeen, 2006; Crystal, 1999, 2001, 2003; Crystal et al., 1997). Regions of maximal sensitivity have similarly been found in humans at points ranging from 272 ms to 800 ms (Collyer, Broadbent, & Church, 1994; Drake & Botte, 1993; Fetterman & Killeen, 1990; Friberg & Sundberg, 1995; Grondin, 1992). In a recent series of temporal discrimination experiments, Grondin (2010) consistently found a smaller CV for 200 ms versus 1000 ms, regardless of the number or range of comparison intervals tested. Interestingly, Lewis and Miall (2009) discovered a steady logarithmic decrease in CV as durations increased from 68 ms to 16.7 min (equally-spaced on a logarithmic scale) in an impressive temporal reproduction experiment. They also found greater precision in a discrimination task for a 3-second duration compared to a 600 ms duration. Despite such clear violations of scalar timing, Lewis and Miall (2009) found little evidence of breakpoints between timing mechanisms. Even though they examined a broad swath of durations spanning multiple timescales for temporal reproduction, Lewis and Miall (2009) did not specifically select their durations to focus on any specific possible breakpoint previously identified in the literature, nor did they conduct within-subject comparisons of performance on both temporal reproduction and discrimination. Moreover, in the reproduction task both encoding and reproduction of durations occurred in the presence of distraction to prevent counting. In the present study, we investigate whether a breakpoint occurs in the region around 1 s where a possible transition between motor and cognitive timing systems might exist. We used no target durations longer than 2 s, both to avoid another proposed transition point and to ensure that our durations would be difficult to support with a counting strategy (Grondin, Ouellet, & Roussel, 2004).

1.3. Task differences in timing

In temporal reproduction, individuals encode a duration and transform it into a motor program to produce the duration via movement. For temporal discrimination, individuals merely compare two or more abstract representations of durations in memory and generate a response to indicate whether or not they match. These different response requirements are presumed to render the tasks more reliant on motor versus perceptual processes for timing, respectively. Some studies point to common mechanism(s) across such tasks for timing in the millisecond range (400 ms: Keele et al., 1985), especially when the response requirements are closely matched (325 ms to 550 ms: Ivry & Hazeltine, 1995). More recent work has revealed hints of cross-task relationships accompanied by task-specific differences in timing variability (Merchant et al., 2008) involving durations of 1 s and less (350 ms to 1000 ms). This latter finding suggests that a distributed network of brain regions might be differentially engaged to time in different task contexts in the sub-second range. Indeed, both patient and neuroimaging studies show that certain brain regions (e.g. striatum, supplementary motor area, etc.) may be involved at different times in different types of timing tasks, depending on task constraints and timescales (Coull, 2004; Harrington, Haaland, & Hermanowitz, 1998; Harrington, Lee, Boyd, Rapcsak, & Knight, 2004; Ivry & Keele, 1989; Lewis & Miall, 2003b,c; Macar, Anton, Bonnet, & Vidal, 2004; Macar, Coull, & Vidal, 2006; Macar et al., 2002). Thus, the number of different timers, their role across tasks, and their neural implementation remain unclear.

Mounting evidence from behavioral, neuroimaging, and pharmacological studies indicates that a dedicated scalar timer may not adequately explain behaviors across motor and perceptual timing tasks requiring judgments of durations spanning milliseconds and

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