Running Head: INDIVIDUAL DIFFERENCES IN TIMING SENSITIVITY

Individual Differences in Timing Sensitivity:
Implications for Interval Timing Models

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Ph.D. Dissertation

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Table of Contents

Abstract

Time discrimination performances ($N = 78$) were examined using either a steadily presented (NFLK) or a heterochromatic luminance flickering (15 Hz; FLK) visual standard-time-interval (STI) stimulus to address the following questions: (1) Are individual differences in time perception reliably observed across durations of less than and greater than one second? (2) What is the relationship between individual differences in time perception and performance on nontiming cognitive tasks that measure processing speed, processing accuracy, and short-term memory? (3) What is the effect of increasing pacemaker speed (through visual entrainment) on time perception, and does this effect vary across individuals who have a low or high sensitivity to time differences? Difference thresholds were measured using the Method of Constant Stimuli (MOCS) in which 7 predefined test interval levels were presented following either a short, 400-ms standard time interval (400-STI) or a long, 1600-ms standard time interval (1600-STI). Two of the 7 levels equaled the standard interval ("blanks") to assess the false alarm (FA) rates. Thresholds and the slopes of transducer functions (d' vs. time increment contrast) were calculated to assess discriminability (*sensitivity*) and *uncertainty*, respectively. Proportion correct (*accuracy*) and decision criterion (*bias*) also served as dependent variables. Difference thresholds were moderately consistent across timing conditions. However, there was a significant interaction of DURATION (400- and 1600-STI) and STIMULUS (NFLK and FLK). The highest and lowest thresholds were obtained with 400-STI FLK and 1600-STI FLK, respectively. Nontiming cognitive tasks (a battery of tests that measured processing speed, accuracy, and working memory) were administered. Greater processing accuracy and working memory scores were associated with those individuals who showed increased sensitivity with NFLK timing, while those who showed increased sensitivity with FLK timing obtained greater processing accuracy, speed, and working memory scores. The results suggest that there is more than one timing system that contributes to time perception over the ms to s range.

Individual Differences in Timing Sensitivity: Implications for Internal Clock Models

Much of our ongoing experience involves the timing of short durations, in the milliseconds (ms) to seconds (s) range. This behaviour permits synchronized interactions with the environment. Interval timing, or judgments about the duration of time intervals, has become the focus of investigation in recent "clock studies," where researchers propose that there is an internal clock or timer that enlists higher cognitive functions such as memory or decision-making processes (e.g., Mattell & Meck, 2000). Described as a "stopwatch" that can be started and stopped at will, the clock accounts for all timing behaviour, whether it be deciding how fast you must run to catch a ball, or how long you can lounge in bed before getting up to go to work. The biological substrate for this interval timing mechanism is not well understood. Some researchers believe that the mechanism(s) involves the concerted activations of neurons within the substantia nigra, striatum, and prefrontal cortex; however, there are experimental data to suggest that almost any area of the brain may be involved (Gibbon, Malapani, Dale, & Gallistel, 1997).

While some researchers (e.g., Ivry & Hazeltine, 1995; Keele, Pokorny, Corcos, & Ivry, 1985; Meck, 1996) have speculated that there is one internal clock or timing mechanism used in perception, memory and movement over shorter time durations (i.e., ms to sec), others (e.g., Church & Gibbon, 1990; Treisman, Cook, Naish, & MacCrone, 1994) have proposed that the brain incorporates many timing skills, and therefore uses many timing systems or pacemakers that are synchronized for adapting to a common psychological experience. Both views are compatible with the idea that information received by specialized neural circuits must be temporally and spatially integrated for internal representations (i.e., perceptions) of the external environment readying the organism for effective behavioural responses.

Interval timing is believed to be mediated and/or moderated by a number of factors, including, arousal, attention, memory, and decision processes (Gibbon, Church, & Meck, 1984; Treisman, 1963; Zakay & Block, 1996). Research that has examined the effect of interference due to competing task demands suggests that interval timing requires effortful processing, cognitive activity that interferes with and is susceptible to disruption by tasks that draw on limited central processor resources such as attention and working memory (see Brown, 1997, for a review). These findings suggest that individual differences related to attention and memory processing may have impact on interval timing performance. There is evidence in the literature that supports this proposal, as dysfunction in one or more of a number of neural circuits associated with attention and memory is associated with less accurate and/or more variable timing performance, for example, schizophrenia (Davalos, Kinsley, & Ross, 2003; Elvevage et al., 2003; Monaco et al., 1998), Attention-Deficit/Hyperactivity Disorder (Barkley, Murphy, & Bush, 2001; Kerns, McInerney, & Wilde, 2001), and head injury (Mangels, Ivry, & Shimizu, 1998; Olton, 1989).

A number of populations are associated with relatively poorer interval timing skill in general, including, young children (McCormack, Brown, Maylor, Darby, & Green, 1999; Zakay, 1992), and the elderly (Block, Zakay, & Hancock, 1998; Lustig & Meck, 2001; Perbal, Droit-Volet, Isingrini, & Pouthas, 2002). However, even in healthy, young adult populations, performance can vary significantly, with some individuals reliably making more accurate time judgments than others (Brown, 1998; Brown, Newcomb, & Kahrl, 1995). These individual differences in timing ability have been observed across tasks and despite practice. Brown proposed that individual differences in "temporal sensitivity" resulted from varying ability to detect small differences in duration, and considered that significant variability due to differences in ability could increase the frequency of type II errors in time research, impeding the refinement of interval timing models.

The present study seeks to reproduce previous findings for individual differences and extend them to timing intervals greater and less than 500 ms. Examination of the psychological time literature led to the consideration of a number of potential sources for variability that may contribute to individual differences. We measured timing interval judgments using established psychophysical methods and compared the psychophysical performances to tasks found in standardized clinical psychometric tests. We believed that cognitive resources similar to those required of a time judgment task could also be expressed psychophysically as a measure of timing sensitivity. The main goals of the present study were to examine the reliability of individual differences in timing sensitivity, and to describe these differences in terms of the perceptual and cognitive processes from which time judgments are believed to be derived.

Terminology and General Methodology

A variety of terms are used to describe time perception. The terms temporal processing, temporal integration, and timing are often used interchangeably for describing a wide range of behaviours. Some researchers argue that the use of vague terms such as these has led to a considerable degree of ambiguity in the time perception literature. This ambiguity is most likely derived from the equivocal research findings and conflicting theoretical models and the proposed timing mechanisms that underlie them. For example, the term "time perception" is used by some researchers to describe timing behaviour that occurs over very short durations, (less than one sec), while "time estimation" is used to describe timing intervals greater than one sec. Other researchers, however, may use these terms interchangeably regardless of duration. The question of whether durations of less than one second and more than one second require similar or different timing mechanisms has yet to be fully addressed.

Humans process temporal information and generate timed behaviours over a large time scale, from microseconds to daily and yearly seasonal patterns, a range of at least 10 orders of magnitude (see Buonomano & Karmarkar, 2002, for a review). Although the terms "time perception", "time estimation", and "timing" may be used interchangeably, some studies have proposed that different neural mechanisms contribute to the temporal processing over the course of microseconds (μs), milliseconds (ms), seconds (s), and circadian rhythms (hrs) (e.g., Buonomano & Karmarkar, 2002; Fraisse, 1984; Rammsayer, 1994, 2002). For example, Kapfer et al. (2002) examined characteristics of neural mechanisms that operate within the μs range, focusing on the axonal conductance of a signal in auditory streams that are involved with isolating the spatial location of a sound source. In humans, the time for a sound signal to travel between the left and right ear is approximately 600 to 700 μs. These intervals are used to calculate the spatial location of a sound source. The neural mechanism proposed to account for such high-speed temporal processing includes delay lines, the axons of neurons in the cochlear nucleus, and coincidence detectors, neurons in the medial superior olive. However, this timing mechanism is not capable of duration or sequence discrimination (Buonomano & Karmarkar, 2002).

Millisecond processing generally refers to those time intervals below 1000 ms. This processing has been referred to as "perceptual timing", and is described as fast parallel processing that is not accessible to cognitive control (Michon, 1985; Rammsayer, 1994, 2002; Rammsayer & Lima, 1991). The ability of athletes and musicians to perform well-timed and coordinated sensory-motor events is believed to rely on trained neural connections that regulate timing in the millisecond range. Although this level of processing is not well understood, it is believed to account for virtually all temporal cues used for speech and vocalization discrimination, as well as, cues for visual, somatosensory, and motor processing (Lewkowicz, 2002; Merzenich, Schreiner, Jenkins, & Wang, 1993).

Psychophysics has determined that the shortest stimulus duration that can be detected ranges from less than 10 ms to approximately 150 ms, depending on the sense modality, the physical characteristics of the stimulus, and the participant's level of practice with the task (see Macar, 1985, for a review). The shortest required duration for detection of a single event occurs with audition, presumably because refined auditory discrimination is necessary for detecting patterns in speech (Coren, Ward, & Enns, 1994). Buonomano and Karmarkar (2002) propose that time perception on the scale of ms represents the most complex form of timing, as it may involve neural mechanisms that rely on independent mechanisms for processing information about order, duration, intervals, inter- and intramodality timing, and motor timing.

Timing on scales longer than a second is often referred to as "time estimation" (Fraisse, 1984; Rammsayer, 1999, 2002). This process is believed to rely more heavily on memory processes (Fraisse, 1984) or on conscious and cognitive control (Rammsayer & Lima, 1991). However, there is dissension in the interval timing literature concerning the necessity for two separate models (i.e., time perception and time estimation) for describing durations that span the one second range. Some researchers (e.g., Buonomano & Karmarkar, 2002; Rammsayer, 1999) argue that distinct neural mechanisms underlie millisecond and second timing, while others (e.g., Ivry & Hazeltine, 1992; Lejeune & Wearden, 1997) argue that timing within these ranges can be explained by a similar timing mechanism.

Humans also track time through circadian rhythms. Circadian timing is involved in the regulation of numerous behavioural and physiological rhythms (see Kalat, 1998, for a review). Sleep-wake behaviours, thermoregulation, fluctuations in appetite, and a variety of hormonal and metabolic oscillations are all examples of cyclical phenomena that occur on a daily basis. Circadian clocks are generally not considered when investigating interval timing behaviour, as they appear specialized for time tracking on a relatively long time scale. However, circadian clocks regulate periodicities (e.g., level of arousal) that influence shorter timing intervals. Level of arousal is included in a number of timing models and is believed to have large influence on the timing accuracy.

Duration judgments are influenced by the experimental methods from which they are derived (see Block, 1989, for a review). Experiments typically use one or more of four major types of duration-judgment methods: production, verbal estimation, reproduction, and comparison. With production methods, the experimenter asks the participant to delimit a verbally-stated duration. For example, a participant may be told to press a key on a keyboard at the start and end of what is to be judged a 60-s interval. With verbal estimation methods, the experimenter delimits a duration by presenting a signal that marks the start and end of a time interval, and the participant is asked to estimate the duration in conventional time units. Both production and verbal estimation methods require a “translation” of duration into conventional time units (Block, 1989, p. 337). The translation process is believed to account for the greater intersubject variability found with these two types of time estimation tasks. With reproduction methods, the experimenter delimits a duration, and then the participant is asked to delimit a duration of equal duration. Because reproduction and production methods require that the participant activate and terminate some response device, these estimates involve motor response latencies which may contribute to timing measure variability, particularly for shorter durations. Finally, with comparison methods, the experimenter delimits two successive durations and the participant is asked to make a judgment concerning their relative lengths. For example, the participant may be asked whether the second of two successive durations is longer or shorter than the first. It is this method that requires prothetic response judgments (e.g., “shorter”, “longer” or “the same”), thus allowing experimenters to ascertain difference thresholds based on temporal discrimination performance. It is through the use of psychophysical methods that a researcher can truly evaluate the timing *sensitivity* (i.e., inverse of threshold) of an individual.

Experimental results must be interpreted within the context of the experimental method used. Seemingly opposite results, such as “overestimation” and “underestimation,” have been observed when comparing different methods. For example, a participant may underestimate a 30-second duration by producing a 20-second duration while the same participant may overestimate a 30-second duration by verbally judging it to be 40 s long. In both cases, the participant’s experience of duration is lengthened relative to an objective clock time.

People can judge duration in a veridical way if an event lasts more than a few hundred ms. As durations increase, so do time judgments in an approximately linear way within 0.5 seconds to a few minutes (Block, 1990). There has been much debate in the time perception literature concerning the psychophysical nature of time. Research was focused on determining whether the relationship between clock time and subjective time is a power function, as is the case for most prothetic continua, or a linear function, described by Weber’s Law. Early research generally presented data in terms of over- and underestimation of time intervals (i.e., subjective estimates described in terms of its proportion to the objective duration). These results were mixed, with support for both linear and power characterizations (see Allan, 1979, for a review).

For prothetic continua, the psychophysical law governing the relationship between stimulus magnitude and psychological magnitude is generally accepted to be a power law, where the psychological magnitude (P) grows as a power function of the stimulus magnitude (S).

$$P = k S^x$$

In the formula, the value of the constant k depends on the units of measurement and the value of the exponent x differs from one sensory continuum to another. For time duration, x was often found to be 0.9 or 1.0, leading researchers and theorists to consider that the data could be adequately fit with a linear function, such as Weber's Law (Getty, 1975). Weber's Law asserts that the increment in duration, $^{\Delta}T$, required to produce a fixed level of discriminability is a constant proportion of the standard duration, T (Getty, 1975). This increment, $^{\Delta}T$, is described as the just noticeable difference (*JND*) found between two stimulus durations, and in a discrimination task, can be estimated from the slope of the psychometric function. One statistic that has been used to describe the *JND* is the standard deviation (*SD*). Thus, if Weber's law holds, the *SD* of the distribution of temporal intervals generated in a scaling task should be directly proportional to the mean duration value being estimated, and the ratio $SD\ (T) / T$, the Weber fraction, should be a constant, independent of T. The time perception literature reports this to be true for interval timing across the hundreds of ms to seconds range, with Weber fractions ranging from approximately 5% to 10% (Allan, 1998).

Past Research

The study of psychological time has spanned more than 140 years. Due to the volume of literature associated with this area of research, a thorough review of the subject matter will not be presented here. Alternatively, a review of the literature judged to be critical to the development of our present knowledge concerning time perception and interval timing, and, in particular, those research findings that provide a framework for the methodology of the present study are presented. Readers who wish to learn more about the research area are referred to general reviews of the time perception and estimation literature (e.g., Allan, 1979; 1998; Block, 1990; Block & Zakay, 1997: 2001; Fraisse, 1984).

The Perception of Simultaneity, Succession, and Order

In 1890, William James speculated about many issues concerning temporal experience that would continue to challenge researchers for more than a century. James described temporal experiences such as simultaneity versus successiveness, the "specious present," and memory for duration. He proposed that the specious present or our experience of "now" represents the few seconds of our current experience that is neither past nor future. More recently, it has been proposed that, depending on the state of the participant, the perceptual experience of ongoing events (i.e., the length of "now") can vary (Michon, 1985), where the magnitude of the difference between internal and external event onset (as assessed by the internal successions of biochemical and electrical events) determines the subjective experience of the speed at which time passes. If the onset of internal events occurs relatively early with respect to corresponding external events, then the argument goes that time will appear to pass slowly, expanding the subjective duration of "now." Conversely, if the onset of internal events occurs relatively late with respect to corresponding external events, then time would appear to pass quickly, shortening the experience of "now."

Some of the oldest questions in experimental psychology concern the perception of simultaneous events and how far apart these events have to be before participants can perceive them as sequential (see Fraisse, 1984, for a review). The transition from simultaneity to succession can be studied by presenting participants with a series of pairs of stimuli of variable duration, and having the participants judge whether two stimuli, a standard and a comparison test duration, are same or different. For time intervals in the 150 to 1500 ms range, the difference-discrimination thresholds are about 5% to 10% of the standard. However, the value of this Weber fraction varies depending on sense modality. Further, thresholds are higher when (1) a time signal in one modality is compared to one in another modality, (2) when two different modalities are involved in the delineation of a single time interval or (3) when the onset and offset of a time signal is presented to one modality but delivered to opposite cortical hemispheres (Grondin, Ivry, Franz, Perrault, & Metthe, 1996; Rousseau, Poirier, & Lemyre, 1983). The perception of successiveness by a trained participant is near 10 ms for auditory stimuli and 30-40 ms longer for visual stimuli (Fraisse, 1984). This difference is believed to be due to the longer latency for perceiving visual stimuli. Researchers have noted that an auditory stimulus is generally perceived as being longer than a visual stimulus, even when the two are presented simultaneously (see Wearden, Edwards, Fakhri, & Percival, 1998, for a review). Some researchers propose that an internal clock pacemaker may run faster for auditory than for visual stimuli (e.g., Wearden et al., 1998), while others consider that intermodal differences in thresholds reflect variable access by different modalities to a central timing mechanism (e.g., Westheimer, 1999).

Perception of order is also a fundamental aspect of temporal experience. Hirsh and Sherrick (1961) conducted a series of experiments that measured the duration required to perceive an order to stimuli of different attributes presented during different time intervals. They concluded that the perception of order requires approximately 20 to 40 ms, regardless of sense modality, stimulus intensity, or spatial location of the stimuli. However, other researchers found discrepancies between successions of stimuli (i.e., acoustical clicks, flashes of light) and successions of perceptions reported (e.g., Oostenbrug, Horst, & Kuiper, 1978; see Fraisse, 1984, for a review) thus indicating that judgments are subject to stimulation bias.

The different sensory systems are characterized by principally different mechanisms of transduction. As a consequence, the time course for transduction is also different and this could account for inter-modal time judgment differences. One popular explanation for the perception of succession and temporal order between two stimuli is the independent channels theory (e.g., Sternberg & Knoll, 1973). According to this theory, information is transmitted through specific channels and reaches a central processor at an arrival time that is determined by the interaction of the signal's specific characteristics (e.g., modality, intensity) and detection criteria. Order judgments are determined by the difference between the arrival times of the information presented through distinct channels. However, cross-modal studies, where different stimuli are presented to different sensory systems, suggest that perceptual experience may not match the actual sequence of external events. The independent channels theory proposes that information transmitted through different channels cannot enter the central processor at the same time, thus, the theory describes the correspondence (or lack of) between external events and perceptual experiences as due to the interaction of signal characteristics and detection criteria. As mentioned previously, thresholds for time discrimination tasks (i.e., judging which of two intervals is "longer" or "shorter") are lower when time intervals are bounded by similar stimuli operating within the same modality, for example, tones or flashes of light (Grondin & Rousseau, 1991; Rousseau, Poirier, & Lemyre, 1983) versus an initial tone and a terminal flash of light (and vice versa). Researchers speculate that the modality of a stimulus interacts with the expected probability of a particular signal type, and so increases or decreases in the latency to begin and/or end timing depend on the experimental context (Meck, 1984; Penney, Holder, & Meck, 1996).

Retrospective versus Prospective Experimental Paradigms

Early time perception researchers have speculated that retrospective time judgments, where a participant is not forewarned that a time estimate is required, invoke different mechanisms than prospective time judgments, where a participant knows in advance that a time estimate is required (e.g., Gilliland, Hofeld, & Eckstrand, 1946). Retrospective estimation was observed to be dependent on the memory of events that occurred within the time interval. Researchers noted that if the interval was filled with many events, it would be remembered as long, and if the interval was uneventful or unfilled, it would be remembered as short. Prospective estimation was also observed to depend on the amount of events during the interval. However, early experimental results were equivocal (see Gilliland et al., 1946; Harton, 1938a, 1938b, for a review).

The retrospective method was extensively used by Ornstein (1969), who asked participants to perform various memory or discrimination tasks that involved more or less complex stimuli (e.g., words, geometric figures). After a specified time period, participants were then asked to estimate the duration of the tasks. Subjective duration was observed to increase with the quantity and complexity of the information that was processed. From his observations, Ornstein (1969) proposed that psychological time is a cognitive construct that uses retrieval to gain information about the stimuli encoded during the time interval. His model, called the storage-size model, proposed that when more stimuli are encoded during a measured time period or if stimuli are encoded in a more complex way, the duration experience is lengthened.

There was little agreement on the basic phenomena that contribute to the estimation of time intervals until the seminal work of Hicks, Miller and Kinsbourne (1976). These researchers identified specific factors that contributed to prospective or retrospective time judgments. They concluded that in the case of retrospective judgments, because there is no deliberate attending to time, estimates are directly related to the number of stimuli processed during the time interval, and are highly variable due to individual differences in memory and/or encoding processes.

Conversely, in the prospective paradigm, because participants know they will be asked to make a time judgment, they actively attend to the passage of time which facilitates the proper encoding of stimuli germane to cognitive time estimation. Hicks et al. argued that as the amount or complexity of stimuli presented during a prospective timing task increases, attentional resources available for the encoding of relevant temporal information are reduced, therefore shortening time estimations. Thus, in contrast to retrospective estimates, prospective estimates are inversely related to the amount or complexity of stimuli processed during the time interval.

A recent meta-analytic review of prospective and retrospective time studies (Block & Zakay, 1997) concluded that prospective judgments are longer and less variable than retrospective judgments. Level of difficulty of a concurrent nontiming task was identified as the most important moderator of prospective judgments, with judgments decreasing in length as the difficulty of the task increased. Retrospective judgments however, are selectively influenced by duration length and stimulus complexity, with judgments increasing in length as the complexity increased, particularly within the context of relatively shorter durations.

In prospective time experiments, the participant's timing behaviour is often described as "attending to time." Block (1990) has objected to the use of this term and others such as "attention to time," stating that these terms are too vague. Some researchers have elaborated on the meaning of these terms (e.g., a perceptual readiness to process temporal cues, Zakay, 2000), however, attentional mechanisms remain poorly explained within prospective timing models, and there is considerable debate about the relative contributions of attention, memory, and arousal, to accurate timing (see Lejeune, 1998, 2000; Zakay, 2000, for a review).

Some researchers consider attention to time to be similar to attention to any other perceptual or cognitive event (Michon, 1985; Michon & Jackson, 1984; Zakay, 2000). Thus, prospective judgments are largely determined by the allocation of attention to time (Zakay, 1993). This view is supported by evidence that suggests time perception to be an effortful process that draws from limited attentional resources (e.g., Brown & West, 1990; Burnside, 1971; Hicks, Miller, Gaes, & Bierman, 1977; Macar, 1996; Macar, Grondin, & Casini, 1994; Marshall & Wilsoncroft, 1989; McClain, 1983; Zakay, 1993). When participants are asked to judge a time interval while performing a nontiming task (i.e., concurrent tasks, or a dual-task time experiment), estimates become progressively shorter as the attentional demands of the nontiming task increase. These results suggest that accurate timing requires attentional resources that may not be fully available when the participant must also attend to other tasks. This idea is substantiated by the effects of prospective versus retrospective methods, where the former induces the increased allocation of resources to time perception.

A limited attentional capacity implies that the more capacity required for one task, the less the spare capacity available for a second task. Consequently, the level of performance on the second task becomes lower (e.g., Kahneman, 1973). In fact, Macar et al. (1994) noted that estimates of duration shortened as the proportion of attention devoted to the timing task decreased (e.g., when participants were instructed to devote 75% of their attention to the timing task and 25% to the nontiming task). The results of dual-task time experiments suggest that the nature of the nontiming task (e.g., sense modality, stimulus complexity) may also determine the extent to which a second task interferes with attention to the primary timing task (Brown, 1997; Brown & Boltz, 2002; Brown et al., 1990). A number of hypotheses have been proposed to account for the sharing of attentional resources (e.g., Navon & Gopher, 1979; Wickens, 1984). For example, multiple resource theory (Wickens, 1984; 1992) proposes that a pool of relatively unspecialized processing resources is available for all tasks, as well as, separate pools of specialized processing resources that contribute preferentially to particular tasks. The model predicts that tasks that draw upon different sense modalities require different attentional mechanisms (i.e., visual versus auditory) thus making the tasks less likely to interfere with each other (Wickens, 1992). Baddeley's working memory model (1990) makes similar predictions, and interference effects due to the performance of a second task in the prospective experimental paradigm have also been attributed to the limited capacity of working memory (e.g., Brown, 1997; Fortin & Rousseau, 1987; Fortin, Rousseau, Bourque, & Kirouac, 1993; Venneri, Pestell, Gray, Della Sala, & Nichelli, 1998).

If time perception involves attention and working memory, cognitive resources that can be limited by processing demands, and specialized processing resources contribute preferentially to particular tasks, depending on the sense modality, then it is important to recognize the influences of working memory and attention mechanisms under all timing intervals and timing tasks. Current theoretical models for interval timing recognize the importance of these influences, however, research that investigates the interaction of cognitive processes with duration-specific or modality-specific timing tasks has been limited.

Current Theoretical Models for Interval Timing

Current theoretical time estimation models are derived from research that describes temporal experience and time judgments in terms of information processing theory. In the 1950's, the integration of theories concerning artificial intelligence, cybernetics, and neuroscience, provided new approaches for investigating the psychology of time, and researchers began to focus on cognitive processes that could account for the psychological construction of time (see Block & Zakay, 2001, for a review). Early models described interval timing as primarily determined by sensory processes (e.g., changes in timing behaviour due to fluctuations in body temperature, Hoagland, 1933, 1935) or alternatively, by cognitive processes (e.g., Ornstein, 1969).

The majority of models proposed that subjective time depends on the accumulation of discrete elements during a time interval, such as the density of perceived changes (Fraisse, 1963), the mean number of events perceived (Frankenhaeuser, 1959), or the number of internal pulses (Creelman, 1962; Treisman, 1963). Sensory-based models described psychological time as relying on a repetitive and cumulative process, where a pulse-dispensing mechanism delivers internal time signals. Cognitive-based models described psychological time as resulting from cognitive factors that underlie the experience of duration, such as the generation of images, changes from one event to another, storage size, or the number of perceived events. More recently, however, to avoid the arbitrary delineation of a disembodied sensory from a higher cognitive or perceptual process, the terms "sensory-process based" and "cognitive-process based" have given way to such terms as "timing-with-a-timer models" or "timing-without-a-timer models" (Ivry & Hazeltine, 1992). Timing-with-a-timer models use terms such as "attention to time" and "temporal information processing" to explain perceived duration (e.g., Gibbon, Church, & Meck, 1984; Thomas & Weaver, 1975; Zakay & Block, 1995, 1996). These models describe mechanisms that involve real-time processes. Timing-without-a-timer approaches do not propose an explicit timing mechanism. While Ivry and Hazeltine use the timing-without-a-timer distinction when they refer to retrospective models, we use the term here when referring to any model that does not include an explicit timing mechanism. These include approaches that focus on aspects of timing, such as, the relationship between timing and the nature or amount of material stored or accessed during an interval, the contextual nature of nontemporal information during an interval, and the temporal patterning of nontemporal information (e.g., words, tonal pitches, lights) in terms of event coherence (e.g., Block, 1989; Boltz, 1991; Fraisse, 1963, 1984; Ornstein, 1969). A more detailed overview of these two theoretical perspectives is provided in the following sections.

"Timing-with-a-timer" Models

These include chronobiological and internal-clock models. Gooddy (1958) proposed that organic periodicities, including glandular, autonomic nervous system cycles, and periodic neuronal discharges, provide the basis for all temporal processing. This idea led to the development of models that are primarily guided by the influence of a nervous system that is linked to neural timers (see Ivry and Hazeltine, 1992, for a review). The scalar timing model (Gibbon, Church, & Meck, 1984), currently the predominant internal clock model in the literature, assumes that the speed of a neural timer is determined by the level of arousal within the nervous system.

A fundamental question regarding temporal processing is whether it relies on a single centralized mechanism (i.e., a single neural timer) or is distributed throughout different areas. Theoretically, if timing is centralized, then performances for time discrimination tasks presented in the visual, auditory or somatosensory modality, as well as, motor timing tasks, would use the same group of neurons, and performances should be highly correlated. Experimenters have tested this hypothesis using data obtained from perceptual and motor timing tasks (e.g., Ivry and Hazeltine, 1995; Keele et al., 1985). Two types of correlations were analyzed, those between different modalities for the same time interval and those between different intervals in the same modality. High correlations in the former analysis would suggest a central timekeeping mechanism that is used across modalities, however, there remains the possibility that independent timing mechanisms are involved in the timing of different durations. If a high correlation is also observed between intervals, the analysis would support the notion that one central clock is being used for all intervals.

Keele and colleagues (1985) studied individual timing variation using trained pianists and nonmusicians. The hypothesis that the production of time intervals by different motor effectors (right forefinger and right foot in right-handed participants) and the judgment of perceptually-based time intervals share a common, central timing mechanism was tested, with the assumption that trained pianists would be “good timers,” exhibiting more accurate and less variable motor production and perceptual judgments than nonmusicians. Measures of timing ability were derived from time judgments in a comparison task, where participants were asked to judge whether a second test interval was longer or shorter than the standard duration (400 ms) that preceded it. Difference scores were calculated using lower and upper threshold measures (i.e., the length of durations necessary for perceiving the comparison as "shorter" or "longer than" the standard). The pianists exhibited significantly smaller threshold difference scores on the perceptual timing task than did non-musicians. Further, this greater temporal sensitivity was associated with greater motor regularity and speed. Keele et al. concluded that motor timing variance is derived from two sources, one in common with perception and the other with motor effector speed. Central clock variance was proposed to account for the former. The musicians were found to be “good timers,” exhibiting reduced central clock variance, as reflected in more accurate and reliable perceptual timing and decreased motor variance.

Ivry and Hazeltine (1995) used slope analysis as a method for measuring variability in time perception and motor tasks (finger tapping) across a range of interval durations. By varying the test interval, growth of the variability function (i.e., ratio of total variability to mean intertap interval) could be compared across time perception and motor tasks. Ivry and Hazeltine proposed that if the perception and production tasks are composed of a separate duration-dependent and a duration-independent source, then the variability function would be equivalent for those tasks that shared a common duration-dependent mechanism. It was assumed that the duration-dependent variance reflected the operation of an internal clock, since other processes, such as signal detection or motor implementation, should remain constant across different durations. Ivry and Hazeltine's experimental results supported their hypothesis, as the increase in the variance as a function of duration was comparable for the two tasks. Assuming this duration-dependent component of the variance provides an estimate of variability in an internal timing mechanism, these results implicate a common timing process in the two tasks.

Ivry and Hazeltine (1995) also noted that variability of perceptual judgments was reduced on many repetitions of a test interval, and was most reduced for perceptual judgments of intervals that were equal in duration to those produced in the tapping task. In other words, finger tapping appeared to assist in the perceptual representation of a test interval. Ivry and Hazeltine proposed that an interval timer was shared by the perceptual and motor tasks, where the timer recorded the duration between finger taps, and this temporal memory was used for making judgments about the relative duration of subsequent test intervals (i.e., equal to, shorter, or longer than).

A common feature of biological clock theories is the presence of some oscillatory process, analogous to the swings of a clock's pendulum, whose cycles can be counted by some other mechanism. Oscillator-based models (e.g., Treisman, Faulkner, & Naish, 1992) assume that oscillator pulse speed is influenced by general and specific states of arousal, with pulses that correspond to times at which stimulus events are expected.

The internal clock and the temporal oscillator. The most influential "timing-with-a-timer" model in the psychological literature has been Treisman's (1963) internal clock model. The clock is a hypothetical, centralized mechanism in which a neural pacemaker generates pulses. It includes a pacemaker and counter mechanism that together facilitate the building of an internal representation of any given time interval. The pacemaker produces a regular series of pulses that travel along a pathway, the rate of which varies as a function of arousal due to external stimuli. The more arousing the stimuli, the more the pacemaker rate increases. The number of pulses generated by the pacemaker within any given time interval is recorded by a counter and transferred to a memory store and a comparator mechanism. Subjective judgments concerning the duration of any given time interval are made by comparing stored representations with the current pulse count.

Treisman's model (1963) has provided the framework for more recent models that describe interval timing, such as the scalar timing model (Gibbon et al., 1984) and the attentional gate model (AGM, Zakay & Block, 1995). These "timing-with-a-timer" models will be reviewed following a description of Treisman's more recent research (Treisman, Cook, Naish, & MacCrone, 1994; Treisman, Faulkner, & Naish, 1992; Treisman, Faulkner, Naish, & Brogan, 1990). Treisman and colleagues (1990, 1992, 1994) proposed a model for an internal temporal pacemaker that underlies timekeeping in perception and action. Like Treisman's earlier model, the pacemaker output frequency increases on increased arousal due to sensory stimuli, however, the new model proposes that output frequency may also be influenced by a central monitoring mechanism. The basic idea of the model is that external periodic stimulation, such as auditory clicks and visual flicker, may drive the pacemaker if its frequency is close enough to the pacemaker rate. The pacemaker includes a temporal oscillator, comprised of a self-exciting network of elementary units that emits a regular series of pulses at a characteristic oscillator frequency, and a calibration unit that receives these pulses and emits a new pulse stream to be used for temporal processing demands. When the frequency of an external periodic stimulation is slightly faster or slower than the temporal oscillator, entrainment occurs, leading to prolonged increases or decreases in pacemaker speed, respectively. Using visual and auditory stimulus trains of various frequencies in motor and perceptual timing tasks, Treisman and colleagues proposed that the temporal oscillator's characteristic frequency consists of harmonics of 12.4 Hz.

Variations of Treisman et al.'s (1990, 1992, 1994) methods have been used by a number of time researchers for examining the effects of external signal trains on duration estimates (Burle & Casini, 2001; Droit-Volet & Wearden, 2002; Penton-Voak, Edwards, Percival, & Wearden, 1996). The results of these experiments suggest that Treisman et al.'s method for increasing pacemaker speed lengthens the subjective experience of time relative to objective time (i.e., shorter productions, or greater verbal estimates).

In a number of experiments that used different time-judgment methods, delivery of 25 Hz auditory click trains before or during timing tasks resulted in estimates of duration predicted by an increase in pacemaker speed (Burle & Casini, 2001; Penton-Voak et al., 1996). Burle and Casini reported a dissociation between activation and attention effects in the production of 1100 ms time intervals. When these factors were manipulated jointly, using 62 dB(A) or 77 dB(A) 25 Hz click trains during single or dual experimental tasks, they showed additive effects on the timing performance measures. Distribution analysis using the data from the low (62 dB) and high (77 dB) activation conditions suggested that the high, but not the low, activation condition resulted in a long-lasting effect that increased as the duration being timed increased. In the high activation condition, time performances reflected a lengthening of subjective time relative to objective time (i.e., shorter time productions). These findings suggested that the "louder" auditory click train induced an increase in pacemaker speed with subsequent increased rate of pulse accumulation, as manifest by shorter time productions.

Droit-Volet and Wearden (2002) trained children (from 3 to 8 years of age) on a temporal bisection task in which two standard intervals, one short and one long, are compared to test intervals of intermediate duration (this task is more thoroughly described in the next section). During preliminary training, visual stimuli in the form of a blue circle denoting the standard duration interval preceded by a white circle of five sec duration. Following training, the children were presented with test intervals (visual stimulus same as that during training) preceded by a white circle of five sec duration that was either constant or flickering. Time judgments in the constant white circle and flicker condition varied considerably, and were consistent with the idea that the repetitive flicker had increased the speed of the pacemaker of an internal clock. Specifically, in the flicker condition, judgments of test intervals (i.e., "Is the test interval more similar to the shorter or longer standard duration presented during training?") revealed a subjective shortening of duration with a greater tendency to judge the longer durations as being more similar to the shorter standard interval that was presented during training.

A number of quantitative theories describe faster pacemaker speed as producing less variable memory representations and/or time estimates (e.g., Gibbon, 1977; Killeen & Fetterman, 1988). If the number of pulses counted during a given time interval is the internal representation of this interval, then the greater the internal clock speed, the finer the temporal resolution of the clock. Thus, while the subjective experience of duration is increased under conditions of greater pacemaker speed, individuals may have greater ability to detect small differences in duration given the finer temporal resolution of the clock.

The mechanism for inducing increased pacemaker speed via visual flicker likely involves the interaction of cell assemblies in the visual pathway. Research has shown that the neuronal activity of the retina and the occipital cortex increases as the frequency of flicker increases (e.g., Curran & Wattis, 1998, 2000; van der Tweel & Lunel, 1965). The highest degree of cortical response is observed in the occipital lobe, with additional increased activity present in the temporal and parietal lobes (Curran & Wattis, 1998, 2000; Küller & Laike, 1998). This suggests that the processing of visual flicker is not functionally localized and presents the possibility that flicker may entrain brain regions that are not visual modal specific, but in actuality centralized pacemakers.

The temporal information processing (TIP) model. Theoretical developments in human and animal timing proceeded independently of each other until Gibbon, Church and Meck (1984) presented an internal-clock, information-processing model called the scalar timing model. Designed to predict animal timing behaviour, the model includes attention, memory, and decisional processes. Partially due to its cognitive emphasis, the scalar timing model has become the dominant force in human timing literature (Ferrara, Lejeune, & Wearden, 1997; Rakitin et al., 1998; Wearden, 1991, 1999). The quantitative version of the scalar timing model was derived from the scalar expectancy theory (SET; Gibbon, 1977), which describes animal timing responses as based on the expectancy of reinforcement. The mathematics of SET reflect a relativistic Weber's Law property, where subjective time is produced by an underlying timing mechanism that exhibits two properties: 1) subjective time is scalar in nature, i.e., the distribution of responses is proportionate to the mean; and 2) the central tendency of the response distribution matches real time.

More recently, the scalar timing model has been referred to as the temporal information processing model (TIP; Lejeune, 1998; Zakay, 2000). Descriptions of the TIP are essentially equivalent to those for the scalar timing model. The model accounts for time perception in the millisecond to seconds range; however, experiments typically use durations that are approximately one second or less in length.

The timing mechanism described by the TIP is divided into three sequential stages, as outlined in Figure 1. The first stage involves a clock or pacemaker which emits pulses at a rate determined by the level of arousal (left-most oval in Figure 1). Lower arousal is associated with slower pulse rates, higher arousal with faster pulse rates. The pacemaker is connected to an accumulator (right-most oval at clock processing stage in Figure 1) that stores pacemaker pulses following the flip of a switch (center oval, clock processing stage in Figure 1). The switch determines the mode of information processing, and will allow pulses to pass to the accumulator when it is in "closed" mode. Thus, when the switch is in closed mode, temporal information processing may begin. The switch is closed when the participant has received the signal (auditory or visual) that timing has begun (oval at input stage in Figure 1). The latency to close the switch varies as a function of the expected probability of a particular signal type. Signals that can be reliably anticipated in terms of spatial location, temporal location, and/or sensory modality, allow for the rapid initiation of pulse accumulation. For example, the anticipation of a visual signal allows the participant to direct attention to the "visual channel," before signal onset and this facilitates the initiation of signal processing with an immediate flip of the switch.

The second stage of the TIP involves memory processing. The accumulator, which contains the pulse store, downloads its contents to STM/working memory (left oval at memory processing stage in Figure 1) while another more or less direct copy of accumulator contents is stored in a longer-term memory called reference memory (right oval). The third stage involves decision-making, where STM and reference memory stores are compared (diamond in Figure 1).

The participant makes a judgment concerning the duration of the present interval (i.e., in STM) using the reference memory store as the standard for comparison. Various response behaviours are possible depending on the results of the comparison and the experimental task used.

Research using the TIP model has been reviewed by Allan (1998) and Ferrara et al. (1997). Two types of tasks, the temporal generalization task and the bisection task, are often used by studies examining the TIP. The temporal generalization task involves identification of a single standard duration. Participants are first presented a stimulus of a given standard duration (e.g., a tone of 400 ms duration, Wearden, 1992) and are then presented with stimuli that are longer, shorter, or equal to the standard. The participants must then decide, usually using a binary "Yes" - "No" response, whether the test duration was the same as, or different than the standard. A "gradient" of responses for each individual can be examined by plotting the probability of "Yes" responses as a function of test stimulus duration across trials. For humans, the proportion of "Yes" responses plotted against stimulus duration usually yields a temporal generalization gradient which peaks at the standard duration and is skewed to the right (i.e., positively skewed). Thus, test durations physically longer than the standard tend to be identified as equal to the standard more often than test durations that are physically shorter than the standard. In contrast, rat studies show flatter and nearly completely symmetrical generalization gradients, with test interval durations of equal temporal distances above and below the standard interval producing nearly identical response probabilities (see Wearden & Ferrara, 1995, 1996, for a review).

Another task frequently used in TIP studies, the bisection task, follows a preliminary training period, where the participant receives extensive practice for identifying two standard stimulus durations, one of short duration and the other of long duration (e.g., 200 ms and 800 ms). The participant is then presented with a series of test intervals (trials) of intermediate duration. On each trial, the participant is required to judge the test interval as being more similar to the shorter or longer standard duration that was presented during training.

Research using the scalar timing model (TIP) has found general trends in animal timing, where the accuracy and variability of interval timing performances varies from species to species (Wearden, 1991). Humans produce more sensitive timing than rats and cats, and these animals in turn produce more sensitive timing than pigeons, fish, and turtles. Further, there appears to be an important distinction between animal and human performances as timing tasks become more "difficult." Ferrara et al. (1997), who observed increasing sensitivity to duration as the difference in duration (i.e., between a test and standard interval) approached zero, proposed that difficult time discrimination tasks (i.e., when duration differences are slight) may be more arousing than easier ones. This explanation assumes that humans can modulate their level of arousal for meeting the demands of timing tasks. This kind of adjustment cannot be accounted for with the TIP model, where level of arousal does not affect timing processes already in operation.

Mathematical modeling techniques have been applied to temporal generalization and bisection task data for generating hypotheses concerning human timing sensitivity (see Ferrara et al., 1997, for a review). Based on these analyses, human coefficients of variation derived from the temporal generalization task are typically less than those found in other species. This has been attributed to an accelerated decrease in the response threshold as the length of the test duration approaches that of the standard duration in reference memory. The increased sensitivity of human time judgments on the temporal bisection task has been explained in terms of a decrease in the response threshold under more difficult conditions, rather than changes in the representation of the standard duration. These findings suggest that, for humans, there is more sensitive behavioural adjustment to presented durations under conditions in which the timing task demands discrimination between more closely spaced stimuli. Lejeune and Wearden (1997) acknowledged the possibility that the SET model may need to incorporate explanations for some of these effects in terms of attention to duration and/or arousal-induced changes in the speed of the internal clock. These explanations may more accurately reflect the human advantage of higher-end functioning versus animals lower in the phylogenic scale.

Inter-individual differences in timing sensitivity have not yet been investigated using the TIP model. SET, the mathematical model from which TIP was derived, requires that at least one source of timing variance be scalar (i.e., a constant coefficient of variation), and that this source of variability be larger than all others. However, the literature has yet to identify the source (s) of variance that contributes to the scalar nature of timing (see Wearden, 1999, for a review). TIP research methods are designed to engage all clock, memory, and decision processes. Observations of variability in timing performances may be attributed to a number of sources, including, slower pacemaker speed, slower opening and closure of the switch, inaccurate representations of time intervals in reference memory, and/or reduced timing sensitivity induced by less stringent response threshold(s) (Lejeune, 1998).

Experimental strategies that examine the operations of one or two system components will be necessary for identifying specific sources of variance within the TIP model. However, researchers have considered that the LTM (i.e., reference memory in Fig. 1) or pacemaker speed may largely account for the accuracy and variability of timing performances. The use of experimental methods that do not invoke LTM, such as pair-comparison tasks, should reduce the number of sources of variability that must be considered. However, it would be difficult to identify the source(s) of timing variability within the interaction of pacemaker speed, switch, accumulator, working memory, and decision processes. For this reason, scalar timing research has examined the effects of pharmacological manipulations, neuropsychiatric disorders, and brain damage on TIP component processes that are believed to engage particular neurotransmitter systems and/or neural pathway operations.

Another methodological approach for investigating the influence of TIP component processes on timing sensitivity involves the presentation of a nontiming task during interval timing. Observations of changes from expected patterns of timing performance are attributed to the information processing demands of the nontiming task. The "interference effect" due to nontiming task demands, represented as increases in performance error or variability, is one of the most consistent findings in the time perception literature. Types of interference tasks include motor skills, perceptual discrimination, visual and verbal processing, memory search, and response decision (see Brown, 1997, for a review). As discussed previously, the usual effect in dual-task experiments is a subjective decrease in duration, as manifest in shorter verbal estimations and reproductions or longer temporal productions. This interference effect has been attributed to nontiming task demands on STM/working memory (e.g., Brown, 1997; Fortin et al., 1993) and/or attentional resources (e.g., Brown, 1997; Brown & Boltz, 2002). Within the TIP, STM/working memory is considered critical for holding and comparing representations of test and standard durations. Attentional factors are described at the level of the pacemaker and switch, where general arousal determines the pulse rate and selective attention influences the latency of timing onset. However, it has been argued (Block & Zakay, 1996) that the TIP fails to account for the multi-faceted nature of human attention systems, and so does not adequately describe the mechanisms that underlie human timing, which is often less rigid and more context-dependent than that of animals. For this reason, Zakay and Block (1995) proposed an attention-based model for interval timing.

Attention-based models for interval timing assume that timing operations are limited by cognitive processing demands on a moment by moment basis (e.g., Thomas & Weaver, 1975; Zakay & Block, 1995). Variability in timing is attributed to attentional allocation processes, where the degree of accuracy exhibited in timing performances is largely determined by the extent to which participants can direct their attention to the timing task.

Allocation of attention model. Thomas and Brown (1974) considered that the encoding of temporal information during a time interval is an intermittent process, with attentional resources being allocated to the processing of temporal or "nontemporal" information in an alternating manner. Thomas and Brown's theoretical framework was further developed and tested by Thomas and Cantor (1975) and Thomas and Weaver (1975) who used a mathematical model that described attentional allocation influences on duration judgments. The attentional allocation model assumes that any stimulus presented during test intervals consists of information that is analyzed or processed at various levels. Perceived duration of an interval is a function of the allocation of resources to two parallel processors that encode this information. One processor encodes temporal information, and acts as a timer. The other processor encodes "nontemporal" information about the stimuli, such as its size, intensity, and colour, and produces an output that describes the quantity of processed information, the quality of processing, and the number of changes that occurred during the interval. These two processors compete for the same attentional resources which have limited and finite capacities. Because the model assumes a constant pool of attentional resources, it does not consider the influence of arousal. Perceived duration of an interval is a monotonic function of the weighted average of the amount of information encoded by the two processors. When participants simultaneously perform a time estimate and a nontiming task, and more attention is given to the nontemporal processor, duration estimates will be shorter. Conversely, when more attention is made available for the timer and less attention is given to the nontemporal processor, duration estimates will be longer. Thomas and Weaver suggested that while the nontemporal information processor encodes some temporal aspects of the stimuli, this information is embedded in the encoding of nontemporal stimulus attributes, and must be translated into temporal units when participants are asked to provide duration judgments that are based on nontemporal processing. These judgments are less accurate and reliable than judgments based on information accumulated by the temporal processor.

The attentional gate model (AGM). Addressing the need for theoretical models that describe human time estimation, Zakay and Block. (1995) and Block and Zakay (1996) proposed the AGM (see Figure 2), a model that combines features of the scalar-timing model, Treisman's internal clock model (1963), and the attentional allocation model. AGM is nearly identical to the TIP, however, it incorporates an attentional gate that indicates the degree to which a participant allocates resources to temporal information processing. The gate allows pulses to pass from the pacemaker to the switch mechanism. If increased resources have been allocated for attending to time, either due to instruction or learning, the gate is open wide, and many pulses may pass. If fewer resources are allocated, such as occurs when the participant concurrently performs timing and nontiming tasks, then the gate either restricts the number of pulses passing through it or the opening time is reduced which in turn lowers the number of pulses passing to the switch mechanism.

The AGM proposes that the pacemaker (left-most oval, Figure 2) produces pulses at a rate influenced by both general arousal (e.g., circadian influences) and specific arousal (e.g., stimulus-induced). When attending to time, as opposed to external stimulus events, the attentional gate (second oval from the left) is opened, allowing a stream of pulses to be transmitted to the level of the switch. The degree to which the gate is open is determined by the allocation of attention to the timing task. A start signal (e.g., external stimulus event such as a tone) indicates the onset of duration, and the opening of the switch (center oval) allows the pulse stream to be transmitted to the cognitive counter (second oval from the right). The switch may be closed from a number of events during the timing task, depending on nontiming information processing demands. Within the AGM, the switch mechanism is considered a cognitive element. Governed by "the meaning system," the switch responds to signals that can influence duration estimation in different contexts in different ways (Zakay & Block, 1996, p. 155). This "meaning system" is not well described by the authors. However, it appears that the latency to open and close the switch is determined by a system that influences the degree of receptivity for receiving temporal or nontemporal information

Block and Zakay (1996) used the term cognitive counter rather than accumulator (as in the TIP model) because controlled cognitive processes such as attention, moderate its input. The total pulse count in the cognitive counter is only transferred to STM when attention is deployed; whereas, the TIP assumes that this transfer is automatic and continuous. A reference memory store (upper right-most oval, Figure 2) contains a record of the average number of pulses that have accumulated in the past with respect to specific intervals, and in humans this store may also contain learned correspondences between these pulse counts and verbal labels for specific temporal units such as a second or a minute. When the total pulse count in STM matches that in reference memory, cognitive comparison processes (lower right-most oval) elicit a response that indicates that the time period has ended. If the number of pulses does not yet match that in reference memory, then the participant will wait or judge the interval as being shorter than that in memory (response mechanism, lower-most oval in Figure 2).

While proponents of the AGM argue that there are clear differences between the AGM and the TIP, because the AGM includes multiple facets of attentional processing, TIP advocates disagree (e.g., Lejeune, 1998, 2000). Lejeune (2000) contends that the addition of an attentional gate mechanism does not provide additional explanatory power, as the processing attributed to the attentional gate mechanism could just as easily be accounted for by the functioning of the switch mechanism (see Lejeune, 1998, 2000; Zakay, 2000, for a review of this debate).

In summary, timing-with-a-timer models propose that an internal central timing mechanism governs the perception and production of interval timing. This mechanism involves biologically driven processes (i.e., an internal clock or pacemaker) and cognitive processes (i.e., attention, memory, and decision processes) that together contribute to the accuracy and variability of timing performances. Conforming to these models allows researchers to try and disentangle each of the model's components to better understand the complete time perception system. For example, entrainment might be used to manipulate low-end, biologically-driven processes, or cognitive influences on timing might be distinguished by introducing nontiming tasks that compete for common cognitive resources. Conclusions concerning the relative contributions of cognitive component processes to timing accuracy and variability might be inferred from the nature of the nontiming task. However, it should be noted that any systematic change in timing behaviour can be attributed to any of several high-end complex processes such as attention, memory, and/or decision processes. The challenge for research that employs the TIP or AGM models is to specify the unique and combined dynamics of pacemaker, attention, memory, and decision components that contribute to time judgments.

Timing-without-a-timer Models

It is important to note that the results of a number of interval timing studies can be explained without reference to an internal clock or pacemaker (e.g., Staddon & Higa, 1999). These explanations support memory models that contain intrinsic principles for explaining why timing should differ substantially depending on the precise conditions under which it is studied. Some proponents (e.g., Zeiler, 1998) have argued that the explanatory power of internal clock models is limited to the experimental methodology from which they were derived, and so they have limited ecological validity. These researchers propose that memory models have a broader scope, describing timing behaviour in interval timing tasks as well as the temporal regularities found with everyday behaviour and the apparent sensitivities to time that can be observed outside the laboratory.

Ornstein (1969) argued that internal-clock models could not explain why information-processing activities strongly influence remembered duration. As stated previously, Ornstein's storage-size in memory model proposed that the higher the complexity of a stimulus, the higher the subjective estimate of the duration of its exposure. At the time of Ornstein's experiments, cognitive psychology used the metaphor of memory processes in digital computers to describe human memory functions. More recent descriptions suggest that memory functions in a more interconnected way, where previously encoded information is continually reorganized.

Cognitive psychologists have proposed a number of different memory models in attempts to explain duration experiences. One explanation is based on the idea that humans construct and represent time by relying on information about various kinds of changes (e.g., Block, 1989; Poynter, 1983, 1989). Block (1989) considered that change and novelty are inherent in observer-environment interactions, and that a contextualist approach to understanding timing behaviours may be more useful for classifying experiments and for evaluating theories and models of psychological time. The contextualist model describes temporal experience as a changing cognitive construct that is based on the interactions of four major contextual factors: (1) the characteristics of the experiencer (e.g., sex, personality variables, animal species type), (2) the kind of temporal behaviour under consideration (e.g., simultaneity, order, duration), (3) the duration of the time period, and (4) the sensory events and activities that occur during the time period. All contextual factors are believed to interact for producing a range of temporal experiences.

Researchers have also proposed that there are different strategies for processing information about time. Losses of temporal information are observed when participants deal with structurally complicated nontemporal information. As events define time intervals, Jones and Boltz (1989) suggested that any rhythmic patterning will affect the way people attend to and judge time interval durations. These researchers examined the influence of event structure on temporal expectancies. Depending on whether events are more or less coherent, participants will adopt different strategies for attending to this information. Thus, responses to event time are shaped by the event itself. For more highly coherent temporal events (i.e., where rhythm is easily detected), time judgments are influenced by the way the event confirms or violates temporal expectancies. In the case of incoherent events, people may resort to analytic attending, where some form of rhythmicity such as counting or grouping is generated by the experiencer.

Michon (1989) proposed that two strategies may be used for processing temporal information in timing experiments: "timing your mind," and "minding your time." Timing your mind relies on the ability to attune to highly complex temporal relations in a dynamic environment. This strategy is primarily a matter of automatically processing external and internal information, a method that is continuously used for relating with an intrinsically temporal world. Conversely, minding your time is a rule-driven, conscious act that requires specific modes of abstract representation and metaphorical or formal thought. Michon provides an example of this distinction by comparing human and animal behaviours in time experiments. In a prospective time estimation experiment, a human participant is minding time because they are allocating attention to the timing task. However, a pigeon who responds to temporal cues for obtaining food rewards is timing its mind, as it associates external and internal cues through automatic processes.

In summary, timing-without-a-timer models emphasize the perspective of the time experiencer for making judgments about duration. Timing-with-a-timer models emphasize the biological and cognitive processes that mediate interval timing. However, the potential impact of certain constitutional variables has been largely ignored. Although the timing-with-a-timer and timing-without-a-timer approaches to the psychology of time appear to have developed from seemingly antithetical philosophies about perception (i.e., top-down vs. bottom-up), there are empirical findings from each that are useful for furthering the development of the other. Constitutional variables may provide a venue for the meeting of these two approaches, where cognitive mechanisms are understood as mediating temporal behaviour, and individual or group differences are examined for elucidating the parameters of cognitive processing within interval timing models.

Individual Differences in Time Estimation

In the late 1800's, important experimental work in the psychology of time examined individual differences in time duration judgments (e.g., Gilbert, 1894; Seashore, 1899). Early large-sample experiments determined that time estimation abilities differed considerably across individuals of various ages. Other early studies examined the relationship between personality traits and differences in timing behaviour (e.g., the tendency to underestimate or overestimate standard durations; see Brown, 1998, for a review). However, much of this research was unsystematic and the results were often contradictory. Inconsistencies in timing performance across a range durations (e.g., from seconds to minutes) led researchers to consider that different timing intervals may activate different timing processes. However, evidence also suggested that there is a significant degree of consistency in timing performances across minutes, hours, or even weeks (e.g., Brown, 1998; Brown et al., 1995; Danziger & du Preez, 1963; Gilliland & Martin, 1940; McCauley, Kennedy, & Bittner, 1980; Schaefer & Gilliland, 1938; Young & Summer, 1954).

Many researchers have recognized that the performances of different individuals can be extremely divergent (Fraisse, 1984), and preferred to employ trained participants for investigating invariant characteristics of temporal perception (e.g., Efron, 1974; Kristofferson, 1976, 1980; Wing et al., 1973), as the ability to discriminate between two intervals of similar duration was found to increase with repeated practice. However, individual differences in timing performance have been observed even among trained participants (e.g., Efron, 1974).

Few studies investigating individual differences in timing ability were conducted during the mid to latter half of the 20th century. However, there has recently been a renewed interest in this area of research (e.g., Block & Zakay, 2001; Brown et al., 1995; Brown, 1998; Rammsayer, 1997a). Researchers that have examined group (e.g., age, clinical group) differences interpret results in terms of timing-with-a-timer models such as the TIP and the AGM (e.g., Craik & Hay, 1999; Kirkcaldy, 1984; Perbal, Droit-Volet, Isingrini, & Pouthas, 2002; Rammsayer, 2002; Wearden, Wearden, & Rabbit, 1997). Sources of variability in these cases are described from a pacemaker, processing speed, attention and/or memory perspective.

Evidence for Individual Differences.

Eysenck (1959) introduced the idea that constitutional variables (i.e., introversion and extraversion) may account for individual differences in timing performance. Some researchers have replicated Eysenck's (1959) findings that suggest extraverts tend to estimate duration to be longer compared with introverts (e.g., Zakay, Lomranz, & Kaziniz, 1984), while other researchers have found no substantial extraversion-related differences in time judgments (see Rammsayer, 1997a, 2002, for a review). Measures of psychoticism have also been associated with individual differences in timing ability (Kirkcaldy, 1984). Rammsayer (2002) reported a relationship between psychoticism scores on the Eysenck Personality Questionnaire-Revised (Eysenck & Eysenck, 1991) and time thresholds for a duration discrimination task. Using the weighted up-down adaptive psychophysical method, and 50 ms and 1000 ms standard durations, Rammsayer presented pairs of time intervals to university students (all male, $n = 60$) who judged whether the durations were of the same or different. After each correct response, the duration of the comparison interval was made more similar to that of the standard, and after each incorrect response the duration differences were increased. The up-down procedure converged on a probability of hits of 75%. Statistical comparisons showed a significant relationship between the psychoticism dimension and timing sensitivity. Participants with higher psychoticism scores made more accurate time judgments than did those with lower scores, but only with a 1000 ms standard duration. The statistical analyses did not detect a main effect of Eysenck's basic personality dimensions for temporal processing associated with 50 ms timing.

Rammsayer (2002) interpreted these findings within the framework of the AGM (Zakay & Block, 1995, 1996) and proposed that a cognitive mechanism called latent inhibition (LI) might account for psychoticism-related differences in attentional processes. Latent inhibition (LI) refers to the phenomenon in which a previously experienced irrelevant stimulus enters into new associations less readily than a novel stimulus, presumably because of a decline in stimulus-specific attention (see Lubow, 1989, for a review). There is evidence to suggest that the magnitude of the LI effect, based on reaction times, is moderated by the dimension of psychoticism, where the effect is reduced in individuals with higher psychoticism scores (Eysenck, 1995). Because LI essentially involves screening out irrelevant information from awareness, reduced cognitive inhibition as manifest by low degrees of LI in high-psychoticism scorers is believed to account for the link between psychoticism and creativity (Eysenck, 1995). Rammsayer proposed that, in everyday life, attention is mainly focused on relevant stimulus characteristics such as intensity or colour, while temporal information may be ignored because they are common to all environmental stimuli (i.e., the participant has learned not to attend to them). Using the AGM as an explanatory model, Rammsayer further proposed that participants with low psychoticism scores have lower ability than those with high scores for directing attention to formerly irrelevant temporal information, resulting in relatively fewer resources for processing temporal information and less accurate time judgments. Kirkcaldy (1984), who obtained similar findings, proposed that individuals with high psychoticism scores have faster internal clocks, and hence increased resolution for timing, than low psychoticism scoring individuals. Both interpretations are plausible within the framework of the TIP and AGM models.

Although individual differences in time estimation continue to appear in the literature, most studies investigate these differences in relation to personality characteristics or other patterns of behaviours, such as impulsivity and locus of control (e.g., Bachorowski & Newman, 1985; Davidson & House, 1982; Stewart & Moore, 1978; Warner & Block, 1984; Zakay, Lomranz, & Kaziniz, 1984). Although significant relationships with time estimation have been reported, it is difficult to interpret these findings within an internal clock model perspective that attributes performance variability to clock speed, memory, attentional processing or some combination of these factors.

The most rigorous methods for examining individual differences in time literature were conducted by Brown et al. (1995) and Brown (1998). Here, university students were classified along a timing sensitivity continuum that was based on the reliability of timing performance measurements across a number of different timing tasks. Brown et al. conducted three separate experiments. In the first, timing sensitivity for relatively short (2 and 2.2 s) and long (12 and 13.2 s) durations was measured using a time discrimination signal-detection theory (SDT) task. Participants attended to a series of time intervals (separate trials for short and long intervals), and then judged whether the interval was the same as, or longer than, the target interval. Using *d'*, the sensitivity measure for performances on each of the short and long duration trials, participants were classified into two groups: one based on above-the-median performance and the other below-the-median. Sensitivity and response bias measures were consistent within individuals in 70% of cases.

In Brown et al.'s second experiment (1995), participants completed a detection task with short (5 s and 5.5 s), medium (10 s and 11 s), or long (15 s and 16.5 s) targets, and then performed a temporal-reproduction task (stimulus durations from 3 to 17 sec). Participants with low temporal sensitivity exhibited more absolute error on the temporal-reproduction tasks than did those with high temporal sensitivity. Further, participants whose temporal sensitivity was assessed on the basis of short, medium, or long durations did not differ with respect to their performances on short, medium, or long duration reproductions. Low and high sensitivity groups generally showed greatest error for short reproductions, with declining error from the short to medium and long reproductions. In the third experiment, participants completed a detection task (12 and 13.2 s) and then performed a duration production task (12 s), under either control or feedback (i.e., regarding the accuracy of their performance) conditions. This experiment was designed to assess the strength and stability of individual differences in temporal sensitivity. While feedback improved accuracy and reduced the variability in duration productions, under both conditions the low temporal sensitivity groups were more variable in their responses versus the high temporal sensitivity groups. The effect due to sensitivity group was large by behaviour-science standards, accounting for more approximately 16% of the variance. In comparison, the effect due to condition (i.e., control versus feedback) accounted for approximately 10% of the variance which suggests that individual differences in sensitivity is a better predictor of timing performance than practice with feedback.

Brown (1998) continued to examine individual differences by observing low and high sensitivity group performances in a dual-task experiment. Participants were required to reproduce a range of durations while completing a second nontiming task. Interval durations ranged from 8 to 16 s. During the timing task, participants were presented a stimulus display of seven two-digit numbers on a computer screen. Participants either viewed the numbers with no mnemonic demand (control condition), or were required to remember three (easy task condition) or seven (difficult task condition) marked digits. Participants reported digits from memory either before or following interval reproductions. Regardless of preliminary group classifications, interference from the mnemonic tasks resulted in absolute errors for timing that increased linearly as a function of task difficulty. However, the low-sensitivity group was less accurate overall in their reproductions than the high-sensitivity group. The second task required that participants tap on a mouse button at a steady rate (2- and 5-s duration productions). Participants classified as having low time sensitivity produced less accurate and more variable responses than those in the high sensitivity score group.

The Brown et al. (1995) and Brown (1998) studies demonstrate that there are significant individual differences in timing sensitivity, with cross-situational consistency in timing performance being found across different tasks, stimulus durations, and time judgment methods. This is of particular importance considering the performance classifications were based on established SDT methodologies. These findings suggest that there are individual differences that exert systematic effects on timing processes and mechanisms. Such effects may be manifest during the encoding, processing, retention, and/or reconstruction of temporal information. Brown (1998) describes individual differences in timing ability as reflecting varying levels of temporal sensitivity, which is defined here as the ability to detect small differences in duration. Individuals who exhibit low temporal sensitivity also exhibit greater variability in their time judgments with the reverse being true for individuals who exhibit high temporal sensitivity.

Evidence for Group Differences

Brown (1998) proposes that individual differences in temporal sensitivity have important implications for time research, particularly research that seeks to elucidate the processes and mechanisms of time perception. Variability in timing behaviour can obscure experimental findings, increasing the frequency of type II errors. For example, preselecting a sample of individuals who exhibit high temporal sensitivity may increase the power of timing research. Such measures may assist in our understanding of components such as those described in TIP, and the possible sources of variance that contribute to interval timing behaviour.

Age differences, sex differences, and neurological and neuropsychiatric group differences in timing behaviour have all been attributed to aberrations or variability in pacemaker speed or cognitive processes that contribute to interval timing. Explanations for these group differences often include references to constitutional variables in the general population such as the capacity to allocate attentional resources or the ability to encode and retrieve information.

Age-related differences. A number of early theorists speculated about possible age-related differences in duration judgments (e.g., Nitardy, 1943), and suggested that older adults experience time as passing more quickly than younger adults. More recent research suggests that older adults generally report faster time passage, particularly when asked to compare the rate to when they were younger (e.g., Baum, Boxley, & Sokolowski, 1984; Schroots & Birren, 1990), however, it is unclear whether these findings are related to the age-related differences in duration judgments that are observed in the laboratory.

Advancing age is commonly accompanied by a decline in performance on a wide variety of cognitive tasks, both in the laboratory and in everyday life (Johansson & Wahlin, 1998). In general, aging appears to be accompanied by a slowing of the elemental processes associated with cognitive tasks that heavily involve working memory, memory retrieval, and divided attention (Hartley, 1992; Light, 1991; Salthouse, 1991, 1992). It has been proposed that reduced processing speed is a major factor in cognitive aging (Salthouse, 1994, 1996). In the time perception literature, direct parallels have been drawn between the age-related reduction in processing speed and a hypothetical age-related reduction in clock or pacemaker speed, where the latter is proposed to account for older adults' reduced speed on motor tasks as well as perceptual nontiming tasks (Schroots & Birren, 1990; Surwillo, 1968; Wearden et al., 1997).

Within "timing-with-a-timer" models, timing accuracy and variability is attributed to component system processes such as pacemaker speed, memory, attention, and decisional processes. Because there are age-related reductions in basal metabolism and brain temperature, some researchers speculate that pacemaker speeds may be reduced in the elderly population (e.g., Wearden & Penton-Voak, 1995). The slowing of a biological clock could presumably account for elderly reports that time passes more quickly. Cognitive processes that mediate the relationship between external and internal events, such as those that allocate attentional resources or memory processes, may become less efficient or more sluggish with age.

A review of the aging and duration judgment research (Block et al., 1998) suggests that, contrary to conventional wisdom, the elderly exhibit timing behaviour that reflects a subjective lengthening of duration, as manifest by shorter productions and greater verbal estimates. These findings are reported by researchers who present "unfilled" interval durations (i.e., no sensory stimuli except onset and offset signals). Block et al. (1998) suggested that because these experiments did not require the elderly to divide their attention between temporal and nontemporal information, they found the task unusually easy to perform, unlike more natural, everyday situations. Additional research findings include those for an age-related increase in the variability of time estimates (i.e., increasing coefficient of variation with increasing age).

Lustig and Meck (2001) proposed that age-related declines in physical and cognitive function may alter patterns of resource allocation, in which older adults become "cognitive misers" who devote their resources to one aspect of a task at the expense of others. The age-related performance declines found with divided attention tasks supports this view. AGM predicts that the difficulty of a nontemporal task will moderate age-related effects. As nontemporal task difficulty increases, older adults may accumulate less temporal information than younger adults, and as a result of being a "cognitive miser," the older person may compensate for this vulnerability by attending more to "nontemporal" aspects of the task (e.g., visual aspects of external stimuli). Because this information provides less reliable information about duration, time estimates by the elderly would be less accurate and more variable than estimates made by younger adults. Lustig and Meck's proposal can also explain the general aging trends reported by Block et al. (1998) who noted that in everyday situations, older adults are less likely to attend to the passage of time, thus accumulating fewer temporal pulses that represent a particular time interval. The argument continues that when older adults are required to attend to time during "unfilled" experimental tasks, they overestimate the passage of time as their memory representations for events favour nontemporal information capture.

Perbal et al. (2002) examined the relationship between age-related differences in time estimation and age-related differences in cognitive functioning. Age-related differences in time estimation were determined by younger (*n* = 22, 20-34 yr) and older group (*n* = 24, 61-77 yr) performances on reproduction and production tasks (test durations ranged from 5 s to 38 s). They manipulated the degree of attentional resource allocation to these timing tasks by having subjects perform a concurrent reading or counting task. Perbal et al. hypothesized that older adults would perform more poorly in the concurrent reading task condition where the need for divided attention would demand efficient allocation of attentional resources. Age-related differences in cognitive functioning were determined by group performances on neuropsychological tests that measured processing speed (simple reaction time tasks) and memory (episodic, STM, and working memory tasks). Significant age-related reductions in performance were noted for simple reaction time tasks, episodic memory (i.e., word list learning), digit span (i.e., STM), and delayed recall for spatial locations in a block tapping task (i.e., working memory). As predicted, performances in the counting condition did not reflect age-related differences. In the reading condition, shorter reproductions and longer productions were made by both groups. These effects, however, were larger for the older group. Approximately 30% to 40% of the variability in performance could be attributed to age. Age-related differences in the accuracy of reproductions were better predicted by performances on episodic and working memory tasks, while processing speed scores accounted for a greater proportion of the age-related variance in the accuracy of productions.

Perbal et al.'s (2002) findings suggest that measures of cognitive processing may account for age-related differences in time estimation in different ways, depending on the timing task condition used to collect the duration judgments. Reproductions tasks are believed to heavily rely on memory processes, as they involve a comparison of durations in memory. As noted by Perbal et al., age-related differences in episodic and working memory were most greatly associated with age-related differences in the accuracy of duration reproductions. Conversely, production tasks are believed to involve a translation of present duration into conventional time units. Perbal et al. considered that the age-related association between performances on processing speed tasks and duration production tasks may be due to age-related declines in ability to divide attention, and proposed that timing accuracy suffered due to the older adult's inefficiency for redirecting attention between the timing and reading tasks.

Researchers have suggested that there is an important relationship between measures of information processing speed and measures of intelligence (Cerella, 1990; Salthouse, 1991, 1994; fluid intelligence, Zimprich & Martin, 2002). Wearden et al. (1997) proposed that there may be a direct link between the variability in precision of estimation of very short time intervals, intra-individual variability of choice reaction time (CRT) measures associated with age, and measures of intelligence. This argument is based on observations of "coarser" trial-to-trial adjustment of response speeds (i.e., during the CRT task) by older adults and individuals with lower intelligence scores (e.g., Smith & Brewer, 1995, p. 244), as well as observations of older adults' relatively reduced capacity for optimizing speed while minimizing errors in temporal tracking tasks (Rabbitt & Vyas, 1973).

Wearden et al. (1997) examined the relationship between age and general intellectual ability (IQ scores, Culture Fair Intelligence Test) and interval timing task performances in groups of active, older community residents (*n* = 90, 60 to 69 year-old group and 70 to 79 year-old group). Timing tasks included the temporal generalization task, the bisection task, and comparison and production tasks. All test intervals were of less than one s duration. IQ and timing performances of the older community resident sample were compared to archival data for a young adult (university student) sample. Poor timing performance (i.e., greater variability) was associated with increased age across tasks, however, was more greatly associated with lower IQ. The findings suggested that the effect of age was small, with many older participants able to perform as well as their younger counterparts on timing tasks that provided consistent, prompt, and accurate feedback, and/or frequent repetition of distinctive standard stimuli. These results are consistent with previous studies that have found that although older adults generally produce more variable time judgments, they are able to improve their performances with practice and external feedback. Lower IQ was associated with less accurate and more variable time performances, regardless of age, however, the relationship between IQ and temporal sensitivity was less clear in the above average IQ range. Wearden et al. (1997) considered the steepness of the generalization gradient to be an indicator of the precision of timing, with steeper gradients representing more precise timing. Their results suggest that there is a slight decrease in timing precision with increasing age and a marked decrease in precision with decreasing IQ.

As do the elderly, children generally exhibit reduced information processing speed (e.g., greater simple reaction times, Kail, 1991), and they perform more poorly on working memory, memory retrieval, and divided attention tasks than young adults. Similar to older adults, children tend to make larger time estimates and produce shorter time durations when compared to young and middle-aged adults (Zakay, 1992). Further, children exhibit reduced timing sensitivity, making significantly more variable and less accurate time estimates than young to middle-aged adults (McCormack et al., 1999; Zakay, 1992). McCormack et al. (1999) who used SET timing task methods for comparing performance across children, young adults, and the elderly, speculated that the reduced accuracy and variability in timing exhibited by children is due to reduced acuity during initial perceptual stages of encoding, which reflects timing-specific developmental effects, while elder adults tend to make errors that are associated with distortions in memory (e.g., tend to remember durations as being longer than they actually were).

In summary, aging studies demonstrate a task-specific property to time perception, where separate components of our time perception system are affected differently by the aging process. How these age-related differences in the component functionality are expressed depends on the demands of the timing and nontiming tasks. The one aspect of timing performance that is shared by children, older adults and low-sensitivity timers, however, is that of increased variability of time estimates (e.g., Block et al., 1998; Brown et al., 1995; Brown, 1998). Researchers speculate that this increased variability may result from greater inter-individual variation in component processes that mediate time judgments, including pacemaker speed, attention, memory, and decision processes.

Sex-related differences. Sex differences in cognitive abilities (see Halpern, 1997, 2000, for a review) raise the possibility that males and females differ in their ability to judge duration. However, there is no clear evidence of sex differences involving memory, attention, or other cognitive processes associated with interval timing. In general, research suggests that males outperform females on tasks involving spatial ability, whereas females outperform males on tasks involving verbal ability. Block, Hancock, and Zakay (2000) provide a review of the literature concerning sex differences in cognitive ability. They note that females outperform males on verbal comprehension and fluency, episodic memory, fine motor skills, and perceptual speed. However, males outperform females on tasks involving fluid reasoning, visuospatial transformations, and spatiotemporal operations.

Prior to the 1950’s, some researchers agreed that females experienced time intervals as being longer than clock time (i.e., larger ratio of subjective-to-objective duration judgments) and that they made more variable duration estimates than males, (see Block et al., 2000, for a review). A more recent meta-analytic review of the literature concerning sex and duration judgments (Block et al., 2000), however, concludes that any sex differences in duration judgments are small effects and only observed for retrospective conditions, where females show a larger ratio of subjective-to-objective duration judgments than males.

Block et al. (2000) describe the overall effect of sex on time estimation within the hypothetical situation of any male or female group asked to estimate the duration of a 100 sec time interval. On average, females would verbally estimate this duration to be 110 sec, while males would estimate it to be 98 sec. Three variables moderate this effect. Females show a larger ratio of subjective-to-objective duration when the number or complexity of stimuli is increased and when there is a greater delay for reporting time judgments. Block et al. propose that sex differences in time judgments may be attributed to sex differences in memory processes. Because females perform relatively better on episodic memory tasks than do males (e.g., Herlitz, Nilsson, & Bäckman, 1997), they may remember more events from a target duration. If many or more complex stimuli are presented during a time interval, females will overestimate the duration because they remember more events and the contextual changes that accompany them. Sex differences in episodic memory may also account for sex-differences in timing tasks where there is greater delay between the presentation of the target duration and the time judgment. Males, forgetting presented information at a faster rate than females, would give a smaller ratio of subjective-to-objective duration. However, greater inter-individual variability for female versus male performances detracts from the generalizability of this explanation.

Prospective duration judgments did not show significant sex differences (Block et al., 2000). However, there was greater inter-individual variability for duration judgments made by females (15% greater). Block et al. report that females may exhibit greater ability for sustained attention to time over prospective timing task trials, as the accuracy of male group performance declines with increased number of trials.

Neurological and neuropsychiatric clinical group-related differences. There has been a surge of research that uses pharmacological interventions and functional neuroimaging techniques for investigating the neural underpinnings of temporal processing and timing sensitivity (see Gibbon et al., 1997; Harrington & Haaland, 1999; Ivry, 1996; Meck, 1996, for a review). Converging evidence provides support for the role of the basal ganglia and the cerebellum in time keeping operations for a wide range of short (ms) and long (s) test intervals; however, controversy remains with regard to how these two structures together influence timing behaviour. Meck (1996) proposed that the neural circuitry of the frontal lobes with the basal ganglia provide the functional setting for an interval time keeper. Abnormalities in morphology, cytoarchitecture, regional blood flow, and neurotransmitter activity in these regions and in their projected connections have been associated with disorders such as Attention-Deficit/Hyperactivity Disorder (ADHD), Parkinson's disease, Schizophrenia, and Huntington's disease; clinical groups that exhibit relative impairments in timing ability (Malapani et al., 1998; Melges, 1989; Smith, Taylor, Rogers, Newman, & Rubia, 2002). Researchers have considered that the impairments in cognitive functioning and/or dysregulated movement associated with these disorders may reflect aberrations in internal clock processing (Mangels, Ivry, & Shimizu, 1998; Meck, 1996; Olton, Wenk, Church, & Meck, 1988).

There have been few studies of the effect of frontal lobe lesions on human timing behaviour. However, nonhuman primate research suggests that neural discharges in the prefrontal cortex during interval timing may be related to an internal counting mechanism or active maintenance of an internal representation of duration in working memory (Mangels et al., 1998; Olton, 1989). Observations of performance on paired comparison timing tasks in brain-injured samples suggest that different brain regions support time judgments for durations in the milliseconds range (400 ms) and seconds (4 s) range. Patients with prefrontal lesions perform more poorly on longer duration comparison tasks, while patients with neocerebellar lesions performed poorly on both shorter and longer duration tasks. Poorer performances by patients with prefrontal lesions were associated with relative deficits in the ability to acquire, maintain and retrieve information as measured by tests of verbal fluency and STM. Patients with neocerebellar lesions demonstrated reduced processing speed in the presence of preserved short term memory. Based on these findings, Mangels et al.(1998) proposed that neocerebellar regions subserve a central timing mechanism, whereas the prefrontal cortex subserves supportive functions required for acquiring, maintaining, monitoring and organizing temporal representations in memory for judging longer durations.

Interval timing research has also used psychopharmacological methods to probe putative neural timing mechanisms. This research generally concludes that neurotransmission associated with the basal ganglia and frontal cortex is critical to timing behaviour. The effects of antipsychotic drugs and stimulants on interval timing are well established in the literature (see Meck 1996, for a review). Antipsychotic drugs such as dopamine antagonists in rats show temporal overshoot behavior (i.e., slowing of the clock), resulting in longer time productions relative to objective time. This timing sensitivity to dopaminergic interventions is also evident in Parkinson's disease where dopaminergic dysfunction in the striatum results in a temporal information processing deficit which disappears when patients are on L-dopa, and reappears when patients go off the drug (Malapani et al., 1998).

Distortions in temporal discriminations due to manipulations of dopaminergic activity in the nigrostriatal system are attributed to changes in the speed of the clock, while distortions due to manipulations of cholinergic and noradrenergic activity in frontal cortical regions are attributed to the consolidation of information processing and/or attentional processes that mediate the latency to start timing (Meck, 1996; Penney et al.,1996). Noradrenergic system functioning accounts for orientation to stimuli in the environment and viscera, mediating the efficiency for selective attention. In trained rats, decreases in brain NE levels are associated with increased latency to onset of timing (and overshoot for obtaining a food reward) while increased brain NE levels are associated with more accurate performances (Penney et al., 1996). Manipulations of acetylcholine function in the frontal cortex are associated with changes in the accuracy of interval timing, findings that are attributed to changes in the consolidation of temporal information in memory (Malapani et al., 1998; Meck, 1996). Stimulants such as methamphetamine produce temporal undershoot (i.e., speeding up the clock), resulting in shorter time productions relative to objective time. Research that examines the effect of cholinergic manipulations on timing behaviour displayed by adult rats shows that cholinergic supplementation improves, and choline deficit impairs, temporal processing (Meck & Williams, 1997).

A number of neuropsychiatric groups show impaired timing ability. Attempts have been made to try and identify possible information processing deficits that may be associated with these reduced timing performances. The contribution of attention to the capacity or efficiency of working memory is evident in individuals with ADHD, where reduced executive control for alternating, dividing, focusing and/or sustaining attention contributes to reduced general memory and working memory performances (Johnson et al., 2001; Tannock, 1998). Quantitative and qualitative deficits in timing performances with ADHD patients have been shown (Barkley, Murphy, & Bush, 2001; Kerns, McInerney, & Wilde, 2001; Smith et al., 2002). Kerns et al. (2001) reported that the association between timing performance and cognitive performance was greater for tasks that placed greater demand on selective and sustained attention than for tasks that measured working memory. However, other researchers have noted timing performances to be associated with more generalized relative deficits.

Individuals with schizophrenia show compromised cognitive abilities in a variety of domains. Impaired timing abilities have been noted in a number of studies (e.g., Davalos, Kinsley, & Ross, 2003; Elvevage et al., 2003; Monaco et al., 1998). In a recent study that used temporal generalization and temporal bisection tasks, Elvevag et al. (2003) noted that schizophrenic patients were less accurate in their judgments of brief durations (i.e., < 1 s) compared to the controls. Performances on a working memory task (digit span) were not significantly associated with performances on the duration judgment tasks. Davalos et al. (2003) explored the possibility that temporal deficits associated with discrimination judgments by schizophrenia patients were due to modality-specific factors. As the schizophrenia group exhibited deficits in discriminating subtle differences in intervals in the tens of milliseconds range on both auditory and visual time perception tasks, compared to normal control peers, the researchers concluded that schizophrenia is associated with a general versus modality-specific temporal processing deficit.

In summary, a number of neurological and neuropsychiatric clinical groups are associated with poorer performance on interval timing tasks. Further, pharmacological manipulations may influence clock component processes, by means of altering arousal and attention mechanisms, leading to reduced or enhanced timing performance. Thus, for the purposes of the present study, individuals will be excluded from participation if they meet one or more of following criteria: 1) they have a clinical disorder associated with reduced temporal sensitivity (e.g., ADHD), 2) they are using prescribed or over-the-counter drugs with psychoactive properties associated with changes in ACh, NE, and/or DA transmission, or 3) they have sustained a mild head injury within the past 12 months or have a history of moderate head injury.

Factors that may Contribute to Individual Differences in Timing Sensitivity

The speed or frequency of an internal pacemaker, the amount of attention given to a timing task, the stability or reliability of perceptual representations of time intervals, the stability or reliability of cognitive decision making (i.e., establishment of criteria), and the effectiveness of motor response to those decisions can influence the accuracy of time judgments. Experimental research typically focuses on manipulating one of these factors in order to observe the effects on group performance. For example, dual-task time experiments introduce interference that results in an overall subjective shortening of duration. The administration of neuroleptics results in an overall subjective lengthening of duration. However, individual differences in timing sensitivity do not appear to be related to the individual's propensity to either underestimate or overestimate the passage of time. Rather, individual differences differ with respect to the absolute deviation value from the standard duration, the frequency of missed targets, and the accumulated sum of absolute deviation values over the course of testing (e.g., Brown, 1998; Brown et al., 1995).

Brown (1998) proposed that low temporal sensitivity may result from one or more of the following clock process aberrations: a central timekeeper that operates with more error and variability, an accumulator or memory store that fails to encode or retain temporal information, perceptual processes that fail to capture important temporal cues, and decision-making processes that bias temporal judgments and resultant motor responses. Within "timing-with-a-timer" models, these aberrations would be manifest by reduced pacemaker speed, increased latency to switch time, a narrower attentional gate, and/or inaccurate representations of duration in memory. It is difficult to extrapolate from the TIP and AGM models for making predictions about the relationship between individual differences in time perception and decision making processes. Brown et al. (1995) and Brown (1998) found no relationship between temporal sensitivity measures (*d'*) and response-bias measures (β) that describe decisional or nonperceptual processes in SDT tasks. Brown (1998) suggested that the lack of association between temporal sensitivity measures and measures of response bias or directional trends towards overestimation or underestimation implied that the main feature of temporal sensitivity is the ability to time events in a consistent fashion.

As discussed previously, attentional processes likely have significant modulatory influence over all timekeeping operations (Macar et al., 1994; Penney et al., 1996; Wearden et al., 1997). For example, central nervous system norepinephrine may enhance selective attention by accentuating activity of neurons that are transmitting the presence of significant stimuli and inhibit the activity of other neurons. The net effect is an improvement in signal-to-noise ratio that reduces the latency to time signal detection, increases temporal resolution and the stability of internally represented temporal intervals, and increases flexibility and speed for fine tuning decision criteria. Individuals with low temporal sensitivity on the other hand may exhibit reduced ability to direct and sustain attention to timing tasks. If these attentional processes are similar to those involved in other cognitive tasks, then individuals with low timing sensitivity may also show reduced performance on nontiming tasks that draw on similar resources.

This study adopts the position that the processing of temporal information in duration discrimination tasks is largely a deliberate cognitive activity that involves the allocation of cognitive resources. Thus, the level of accuracy reflected in timing performances will be determined primarily by the experimental task and the individual's capacity for attention and working memory processing. This position is supported by research that has examined the influence of a concurrent nontiming or additional timing task on time judgments. Interference by concurrent nontiming tasks that require attention and working memory generally leads to shorter, less accurate, and/or more variable estimates. The effect of attentional allocation on time judgments is quite robust, as the results of recent research suggest (Fortin & Massé, 2000). Time-sharing between an interval timing task and the mere expectation of its interruption produces interference effects that are similar to those that are produced in dual-task time research.

Attention and processing speed and accuracy. Theories that integrate findings from both cognitive laboratories and the study of clinical populations concur in viewing attention as the confluence of a number of separate but interrelated aspects of a neural network (e.g., Luria 1973;

Mesulam, 1990). Importantly, together the various components of activation and attention are viewed as the necessary foundation on which all other cognitive functions rest.

The interaction between the prefrontal cortex and its projection areas is believed to be the basis for cognitive control (e.g., Miller, 2000). Imaging studies provide evidence for top-down attentional modulation that increases visual stimulus-specific responsiveness (e.g., Hopfinger, Buonocore, & Mangun, 2000). This top-down attentional modulation is also active during the monitoring, manipulating, or selecting between items in memory (e.g., D'Esposito, Postle, & Ryman, 2000; Petrides, 1995; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000). Miller (2000) proposed that cognitive control is reflected in the attentional selection of neuronal representations, and that this may be applicable to sensory stimuli, thoughts, memories, or motor actions. Experimental evidence suggests that neuronal populations that are targeted for modulation are specific to the object of attention. Thus, their activation does not simply reflect a general state of greater attentiveness. Evidence from imaging research suggests that such attentional selection operates within the motor, as well as in sensory and mnemonic domains (Rowe, Friston, Frackowiack, & Passingham, 2002).

As noted by Block (1990), the time literature is often careless with regard to its conceptualization of attention within timing models. Incorporating scientific theories of attention within interval timing models may improve their predictive validity. It is possible that the speed of the pacemaker may not exert as much influence on timing as the size of the "spotlight of attention" (Iwasaki, 1993) which determines the enrichment of internal representations devoted to any given moment. Operations of the switch could be modified to account for the efficiency of divided or alternating attention for sampling temporal and nontemporal stimuli. Within the comparator component of the interval timing models, executive attentional processes could influence threshold levels, based on the degree of arousal or alertness and the demands on processing resources.

One of the difficulties for incorporating attentional influences within interval timing models stems from the multidimensional nature of attention. Fan, McCandliss, Sommer, Raz, and Posner (2002) tested the efficiency and independence of Posner and Peterson's (1990) three system model (i.e., alertness, orienting and executive functions) for attentional processes in the vision modality, using reaction time tasks. Although levels of alertness are believed to have no effect on the accumulation rate of sensory information, when alertness is low, the criterion for response is more stringent. This increase in criterion is associated with longer reaction times. The TIP and AGM propose that the speed of pacemaker pulses and the rate of their accumulation increases as levels of arousal increase. When arousal is low, pulses accumulate more slowly, and it is the increase in time required to accumulate pulses that match the number of those in reference memory that is believed to account for longer time productions. However, it is also possible that these overestimations are due to changes in criterion for decision making and/or longer motor response times.

In the AGM, the criterion for making a response is believed to be a function of the cognitive comparator, a mechanism that requires attentional resources for its operations. However, Zakay (2000), one of the creators of the model, states that the manner in which attentional processes influence decision criteria has yet to be determined. The TIP model proposes that response criteria are a function of a comparator that operates within working memory. As the TIP was derived from the scalar timing system for describing animal timing behaviours, it uses the scalar mathematical decision formula to describe human decision making during timing tasks. However, the fact that the decision formula works well for describing timing accuracy in animals does not mean that the decision process in humans is well understood. Wearden (1999), a proponent of the TIP model, stated that decision processes, like memory processes, were invented merely for the purpose of describing the available data.

In vision research, attentional facilitation is believed to involve a combination of mechanisms or processes, including noise reduction, decisional factors, and/or signal enhancement (Kinchla, 1992; Lu & Dosher, 1998; Wilkinson, Halligan, Marshall, Buchel, & Dolan, 2001; Yeshurun & Carrasco, 1998, 1999). Ciaramitaro and colleagues (2001) were able to separate the contributions of sensory from decision-making processes using probability cueing. Improvements in performance were associated with increases in the probability of perceiving a signal embedded in noise, however, were not associated with criterion changes in decision processing. This methodology may prove to be a particularly effective approach for examining the effect of attentional allocation on timing accuracy and variability, as it allows manipulations of the expected probability of a particular signal type within an interval.

Separating the influence of processing speed and attention within interval timing models will be a challenging task. Differentiating between working memory and attentional allocation contributions to time performances presents a similar challenge. The AGM and TIP propose that internal representations of time intervals are created within a perceptual store that is held in mind and reaccessed for comparison judgments. These processes are traditionally attributed to working memory, a theoretical construct that subsumes attention and executive processes. There is considerable debate in the time literature concerning the relative influence of attention and working memory on time judgments, with some researchers suggesting that interference effects are primarily due to nontemporal processing demands on working memory. These arguments ignore the fact that increasing demands on working memory necessarily involve increased demands for attentional resources, with attentional facilitation ultimately determining the resolution and meaning of internal representations, as well as the rate of alternation and rehearsal of items in memory.

Short-term and working memory. Short-term and working memory are essential components to the AGM and TIP interval timing models. Working memory is described as a distinct memory system that is similar to short-term memory in terms of capacity limitations, but also is a dynamic system that influences aspects of attention and executive functioning (Baddeley, 1990). Working memory has three components: the central executive, the articulatory phonological loop, and the visual-spatial sketch pad. The central executive is an attention-controlling system that supervises and coordinates slave systems. The articulatory phonological loop and the visual-spatial sketch pad are modality-specific slave systems where speech-based information and visual images are stored and manipulated. Brown (1997), who examined interference effects for a range of concurrent nontiming tasks, suggested that timing is associated with central executive processing and to a lesser extent the phonological loop, as mental arithmetic, a task primarily associated with the central executive (but also sensitive to demands on phonological loop processing resources) leads to mutual interference with concurrent timing tasks (i.e., disrupting both timing and nontiming task performance).

The Present Study

The present study was designed to advance the findings of previous research that has examined individual differences in time perception and to investigate the psychophysical characteristics of interval timing across durations of less than and greater than one second. The methodology was designed to address three questions concerning the nature of interval timing and the sources of variability that may contribute to individual differences.

(1) Are individual differences in time perception reliably observed across durations of less than and greater than one second? If consistent differences in psychophysical measures of interval timing are observed across these durations, they reflect the functioning of a general timing system. A time discrimination task (visual modality) that involved random presentation of shorter (400 ms range) and longer (1600 ms range) time intervals was selected for the present study. The task allowed us to construct psychometric functions that produced psychophysical measures of time perception. This task is described more fully in the methods section. As there is debate in the literature concerning the necessity of different models that describe interval timing across this range of durations, we made no predictions concerning the consistency of individual differences across this range.

(2) What is the effect of increasing low-end pacemaker speed on time perception, and does this effect occur equally for low and high temporal sensitivity individuals? Research findings suggest that the presentation of repetitive stimuli during an interval increases the speed of the hypothetical internal clock's pacemaker mechanism. We used Treisman et al.'s method (1992; 1994) for increasing pacemaker speed in order to test the hypothesis that neural entrainment by a repetitive visual stimuli would improve the resolution of internal representations of duration, resulting in greater sensitivity for time perception. A priori, it was hypothesized that flicker effects would be greatest for 1600 ms timing, as previous research suggests that the effect increases with increases in the duration being timed (Burle & Casini, 2001). Further, because pacemaker speed is one possible source of variability that may contribute to individual differences in time perception, we considered the possibility that individuals with low temporal sensitivity due to slower and/or more variable pacemaker speed may show significant improvements in their ability to discriminate time intervals that are

denoted by repetitive stimuli.

(3) What is the relationship between individual differences in time perception and performance on nontiming cognitive tasks that measure processing speed, processing accuracy, and short-term memory? As internal clock models include cognitive components (i.e., memory, decision or comparator mechanism), individual differences attributable to cognitive variables may have impact on time perception. Working memory, processing speed and accuracy tasks were selected for the present study. They are described more fully in the methods section. We compared measures of cognitive performance across groups that differed with respect to their level of accuracy or sensitivity (i.e., low versus high) for time discrimination. We predicted that individuals who exhibited greater sensitivity and accuracy for time discrimination would obtain higher scores on working memory, processing speed, and processing accuracy tasks.

Method

Experimental Design

Psychophysics and SDT Methods

We used psychophysical and SDT methods to provide rigorous measurements of time perception (Cohn, 1981; Klein, 2001; Macmillan & Creelman, 1991). The basic assumption of classical psychophysics is the existence of a threshold, which can be thought of as a boundary by which a stimulus energy or pattern must exceed before it can be perceived. In terms of temporal processing, the threshold can be a difference in temporal duration between two successive intervals (i.e., the difference between a standard and test interval).

With the Method of Constant Stimuli (MOCS), the experimenter can use a predefined set of two-interval trials that are presented randomly to the participant. We adapted the MOCS for a signal detection discrimination task, where standard intervals were followed by various comparison "test" intervals. In SDT, the sensory process has no sensory threshold, rather, the sensory process is assumed to have a continuous output based on random Gaussian noise (Macmillan & Creelman, 1991). When a signal is present, the signal combines with the noise. Measures of the sensitivity of the sensory process are based on the difference between the mean output under no signal and signal plus no signal (noise) conditions. Within the context of the present study, participants were asked to discriminate outputs under "no signal" successive durations, (where both standard and test intervals were equal) and under "signal" successive durations, (where the test interval was longer than the standard). Test intervals were filled, with visual stimuli denoting the duration of the interval.

For comparisons of successive durations, Hellström's (1985) sensation-weighting model predicts that the first of these will be underestimated relative to the second resulting in a negative time-order error (TOE). Accuracy of judgment is better when the second interval of the pair is the comparison interval. Also, interstimulus intervals (ISI) can have a large effect on the size of TOE. For example, Wearden and Ferrara (1993) noted that negative TOEs tended to increase with longer ISIs in the seconds range. Therefore, this study used a 900 ms ISI, as determined appropriate for 50 ms and 1000 ms durations by Rammsayer (2002) who also examined individual differences in timing accuracy.

Visual aspects of the discrimination timing task: no-flicker and flicker. The photopic visual stimuli that demarcated the standard and test time intervals were designed to favorably weight activity from the middle-wavelength (MWS) and long-wavelength (LWS) sensitive cones in the fovea. Research shows that short wavelength chromatic responses involving the short-wavelength sensitive (SWS) cones are less *temporally* responsive to changing stimuli than the LWS- and MWS- cones. The LWS- and MWS-cones along with their connections to the r-g chromatic system are also tied to the faster responding photopic luminance channels (see Smithson & Mollon, 2001, for a review). Further, foveal and peripheral retinal regions are associated with different timing behaviour, with the former described as more precise for detecting incremental changes in the time between the onsets and the latter described as showing a faster time course for responding to high frequency changes in luminance (e.g., flicker) with response nonlinearities that may obscure observations of foveal timing (McKee & Taylor, 1984; Smithson et al., 2001). For this reason, the chromaticity of the foveally displayed visual stimulus was "yellow" with a dominant wavelength (λ_d) of 577 nm, based on 1931 CIE calculations. To minimize rod photoreceptor involvement, the chromaticity of the large background was a "violet" light adaptation field with a calculated CIE nonspectral λ_d of -510 nm. Thus, we were fairly confident that the sensory processes involved with our timing data were primarily attributed to LWS and MWS parvocellular luminance signaling.

Flicker stimulus durations were synchronized with sinusoidal modulated 15 Hz flicker (67 ms per cycle), in phase with the luminance timing interval onset and offset, thereby facilitating timing accuracy (Westheimer, 2000). A 15 Hz frequency is compatible with previous research that has examined the effects of flicker on interval timing (Treisman & Brogan, 1992), and provided a phasic match to 400 ms (6, 66.7 ms cycles), 800 ms (12, 66.67 ms cycles) and 1600 ms (24, 66.7 ms cycles) standard durations.

Preliminary psychophysical assessment. Sensitivity experiments often use uniform stimulus distributions (where successive increases in contrast are of equal magnitude). However, according to Macmillan et al., (1991) these distributions need not be uniform. It could be argued that in natural situations, timing involves stimulus distributions that are less uniform than those that are presented in interval timing experiments. We decided to make more "naturalistic" observations of individual differences in timing perception by randomly presenting a range of standard durations that were associated with non-uniform distributions.

Standard duration values and test ranges were assessed using a series of preliminary experimental runs (*n* = 10). We chose a 400 ms standard interval for observing time discrimination for relatively shorter durations, an 800 ms standard interval for observing time discrimination for mid-range durations, and 1600 ms for observing time discrimination for relatively long durations (i.e., longer than the 1 sec arbitrary boundary as set down by Rammsayer, 1994, 2002). Test interval durations were selected based on the need for reliable measures across a subthreshold to suprathreshold range, and so were non-uniform, representing test increment contrasts over 50 to 150 percent ranges. The preliminary findings showed that this resolution and range were adequate to calculate not only threshold but slope of the psychometric function as well.

Feedback from participants in our preliminary study generally revealed that the interleaved use of shorter and longer standard durations during a single experimental session reduced feelings of boredom and decreased the opportunity for subjects to use a counting strategy in assisting them with their performance. However, overall they also reported that the timing sessions were uncomfortably long (75 minutes) with fatigue and distractibility occurring in the latter blocks of trials. The data supported these reports, as sensitivity for timing was reduced over the final blocks of trials. To prevent the experimental session from exceeding two hours, we dropped the 800 ms standard interval condition in the main study and used the 400 ms and 1600 ms standard durations to make the distinction between a "short" duration and "long" duration, as did Rammsayer (50 ms and 1000 ms intervals denoted by auditory stimulus, 1999, 2002). We hypothesized that 400 ms and 1600 ms intervals may invoke a more immediate physiological and greater end cognitive response, respectively. Reducing the number of standard durations for the final study reduced the duration of the timing sessions (from 70 to 55 minutes), while permitting an increase in the number of trials for each standard (from 120 to 154). Forty-four "blank" trials (i.e., test duration is equal to standard duration) were included in this number.

We selected threshold, decision bias, proportion correct, and slope measures to represent our psychophysical characterization of interval timing across 400 ms and 1600 ms standard duration tasks. Threshold measures are our primary measure of time interval discrimination, as they represent measures of sensitivity. Decision bias, proportion correct, and slope measures afford an expanded framework for our characterization of time perception across relatively short and long durations.

Psychophysical and SDT methods: Threshold and decision bias calculation. Test intervals were always equal to or greater than the standard interval, and they spanned the subthreshold to suprathreshold range. The difference between standard and test interval can be best characterized as "msec time increment contrast," where time increment contrast equals the test interval [ms] / standard [ms]). Participants were required to discriminate standard-test pairs by indicating whether the test intervals were the same or different from the standard. SDT methods were used to define false alarm rates. This enabled us to plot mean transducer functions (d' as a function of time increment contrast) as well as mean psychometric functions (proportion correct versus time increment contrast). In SDT, discriminability is described by d', where $d' = z(H) - z(FA)$, H is the proportion hit rate and FA is the proportion false alarm rate. These calculations provided a reduced decision-based criterion bias of discriminability, where the FA trials (i.e., zero time increment contrast, "blank") provided the unidimensional measure of decision bias (c) over the range of contrasts, $c = -z(FA)$ (Macmillan et al., 1991). When d' values describe performance over a range of contrast values, a curve fit to these points is called a transducer function. For comparing sensitivity across individuals, measures of threshold were obtained from fits to *d'* versus time increment contrast plots. In this study, threshold was set arbitrarily by the experimenter. In the literature, this is generally set to 1.0, however, higher *d'* values have been used to better characterize the point of threshold (e.g., Klein, 2001; Macmillan et al., 1991).

Distributions for test intervals were adjusted in order to capture observations of sub- and supra-threshold responses. Thresholds were greater than the 5% to 10% Weber fractions that are generally reported in the literature. They ranged from approximately 20% to 70%, depending on the standard duration. Thresholds were largest for 400 ms timing, smallest for 800 ms timing, and intermediate for 1600 ms timing. These thresholds are much larger than those reported by Rammsayer (2002) who also used MOCS for observing individual differences in timing accuracy. The method included an adaptive psychophysical procedure (i.e., a response-based increase or decrease in the differences between standard and test interval) where 50 ms and 1000 ms standards and test durations were presented in separate blocks of trials. Seventy-five percent difference thresholds for the 1000 ms auditory standard (white noise) varied across groups, and ranged from 130 ms (*SD* = 55 ms) to 199 ms (*SD* = 121 ms). Thus, thresholds for 1000 ms timing varied significantly, with approximately two-thirds of the sample obtaining thresholds at time increment contrasts between 7.5% and 32%. Conversely, difference thresholds for 50 ms timing were proportionately smaller and spanned a shorter range for the majority of individuals representing 4% to 9.5% of the base duration. With respect to visual timing, Brown (1998) noted that median sensitivity scores (*d'*) were progressively higher for longer standard durations; however, these scores were derived from single interval discrimination trials where a limited number of test intervals were randomly presented, specifically, the standard (5 s, 10 s or 15 s) or standard plus ten percent. Westheimer (1999) reported Weber fractions for visual comparison task timing obtained for a very small sample. Fractions were reduced on extended practice, and generally ranged from 5% to 10% across a range of timing tasks, from 500 ms to 1500 ms duration. As did Rammsayer's threshold measures (2002), Westheimer's measures proceeded from runs of trials with just a single duration per run.

Psychophysical and SDT methods: Proportion correct calculation. Correct responses over the test interval range were summed and divided by the total number of trials (i.e., number correct across range [including blank trials] / total number of trials). This calculation produced a proportion correct measure that reflects the degree of accuracy for time discrimination over the test interval range.

Slope calculation. Using a wide range of test intervals the MOCS allowed us to calculate the slope of the transducer function, a measure that cannot be easily obtained using more modern adaptive procedures (see Klein, 2001, for a review). Research examining psychometric functions for luminance detection have shown that subject uncertainty (e.g., Cohn, 1981) and overall reliability of sensory performance (e.g., Pelli, 1985; Strasburger, 2001) can be directly related to a psychometric function's slope. Generally, increases in slope reveal increases in uncertainty and poorer overall performance of the task.

We also considered that a measure of "efficiency," might provide additional information about time perception, and borrowing from colour vision psychophysics (which often relates the response ratio of two cone systems) we calculated measures of efficiency using the ratio equation, $S / S + s$, where S = sensitivity (i.e., 1/threshold) and s = slope. However, efficiency measures were very highly correlated with threshold and slope (i.e., provided redundant information) and were not included in the data analyses.

Preliminary and Cognitive Psychometric Evaluation

All individuals were administered Ishihara pseudoisochromatic plates (1993, 24–plate edition) to test for colour blindness. In order to examine the relationships between individual differences in time interval discrimination and nontiming task performances that demand central processing resources, a number of standard cognitive tests were administered, including tests which assess processing speed and accuracy, and working memory. These tests were selected based on their psychometric properties and continued use in experimental research and clinical settings (Larrabee & Curtiss, 1995; Lezak, 1995). Psychometric properties and apparati used for the cognitive evaluations are provided in the Appendix A.

Processing speed tasks included the California Computerized Assessment Package (CalCAP, Miller, 1999) Simple, Choice, and Sequential Reaction Time tasks, Color and Color-Word tasks from the Stroop Neuropsychological Screening Test (Trenerry, Crosson, DeBoe, & Leber, 1989), and the Symbol Search subtest from the Wechsler Adult Intelligence Scale – Third Edition (WAIS-III, Wechlser, 1997a). Measures of processing accuracy were derived from performances on processing speed tasks. Speed and accuracy measures showed adequate independence for the purposes of data analyses. Pearson correlations among cognitive task measures, as well as, a review of the calculations used to summarize the cognitive task data are reported in the *Results, Preliminary Preparation of the Data* section. Short-term/working memory tasks included subtests taken from the Wechsler Memory Scale – Third Edition (WMS-III; Wechsler, 1997b), including, Digit Span Forward and Backward, Spatial Span Forward and Backward, and Letter-Number. Participants also completed the Seashore Rhythm Test, an auditory timing task from the Halstead-Reitan Neuropsychological Test Battery (Reitan &

Wolfson, 1985). This test is brief and offered us the opportunity to assess its utility for future research purposes. Seashore Rhythm Test performances were not included in the main data analyses that examined the relationship between sensitivity for timing and performances on cognitive tasks.

Participants

None of the 10 participants used in the preliminary study were included in the main study. For the main study, eighty-seven adults (males, *n* = 27; females, *n* = 60) from the Lakehead University student population and surrounding community were recruited. Although Rammsayer's (2002) preliminary data analysis revealed female timing performance varied with menstrual cycle, we felt that there was sufficient evidence in the literature to support the inclusion of females in our study. Psychology students were given extra course credit for their participation and all participants were provided an opportunity to win one of four $50 cash draws. The study was advertised as an investigation of timing ability. Exclusionary criteria were determined a priori for the purpose of reducing performance variability attributed to age or health diagnoses (e.g., ADHD, previous head injury, vision problems, and colour blindness). Data sets for five individuals were excluded due to the presence of ADHD, vision problems, and elder age. Of the eighty-two adults that met criteria for inclusion, four completed only one of the two timing sessions. Seventy-eight individuals (males, *n* = 23; females, *n* = 55) completed all experimental tasks as described. Only the data from these individuals were included in the final data analyses. Ages for these individuals ranged from 19 to 45 years (*M* = 24.2, *SD* = 7.6).

Apparatus and Stimuli

Time Interval Discrimination Tasks

Visual timing tasks were presented using apparati available at the Vision Lab at

Lakehead University. All stimuli were presented on a high-resolution monochrome Nanao 90801 monitor (13 X 16° display). Stimuli were designed and displayed using VisionWorks™ computer software. Duration was denoted by a "yellow" (λ_d = 577 nm) 1.5 ° dial. circular visual stimulus, surrounded by a "violet" (λ_d = -510 nm) adaptive field (luminance = 40 cd / m^2). Participants were required to attend to durations denoted by the onset and offset of the presentation of the visual stimulus in the center of the monitor. The visual stimulus was steadily presented throughout the interval in the no-flicker conditions. For the flicker conditions, the dominant stimulus wavelength was temporally modulated with the background at 15 Hz. The flickering stimulus modulated through chromatic space (i.e., "yellow" to "violet") and through luminance space. A cosine wave setting with 180 degree phase advance allowed the luminance to ramp up linearly with the onset of the stimulus and ramp down linearly prior to stimulus offset.

In both no-flicker and flicker sessions, the visual stimulus was presented for either 400 ms or 1600 ms during the first interval of a trial. Following the presentation of the 400 ms standard interval was the test interval, in which the same visual stimulus was presented for 400, 467, 533, 600, 800 or 1000 msec durations. Following the 1600 msec standard interval was the test interval, in which the same visual stimulus was presented for 1600, 1733, 1867, 2000, 2267 or 2533 ms durations. All of the standard and test intervals were presented randomly (i.e., MOCS) Preliminary trials revealed these test intervals to be resolute enough to define thresholds while extensive enough to define the psychometric slopes (Klein, 2001; King-Smith & Rose, 1997).

Procedure

Time interval discrimination and nontiming cognitive task performances were measured over two experimental sessions, with each session lasting 70 to 90 minutes. The sessions were performed on two separate days (no more than five days apart), at approximately the same time of day. These requirements were imposed for the purpose of reducing performance variability due to changing physiological factors such as daily hormonal shifts. Participants were also advised to maintain a consistent pattern of caffeine and nicotine intake across timing sessions. Information concerning stimulant intake was recorded at each session.

The first experimental session was approximately 90 minutes duration and included initial engagement in a preliminary interview (15 to 20 minutes) for the purpose of obtaining consent, as well as personal information concerning the individual's health and lifestyle, including interests, skills and hobbies. Cognitive tasks were then administered (15 minutes). Tasks and order for administration are presented in the *Cognitive Tasks* section that follows. A time interval discrimination task session followed (55 to 65 minutes). The first session ended with a brief interview for obtaining feedback from participants regarding their timing experiences (i.e., what timing strategies they used, level of confidence for timing shorter and longer intervals). The second experimental session followed the same general procedure. The time to complete cognitive and time interval discrimination tasks in the second session was approximately equal to that for the first session tasks.

Time Interval Discrimination Tasks

Participants were randomly assigned to complete either no-flicker or flicker time interval discrimination tasks during their first timing session. Timing task sessions were conducted in a darkened booth with an average ambient light level of less than 0.01 cd/m^2. Participants were instructed to attend closely to the durations of the foveally-presented "yellow" circle stimuli. By definition, the stimuli were presented during the standard and test intervals and participants were instructed to indicate whether the second presentation was of the same or longer duration. A 3-minute dark adapt period preceded the presentation of 14 practice trials.

For each session, 400 and 1600 ms standard and test durations were randomly presented in order to facilitate sustained attention during the testing and to reduce the effects of practice, expectation, and counting strategies on performance. Three-hundred and eight trials were presented in 22 blocks, each block consisting of 14 trials. A single block contained a random iteration through four blank trials (two for each of the 400 and 1600 ms standards) and one trial for each combination of standard and test durations (five for each of the 400 and 1600 ms standards). The number of blank trials was increased from 22 to 44, as results from the preliminary study suggested that this change would decrease thresholds by increasing the discriminability of standard-test trials. Presentation of one of two standard durations followed a 900 ms delay and then a test duration was presented. A schematic of the spatial and temporal arrangements of the stimuli and trial intervals are shown in Figure 3. The participant pushed either a left or right keypad button to indicate a "same as" or "longer than" response, respectively. The pacing of the trials was set by the participants who pressed a button to start each new trial. Each trial began and ended with a brief warning tone for the purpose of signaling to the participant to attend to the next trial presentation or alternatively that they could press a button to start a new trial.

Cognitive Tasks

These tasks were administered according to standardized test instructions. The order of presentation was fixed as follows: 1) CalCAP Simple, Choice, and Sequential Reaction Time Tasks, 2) the Seashore Rhythm Test, 3) WMS-III Digits Forward and Backward, 4) WAIS-III Symbol Search task, 5) WMS-III Spatial Span Forward and Backward, 6) the Stroop

Neuropsychological Screening Test, and 7) the WMS-III Letter-Number task. Computer administered reaction time tasks and the Seashore Rhythm Test were administered following the initial interview and prior to the start of the first timing session. The remaining tasks were administered prior to the start of the second timing session.

Processing speed and accuracy tasks. For CalCAP Simple Reaction Time tasks, participants were asked to press a key as soon as they saw anything at all on the computer screen (distance between participants and computer screen was 3 feet for all CalCAP tasks). Four practice trials were followed by 12 trials of target presentation (the stimulus was a numeric digit presented for 70 ms) with random ISIs from 1000 to 5000 ms. Participants completed the task three times; once at the start of the CalCAP battery, and again following each of the Choice and Serial Pattern Reaction Time (RT) tasks. The number of practice trials was reduced from four to two for second and third presentations of the simple RT task. For the choice reaction RT task, participants were asked to press a key as soon as they saw a specific number (e.g., 7) on the screen - otherwise they were to do nothing. Digit stimuli for the choice reaction RT task were of degraded visual quality. Ten practice trials that included three target stimuli were presented for 175 ms stimulus duration and 1000 ms ISI. The main task was comprised of 100 trials with 15 target stimulus presentations of 70 ms duration and 800 ms ISI. For the Serial Pattern Matching RT task, participants were instructed to press a key only when they saw two of the same number in sequence, for example, if they saw the number 3 followed by a second occurrence of the number 3. Ten practice trials with two target stimuli were presented. The target stimuli were presented for 175 ms with 1000 ms ISI. The main task was comprised of 100 trials with 20 target stimulus presentations of 70 ms duration and 800 ms ISI. Each of the CalCAP tasks generated a measure of RT (in ms). The Choice and Serial Pattern RT tasks also generated d' estimates of accuracy based on the number of hits and FA rates.

The WAIS-III Symbol Search task (Wechsler, 1997a) was administered using standardized test instructions. Participants were instructed to look at two figures on the left hand side of a 8.5" X 11" paper sheet, then scan arrays of five items to the right of these figures, and check off a "yes" or "no" response to denote the presence or absence of any target figure in the stimulus array. Participants were told to complete items in order and to perform the task as quickly and as accurately as possible. Participants were provided start and stop signals that delimited the 2 min time period allowed to complete this task. Scores were calculated by summing the number of responses and the number of correct and incorrect responses.

The Stroop test included two tasks, a Color Task and a Color-Word Task. The participants were first presented the Color Task stimulus sheet and instructed to read the words in each column, from top to bottom beginning with the column on the left hand side of the sheet as quickly and as accurately as possible, correcting any errors they might make. A stopwatch was used to measure the time to complete Stroop tasks. For the Color-Word Task, participants were presented a stimulus sheet and instructed to name aloud the colour of the ink in which the word was printed as quickly and as accurately as possible, correcting any errors they might make. Correct, incorrect and corrected responses, and completion times were recorded.

Short-term/working memory tasks. All memory tasks were administered using the standardized instructions and procedures provided in the WMS-III manual (Wechsler, 1997b). Digit Span Forward and Backward task test items consisted of two trials of number sequences from two to nine digits in length. Items were administered in order from shorter to longer number sequences, at a rate of one digit per second. The test was discontinued when a score of '0' was received on both trials of any item. Items and administration were similar for the Digits

Backward task, however, the numbers were recited back by the participant in reverse order.

Spatial Span Forward and Backward tasks required that the participant remember a sequence of block taps produced by the experimenter at the rate of one block per second. Each test item consisted of two trials of block sequences. The number of blocks in the sequence increased by one with each new item presented. Following the presentation of each trial of an item, the participant made an attempt to repeat the sequence of block taps as shown. Items were presented until the participant made one or more errors on two trials of the same item. The Spatial Span Backward task required that participants repeat the sequences of block taps in reverse order.

The Letter-Number Sequencing task required that the participants attend to string combinations of numbers and letters that were read to them at a pace of one unit per second. Each item of the test consisted of three trials, and each trial was a different combination of numbers and letters. The first item consisted of a single letter and number, and with each new item the number of letters and numbers increased by one. Participants were asked to repeat back these sequences in the following order: first, the numbers, in ascending order; second, the letters, in alphabetical order. Participants were provided with five practice items prior to beginning the scored task. The test was discontinued when the participant received a score of '0' on all three trials of any item.

Results

Experimental Design, Terminology, and Selected Data Analyses

The primary focus for our experimental design is a within-subjects examination of time interval discrimination across 400 ms and 1600 ms standard time intervals. From this point onward, standard time intervals will be identified as 400-STI and 1600-STI. These standard time intervals represent two levels of DURATION, one of two within-subject factors. All participants completed no-flicker (NFLK) and flicker (FLK) time interval discrimination tasks, representing two levels of the STIMULUS condition, the second of two within-subject factors. Four psychophysical measures of time interval discrimination performance across DURATION and STIMULUS were obtained, including threshold measures (THRESH), decision bias (*c* or DEC), proportion correct (PROPC), and slope measures (SLOPE). Thus there are 16 dependent variables: THRESH, DEC, PROPC, and SLOPE. THRESH is a measure of sensitivity (1 / THRESH), and can take the form of a Weber fraction ($\Delta T / T$) at $d' = 1.5$, where T represents the standard time interval, ΔT represents time increment over standard, and d' represents the degree of unbiased discriminability at threshold. Increases in THRESH represent decreases in sensitivity. THRESH values reflect the influence of *DEC*, a measure of criterion decision-making stringency which is determined by the *FA* rate over zero contrast test time interval. Increases in DEC represent increases in stringency. PROPC is a measure of overall accuracy for time interval discrimination across the range of test interval time increment contrasts associated with 400-STI or 1600-STI. Increases in PROPC represent increases in accuracy. Changes in SLOPE represent the degree of uncertainty for discrimination over the test time interval range. Increases in SLOPE represent increases in uncertainty. Means and standard deviations for THRESH, DEC, PROPC, and SLOPE are presented in Table 1. Pearson correlations among these variables are presented in Table 2. Acronyms are listed in Appendix B.

We selected a number of statistical methods for addressing our research questions concerning the nature of interval timing mechanisms and the sources of variability that may contribute to individual differences in time perception. Level of significance was set at $p \leq .05$. Repeated measures of THRESH, DEC, PROPC, and SLOPE measures were not commensurate.

A 2 x 2 and single-factor repeated measures analysis of variance (ANOVA) across all psychophysical measures of time perception were conducted. For the 2 x 2 analyses, there were two DURATION levels (400-STI and 1600-STI) and two STIMULUS levels (NFLK and FLK).

Of the four psychophysical variables, THRESH represents the dependent variable of primary interest (i.e., sensitivity). We used this measure to form groups of low sensitivity and high sensitivity timers, following the procedure described by Brown (1998). Because we used THRESH to represent sensitivity, individuals were assigned to a low- (high-) sensitivity group if their score fell above (below) the median population threshold. These between-subjects groups were entered to MANOVAs for examining the relationships among psychophysical variables, as well as the relationships between sensitivity groups and cognitive task performances. These latter performances include summary measures of processing speed (SPEED), accuracy (ACCUR), and working memory (MEM).

Preliminary Preparation of the Data

Prior to data analysis, all variables were examined for accuracy of data entry, missing values, and fit between their distributions and the assumptions of multivariate analysis (Tabachnick & Fidell, 2001). There were no missing data. Outliers and low to moderate skew were noted for the majority of variables. However, values were generally within reasonable limits. Extreme outlier scores (i.e., $SD \geq 3.29$) were adjusted. These included four cases 400-STI NFLK: SLOPE, five cases 400-STI FLK: SLOPE, six cases 1600-STI NFLK: SLOPE, three cases 1600-STI FLK: SLOPE, and one case 400-STI FLK: DEC. These outliers were assigned a value one unit smaller (SLOPE) or one larger (DEC) than the next most extreme measure in the distribution. FLK and NFLK 400-STI: DEC showed moderately high negative skews. These variables were transformed as recommended by Tabachnick and Fidell (2001), by first reflecting the variable and then applying a logarithmic transformation. These transformations had no impact on the multivariate data analyses, as F values did not vary for analyses that included original and transformed DEC values. There were no multivariate outliers.

Threshold Calculations

Sensitivity (1/THRESH), was our primary psychophysical characterization of time interval discrimination. These measures were calculated as follows. The signal-detection data were formed into a response matrix for each of the 400-STI and 1600-STI levels of DURATION, for each of the NFLK and FLK levels of STIMULUS, and for each individual. A floor and ceiling of .02 and .98, respectively, was set for FA and hit rates, as is common practice for avoiding infinite values (Macmillan & Creelman, 1991). These proportion limits represent a conversion of 0 and 1 to $1 / (2N)$ and $1 - 1 / (2N)$, where N = the number of trials at each level of test duration.

Figures 4 and 5 show transducer functions which plot *d'* values as a function of time increment contrast (i.e., $\Delta T / T$). The mean sample transducer functions for NONFLK 400-STI and 1600-STI are shown in Figures 4 and 5, respectively. These functions were obtained by averaging *d'* measures across participants for each DURATION and STIMULUS level. The averaging method is considered superior to the *pooling or collapsed d'* method which produces a lower estimate of sample mean *d'* (Macmillan & Creelman, 1991). Measures of *d'* over the range of time increment contrast were fitted to a Weibull curve, producing psychometric transducer fits with corresponding SLOPE estimates obtained from the optimized fitted equations. The Weibull function, a nonlinear regression model for data fit, is commonly used for fitting psychophysical data obtained in vision research (Klein, 2001; Macmillan & Creelman, 1991; Wichmann & Hill, 2001). Transducer functions were plotted for each level of DURATION, for each level of

STIMULUS, for each participant. The majority of R^2 fits ranged from .95 to .99.

A value of d' = 1.5 was selected for determining measures of THRESH. This value is greater than the typical d' = 1.0 generally reported in the literature (Macmillan & Creelman, 1991). However, greater d' values are believed to more accurately represent observations of performance over a range of comparisons (Klein, 2001). The d' = 1.5 value indicator was optimal, as values below and above 1.5 were either lower or higher than respective sub- and supra-threshold values in a number of cases. Measures of THRESH were estimated at the time increment contrast value that corresponded with the ordinal d' value of 1.5 and is indicated in Figure 4 by horizontal and vertical lines.

Cognitive Task Summary Scores

Cognitive test scores were transformed to z-scores and summed to produce summary SPEED, ACCUR, and MEM variables. For some test scores, the sign of the z-score was inversed to maintain a meaningful standard across categories where negative and positive scores reflected relatively poorer or better performance, respectively. SPEED included CalCAP Choice, Sequential, and Simple task RTs (mean RT for the three runs of the task) the number of completed Symbol Search task items, and difference scores for Stroop Color-Word and Color task completion times. ACCUR includes CalCAP Choice and Sequential *d,* Symbol Search task proportion correct, and weighted combinations of Stroop Color-Word task corrections (weight = 2) and errors (weight = 5). MEM includes Letter-Number, Digit Span (sum of Forward and Backward), and Spatial Span (sum of Forward and Backward) task scores.

Main Psychophysical Data Analyses

Prior to the data analyses, a 2 x 4 MANOVA was performed for investigating the possibility that there may have been practice effects on THRESH. The results of the 2 x 4 analysis, with no-flicker-first-session ($n = 40$) and flicker-first-session ($n = 38$) entered as a between-subjects factor and the four THRESH entered as dependent variables were not significant (Wilks's lambda, $F[4, 72] = .13, p = .97$).

Threshold (THRESH)

A 2 x 2 repeated measures ANOVA revealed a large significant effect of DURATION on THRESH ($F[1, 77] = 591.85, p < .001, \eta_p^2 = .89$), as well as, a significant interaction of DURATION and STIMULUS ($F[1,77] = 11.92, p = .002, \eta_p^2 = .13$). The interaction is depicted in Figure 6. The results of single factor analyses showed 1600-STI THRESH were lower than 400-STI THRESH in both NFLK ($F[1, 77] = 311.71, p < .001, \eta_p^2 = .80$) and FLK ($F[1, 77] = 537.86, p < .001, \eta_p^2 = .88$) STIMULUS conditions. However, the THRESH for FLK 400-STI were greater than those for NFLK 400-STI ($F[1, 77] = 6.46, p = .01, \eta_p^2 = .08$), while the THRESH for FLK 1600-STI were lower than those for NFLK 1600 STI ($F[1, 77] = 4.59, p = .03, \eta_p^2 = .06$).

Figure 7 depicts the 400-STI and 1600-STI distributions for NFLK and FLK. Both 400-STI levels of STIMULUS show greater inter-subject variability (interquartile range) relative to 1600-STI levels. This can also be seen with the THRESH standard deviations and ranges in Table 1. The average discrimination performance [d'] as a function of time increment contrast (psychometric transducer functions) for 400-STI and 1600-STI NFLK are shown in Figure 8. As indicated by the horizontal dotted line at d=1.5, the average 400-STI THRESH is greater than the 1600-STI THRESH. This was also the case for FLK results. Average THRESH measures corresponded with hypothetical test intervals of 715 ms ($SD = 126$) and 743 ms ($SD = 125$) for NFLK and FLK 400 STI, respectively, and 2067 ms ($SD = 207$) and 2020 ms ($SD = 178$) for NFLK and FLK 1600-STI, respectively. These measures, particularly 400-STI, are much greater than those reported in the literature (i.e., Weber fractions from 26% to 86%, versus approximately 10% in the literature). *d'* = 1.5 does not account for this discrepancy, as mean proportion correct measures at this value were below unbiased 50% correct for both durations. We considered THRESH correspondence within the context of test increment range, and calculated "range-based" THRESH (i.e., $\Delta T / \Delta T_r$, where ΔT_r is the entire time contrast range used for a given 400 or 1600 ms standard interval). The results of a two factor (DURATION and STIMULUS) repeated measures ANOVA using range-based THRESH showed that there continued to be a significant main effect of DURATION ($F[1, 77] = 23.52, p < .001, \eta_p^2 = .23$) and a significant interaction of DURATION and STIMULUS ($F[1, 77] = 12.07, p = .001, \eta_p^2 = .14$). Because of these similarities, we continued to use our original ΔT-defined THRESH for all subsequent analyses.

The relationships between increasing average discriminability (*d'*) and time increment contrast for both levels of STIMULUS within 400-STI and 1600-STI are depicted in Figures 9 and 10, respectively. A *d'* value of 1.5 was maximally positioned for detecting effects due to an interaction of DURATION and STIMULUS. The effect of FLK on 400-STI was greatest over the subthreshold and threshold range with a progressive decrease in effect over the suprathreshold range. The effect of FLK on 1600-STI was greatest over the threshold and suprathreshold range. The magnitude of effect due to FLK was more consistently expressed over the entire1600-STI range. Note how the dashed fits denoting FLK are to the left of the continuous fits with 1600-STI (Figure 9) and to the right with 400-STI (Figure 10).

Decision bias (DEC)

A 2 x 2 repeated measures ANOVA revealed a large significant main effect of DURATION on DEC estimated marginal means ($F[1, 77] = 124.81, p < .001, \eta_p^2 = .62$). The analysis did not reveal a significant main effect of STIMULUS or interaction of DURATION and STIMULUS. The results of single factor analyses showed DEC with 1600-STI were less stringent (i.e., lower *c* values) than those with 400-STI in both NFLK ($F[1, 77] = 87.83, p < .001, \eta_p^2 = .53$) and FLK ($F[1, 77] = 102.22, p < .001, \eta_p^2 = .57$) STIMULUS levels. Figure 11 shows this main effect for all levels of DURATION and STIMULUS. NFLK and FLK 400-STI distributions reflect reduced inter-subject variability, as seen in Figure 12. There was a large effect of DURATON on DEC. The decision criteria with 400-STI were more stringent (i.e., higher scores) with a negatively skewed distribution, which reflected a significantly reduced inter-subject variability. These properties can also be seen in Table 1, reflecting greater consistency for highly stringent criterion across individuals. As noted previously, data analyses were conducted using transformed and original DEC values. There was no discrepancy between these results.

Proportion correct (PROPC)

A 2 x 2 repeated measures ANOVA revealed a large significant main effect of DURATION on PROPC ($F[1, 77] = 105.71, p < .001, \eta_p^2 = .58$), as well as a significant interaction of DURATION and STIMULUS ($F[1,77] = 35.90, p < .001, \eta_p^2 = .32$). This interaction is depicted in Figure 13. The results of single factor analyses showed 1600-STI PROPC (accuracy) scores were greater than those for 400-STI in both NFLK ($F[1, 77] = 31.57, p < .001, \eta_p^2 = .29$) and FLK ($F[1, 77] = 161.97, p < .001, \eta_p^2 = .68$) STIMULUS levels. However, PROPC for 400-STI FLK was significantly reduced relative to 400-STI NFLK ($F[1, 77] = 13.07, p = .001, \eta_p^2 = .15$), while PROPC scores for FLK 1600-STI were greater than those for NFLK 1600 STI ($F[1, 77] = 16.22, p < .001, \eta_p^2 = .17$).

Figure 14 depicts the 400-STI and 1600-STI distributions for NFLK and FLK. Accuracy was greater for with the1600-STI than with the 400-STI. The relationship between NFLK THRESH and PROPC is illustrated using the NFLK STIMULUS data in Figures 15 and 16. Both figures are overlay plots showing transducer and psychometric (proportion judged "longer") functions for 400-STI NFLK (Figure 15) and 1600-STI NFLK (Figure 16). The discrepancy between proportion "longer" and discriminability (d') for 1600-STI is due to the increased FA rate. The relationship between FLK THRESH and PROPC for 400-STI and 1600-STI showed similar trends.

SLOPE

A 2 x 2 repeated measures ANOVA revealed a modest significant effect of DURATION on estimated psychometric function slopes (i.e., SLOPE) ($F[1, 77] = 12.37, p < .001, \eta_p^2 = .14$), and significant interaction of DURATION and STIMULUS ($F[1,77] = 4.21, p < .05, \eta_p^2 = .06$). These effects are depicted in Figure 17. The results of single factor analyses showed that the effect of DURATION was only significant within the FLK STIMULUS level. SLOPE was greater (i.e., more subject uncertainty) with the 400-STI FLK than with the 1600-STI FLK ($F[1, 77] = 17.25, p < .001, \eta_p^2 = .18$) conditions. As can be seen in Figure 17, the estimated marginal mean SLOPE with 400-STI NFLK was greater than that for 1600-STI NFLK conditions, however, the single factor analysis failed to detect a significant difference ($F[1, 77] = .53, p = .47$). Similarly, although the estimated marginal mean SLOPE with the 400-STI FLK was greater than that with the NFLK 400-STI conditions, the data analysis failed to detect a significant difference ($F[1, 77] = 1.25, p = .37$). Figure 18 shows SLOPE distributions across levels of DURATION and STIMULUS. Reduced inter-subject variability was noted for 1600-STI FLK, as can also be seen from the relatively reduced magnitude for standard deviation (see Table 1).

Summary: Main Effect of DURATION and Interaction of DURATION and STIMULUS

Both NFLK and FLK 400-STI were characterized by increased and more variable THRESH, reflecting significantly reduced sensitivity for 400 ms timing. 1600 ms FLK THRESH were the lowest and 400 ms FLK THRESH were the highest across levels of DURATION and STIMULUS. DEC was greater for 400-STI for both NFLK and FLK timing, and also showed reduced inter-subject variability. It appears that discriminating time intervals from a 1600 ms standard, particularly when the stimulus is temporally flickering , produces greater sensitivity and reduced decision criterion stringency than discriminating intervals from a 400 ms standard. Both NFLK and FLK 400-STI were characterized by smaller PROPC relative to 1600-STI conditions. Thus, 1600 ms timing also shows greater response accuracy. The effect of DURATION on PROPC was greatest for FLK, with 1600-STI FLK measures of SLOPE showing the smallest degree of uncertainty. Analyses that examined the interaction of DURATION and STIMULUS showed that 400-STI FLK produced the poorest performances and 1600-STI FLK produced the best performances, as reflected in THRESH and PROPC measures.

Correlations

Pearson correlations among psychophysical timing variables are presented in Table 2. These relationships provide information concerning the reliability of individual differences as well as the direction and strength of association among the psychophysical measures. We now provide a summary of these relationships. As noted previously, there were no missing data, N = 78. Level of significance for reported correlations is $p \leq .001$ (two-tailed), unless otherwise noted.

No-Flicker. Relationships among 400-STI and 1600-STI *no-flicker* THRESH, PROPC, DEC, and SLOPE varied considerably. Thresholds showed the greatest degree of consistency (*r*

= .55), followed by decision bias (r = .43) and proportion correct (r = .37). There was little association between SLOPE measures across durations.

NFLK difference scores with 400-STI and 1600-STI. As psychophysical timing variables were only moderately associated across durations (i.e., threshold, r = .49, decision bias, r = .46, and proportion correct, r = .37), we decided to examine NFLK THRESH, DEC, PROPC, and SLOPE difference measures between 1600-STI and 400-STI. Decreases in THRESH, from 400-STI to 1600-STI, were moderately to highly associated with increases in PROPC (r = -.70). Decreases in SLOPE, from 400-STI to 1600-STI, were moderately associated with decreases in THRESH (r = .56) and increases in PROPC (r = -.46), suggesting that increased sensitivity and overall accuracy for 1600-STI was associated with reduced uncertainty.

Increases in PROPC, from 400-STI to 1600-STI were modestly related to decreases in DEC (r = -.41), suggesting that individuals were able to increase the number of correct responses over the range of 1600 ms test time increment contrasts by using less stringent criterion.

400-STI and 1600-STI FLK. We noted that while the data analyses detected a significant interaction of DURATION and STIMULUS, with 400-STI FLK reflecting the poorest performances across timing tasks and 1600-STI FLK reflecting the best performances, the intra-subject consistency was greater with 400-STI and 1600-STI FLK than with the NFLK conditions (i.e., PROPC r = .52, versus, r = .37, and threshold r = .70, versus, r = .55). However, there was a reduced relationship between DEC with FLK (r = .25, $p < .05$), versus, NFLK (r = .43). These results and those from the repeated measures data analyses suggest that flicker had a systematic effect on timing processes, irrespective of duration, where DURATION effects were amplified.

NFLK and FLK. Relationships among psychophysical variables across levels of STIMULUS were generally comparable to the DURATION levels. THRESH measured with

400- and 1600-STI were moderately to highly related ($r = .62$ and $r = .51$, respectively), and PROPC measured with 400- and 1600-STI were also moderately to highly related ($r = .67$, both). There was little to no relationship between 400- and 1600-STI SLOPE measures. In contrast, 400-STI DEC measures were modestly related ($r = .25, p < .05$), while 1600-STI DEC measures were moderately to highly related ($r = .67$). In general, these results suggest that individual differences were consistently manifest across levels of DURATION and STIMULUS.

Analyses of Low- and High-Temporal Sensitivity Groups

We continued to examine the nature of timing behaviour across durations by assigning individuals to either low- or high-temporal sensitivity groups. As did Brown (1998), we categorized individuals based on the median average threshold (cut-off point) for each DURATION NFLK condition. Participants with individual thresholds that were higher than the average cut-off for either the 400-STI NFLK or 1600-STI NFLK were considered *low-sensitive timers* for that respective DURATION. Similarly, participants with individual thresholds that were lower than the average median threshold were considered *high-sensitive timers* for each DURATION. Thus, it was possible for some participants (the minority) to belong to a low-sensitivity group with 400-STI and to a high-sensitivity group with 1600–STI while others (the majority) belonged to the same low- or high-sensitivity groups for both DURATION levels. The NFLK threshold-defined group performances were then compared to their FLK performances. Psychophysical data from those individuals who showed consistent timing sensitivity across DURATION and STIMULUS levels were later compared to standard clinical cognitive task performances.

No-flicker (NFLK) Timing

A direct logistic regression analysis (SPSS binary logistic option) was performed on 1600 ms group membership as outcome and 400 ms group membership as predictor. The prediction model was statistically reliable, X^2 (1, N = 78) = 8.81, p = .003, with 52 of the 78 participants, or 66.7% of the sample, reliably distinguished as low-time-sensitive (65.8%) or high-time-sensitive (67.5%). This finding suggests that 400 ms and 1600 ms timing may use similar processing resources as there was considerable consistency for group membership across the no-flicker durations. However, the lack of high consistency between NFLK psychophysical variables noted in the correlational analyses suggests that timing resources also may vary in terms of their contribution to 400-STI and 1600-STI THRESH.

Sensitivity groups based on 400-STI NFLK performances. Low- (n = 38) and high- (n = 40) temporal sensitivity groups, defined by 400-STI NFLK thresholds, were entered as a between-subjects factor to a one-way MANOVA, with PROPC, SLOPE, and DEC as dependent variables. The 2 x 3 analysis detected a significant main group effect (F[3, 74] = 36.06, p <.001, η_p^2 = .59). As expected univariate analyses showed that the high-sensitivity group obtained greater PROPC (F[1, 76] = 78.94, p <.001, η_p^2 = .51; M = .66, SD = .06, versus, M = .53, SD = .06). This group also showed reduced uncertainty for timing as manifest by lower SLOPE (F[1, 76] = 7.33, p = .008, η_p^2 = .09; M = 1.84, SD = .81, versus, M = 2.59, SD = 1.50), although the direct association between reduced THRESH and SLOPE was small. No significant group differences were detected with respect to DEC (F[1, 76] = 3.29, p = .07, η_p^2 = .04).

Sensitivity groups based on 1600-STI NFLK performances. A one-way MANOVA, entering 1600-STI low- (n = 38) and high- (n = 40) temporal sensitivity groups, defined by 1600-STI NFLK thresholds, were entered as a between-subjects factor and 1600-STI NFLK PROPC, SLOPE, and DEC as dependent variables. The analysis detected a significant main group effect (F[3, 74] = 45.02, p <.001, η_p^2 = .65). As was the case with the 400-STI NFLK analyses, the high-sensitivity group obtained greater PROPC ($F[1, 76] = 49.49, p < .001, \eta_p^2 = .39; M = .71, SD = .06$, versus, $M = .59, SD = .08$) and showed reduced uncertainty (lower SLOPE) ($F[1, 76] = 11.21, p = .001, \eta_p^2 = .13; M = 1.63, SD = .80$, versus, $M = 2.52, SD = 1.40$) relative to the low-sensitivity group. The high-sensitivity group also showed increased DEC, (more stringency) than the low-sensitivity group with 1600-STI NFLK ($F[1, 76] = 10.89, p = .001, \eta_p^2 = .13; M = 1.47, SD = .47$, versus, $M = 1.05, SD = .62$).

These findings support the idea that there was little flexibility for adjusting decision criteria in 400-STI NFLK timing, regardless of whether individuals were low- or high-temporally sensitive. They also suggest that PROPC (accuracy) measures more clearly differentiated low- and high-temporal sensitivity groups for 400 ms NFLK timing. Effect sizes suggest that SLOPE (certainty) and DEC (stringency of criterion) more clearly revealed low-from high-temporal sensitivity groups with 1600-STI NFLK trials.

Examining the Effect of Flicker on Low- and High-Sensitivity Timers

We conducted four one-way ANOVAs for examining the impact flicker had on low- ($n = 38$) and high- ($n = 40$) temporal sensitivity group THRESH as defined with 400-STI or 1600-STI. One ANOVA, where we entered 400-STI NFLK groups as a between-subjects factor and 400-STI FLK THRESH as the dependent variable showed that high-sensitivity NFLK timers obtained lower FLK thresholds ($F[1, 76] = 17.97, p < .001$, , $\eta_p^2 = .19; M = .73, SD = .24$, versus, $M = .98, SD = .28$). However, when FLK THRESH minus NFLK THRESH differences were entered as DVs into a second ANOVA, it revealed that low-sensitivity timers showed little change in THRESH with STIMULUS condition ($F[1, 76] = 8.23, p = .005; M = -.02, SD = .27$, versus, $M = .16, SD = .19$), unlike the large differences found with high-sensitivity timers. Figure 19 depicts the effect of flicker on low-and high-temporal sensitivity groups with 400-STI. High-sensitivity timers obtained lower NFLK and FLK THRESH, and showed a significant increase in THRESH with flicker ($t[39] = -5.39, p < .001$). However, THRESH for low-sensitivity timers showed a small shift in THRESH with FLK.

A one-way ANOVA entering 1600-STI NFLK groups as a between-subjects factor and 1600-STI FLK THRESH as the dependent variable showed that high-sensitivity NFLK timers obtained lower FLK thresholds ($F[1, 76] = 30.50, p < .001, \eta_p^2 = .29; M = .21, SD = .09$, versus, $M = .32, SD = .10$). However, group differences with respect to relative changes in 1600-STI THRESH from NFLK to FLK were detected using one-way ANOVA entering THRESH difference scores (FLK minus NFLK) ($F[1, 76] = 8.51, p = .005, \eta_p^2 = .10; M = .01, SD = .10$, versus, $M = -.07, SD = .13$), with low sensitivity timers showing greater reductions in THRESH with FLK. Figure 20 depicts the effects of flicker on low- and high-temporal sensitivity groups in the 1600-STI. High-sensitivity timers obtained lower NFLK and FLK THRESH, and showed a slight trend for increased THRESH with flicker. THRESH for low-sensitivity timers were higher, but the effect of FLK was greater, as can be seen by the lower mean THRESH for 1600 ms flickering stimuli.

To summarize, it appears that the effect of flicker was not manifest equally across low- and high-temporal sensitivity groups. Flicker had a negligible effect on low-sensitivity timers with 400STI, but it had a large effect with 1600-STI. These findings support the idea that flicker may have reduced the variability of pacemaker speed, or it may have impacted on other timing process or mechanism that are more prominent with perceptions involving durations longer than 1 sec. Of course, this was not always the case for a minority of participants. There were a number of individuals who showed an increase or decrease in sensitivity on flicker tasks relative to no-flicker tasks, leading to a change in their group classification (400-STI, $n = 19$; 1600-STI,

$n = 15$), however, the low n together with unequal group sizes precluded further data analyses with this subgroup.

Sensitivity Group Analyses: Cognitive Task Performances

Our results so far suggest that timing component processes may vary in terms of their unique contribution to 400-STI and 1600-STI performances. We observed duration-specific timing behaviour, most notably, large differences in THRESH, PROPC, and DEC measures. Further, there was an interaction of DURATION and STIMULUS, where 400-STI and 1600 FLKR performances represented the least and most sensitive / accurate timing, respectively. However, individual differences were most consistently manifest across FLK sensitivity and accuracy measures, suggesting that this experimental manipulation had a systematic effect on timing across levels of DURATION. Low temporal sensitivity groups showed relatively greater effects due to FLK.

We administered cognitive tests for the purpose of examining the relationships between psychophysical timing performances and measures of processing speed (SPEED), accuracy (ACCUR), and working memory (MEM) -- cognitive processes that are believed to underlie timing. We also administered the Seashore Rhythm Test, an auditory timing task, for comparing these performances with those for visual timing. The Seashore scores were generally poorly associated with visual timing task measures. Exceptions were noted for associations with 400-STI NFLK: PROPC ($r = .30, p = .007$), 1600-STI NFLK: DEC ($r = .34, p = .002$), and 1600-STI FLK: THRESH ($r = -.34, p = .002$). Seashore scores showed modest to moderate direct relationships with cognitive task summary scores, MEM ($r = .45, p < .001$) and ACCUR ($r = .32$, $p = .008$). Direct relationships between cognitive summary scores were significant but generally modest: SPEED and MEM ($r = .38$, $p < .001$); ACCUR and MEM ($r = .35, p = .003$); and

SPEED and ACCUR, (*r* = .30, *p* = .005).

Correlations between thresholds and cognitive task scores showed notable trends. SPEED scores showed highest correlation with 1600-STI FLK THRESH (*r* = -.39, *p* < .001), followed by 1600-STI NFLK (*r* = -.24, *p* = .03), and 400-STI (*r* = -.20, *p* = .08, and, *r* = - .16, *p* = .16; FLK and NFLK, respectively). MEM scores showed highest correlation with 400-STI NFLK THRESH (*r* = -.44, p < .001), followed by 1600-STI NFLK (*r* = -.37, *p* = .001), 1600-STI FLK (*r* = -.32, *p* = .004), and 400-STI FLK (*r* = - .25, *p* = .03). ACCUR scores showed highest correlation with 400-STI NFLK THRESH (*r* = -.45, *p* < .001), followed by 1600-STI FLK (*r* = -.36, *p* = .001), 400-STI FLK (*r* = -.34, *p* = .003), and 1600-STI NFLK (*r* = - .31, *p* = .007). Thus thresholds for no-flicker 400-STI and 1600-STI were most highly correlated with MEM and ACCUR scores, while correlations with 1600-STI FLK were relatively consistent across all measures (from *r* = -.32 to *r* =-.39, SPEED greatest, MEM lowest). Correlations for 400-STI FLK scores were generally lower (ACCUR, *r* = -.34; MEM, *r* = -.25; SPEED, *r* = -.20).The correlations between THRESH scores and cognitive task performance suggest that NFLK performances were most greatly associated with MEM and ACCUR scores, followed by SPEED, and FLK performances were more greatly associated with ACCUR and SPEED, followed by MEM. There were also notable patterns in correlations from NFLK to FLK thresholds within levels of standard duration. Correlations between cognitive performance and 400-STI, from noflicker to flicker, showed reductions in associations with MEM scores and an increase in associations with SPEED on flicker. Correlations between cognitive performance and 1600-STI, from noflicker to flicker, showed a similar pattern, i.e., reductions in associations with MEM scores and an increase in associations with SPEED on flicker, however, also an increase in ACCUR (within 400-STI showed modest reduction in ACCUR).

Because there were a number of cases of group categorization changes from 400-STI to 1600-STI and from NFLK to FLK conditions, we decided to examine the relationship between timing sensitivity and cognitive performance within the context of "consistent" sensitivity groups, that is, within the context of individuals who were either low- or high-time-sensitive across both 400-STI and 1600-STI. Thus, there were two sets of consistent sensitivity groups; one for noflicker timing and another for flicker timing.

Consistent Sensitivity Groups for NFLK Timing

The NFLK consistent sensitivity groups included 26 individuals who were classified as low-sensitive timers and 26 individuals who were classified as high-sensitivity timers. A 2 x 3 MANOVA was conducted, entering groups as the between-subjects factor and SPEED, ACCUR, and MEM, as the dependent variables. The multivariate between-subjects effect was significant ($F[3, 48] = 6.86, p = .001, \eta_p^2 = .30$). NFLK high- sensitivity timers obtained greater MEM scores ($F[1, 50] = 14.91, p < .001, \eta_p^2 = .23, M = 1.25, SD = 1.28$, versus, $M = -1.14, SD = 1.82$) and ACCUR scores ($F[1, 50] = 13.35, p = .001, \eta_p^2 = .21, M = 1.02, SD = 1.48$, versus, $M = -.45$, $SD = 1.44$) than did low-sensitivity timers, however, greater SPEED scores did not reach significance ($F[1, 50] = 3.38$, $p = .07, \eta_p^2 = .06, M = 1.09, SD = 2.84$, versus, $M = -.55, SD = 3.57$). These results are fairly congruent with the correlational data. Greater memory and accuracy scores were most associated with high sensitivity performances across noflicker durations.

Consistent Sensitivity Groups for FLK Timing

The FLK consistent sensitivity groups included 28 individuals who were classified as low-sensitivity timers and 27 individuals who were classified as high-sensitivity timers. A 2 x 3 MANOVA was conducted, entering groups as the between-subjects factor and SPEED, ACCUR, and MEM, as the dependent variables. The multivariate between-subjects effect was significant (F[3, 51] = 6.37, p = .001, η_p^2 = .27). As was the case for NFLK, FLK high-sensitive timers obtained greater ACCUR scores (F[1, 53] = 10.01, p = .003, η_p^2 = .16, M = 1.17, SD = 1.35, versus, M = -.11, SD = 1.63) and MEM scores (F[1, 53] = 8.10, p = .006, η_p^2 = .13, M = .90, SD = 2.37, versus, M = -.83, SD = 2.12), however, they also obtained greater SPEED scores (F[1, 53] = 9.83, p = .003, η_p^2 = .16, M = 1.58, SD = 2.46, versus, M = -.72, SD = 2.95) than did low-sensitivity timers. These results are fairly congruent with the correlational data. SPEED scores showed greater association to individual differences for flicker timing, and MEM scores showed reduced association. ACCUR scores described individual differences to a greater extent than did MEM scores.

Discussion

Individual Differences in Time Perception

The Consistency of Individual Differences across Durations

The present results are in general agreement with Brown (1998) and colleagues (Brown et al., 1995) who examined interval timing within the context of individual differences (Brown, 1998; Brown et al., 1995); individuals vary considerably with respect to their ability to accurately detect differences in duration, and level of ability is manifest fairly reliably across a wide range of timing tasks. Our results extend these observations to timing tasks in the less than one second range. However, while approximately 65 to 70 percent of our sample maintained group classification as time-insensitive (low-sensitivity timers) or time-sensitive (high-sensitivity timers) across shorter and longer task durations, the results did not conform to Weber's Law where the standard deviation of judgments of time is expected to grow as a linear function of the mean duration. Our data show that time discrimination with shorter durations is less than that for longer durations when both duration categories are presented randomly within a series of trials. Further, this reduced discriminability (or *sensitivity* to differences) was associated with greater individual differences, as manifest by greater variance with 400- versus 1600-STI thresholds. These observations support the idea that different mechanisms may underlie the timing of shorter and longer durations. Before examining our findings further, a brief overview of the timing mechanisms is in order.

Is There More Than One Timing Mechanism that Contributes to Time Perception?

A fundamental question regarding the mechanisms that underlie interval timing is whether timing is performed by some specialized central time-keeping system or distributed throughout different brain regions. Currently, the most popular proposal for mechanisms underlying the direct measurement of temporal information favours a centralized mechanism where the passage of time is encoded by an internal clock, a hypothetical neural pacemaker that generates pulses that are recorded by a counter (e.g., Church, 1984; Creelman, 1962; Treisman, 1963). The accumulation or number of registered pulses forms the basis on which time is estimated. The wide-spread acceptance of TIP, an interval timing model that applies scalar timing theory, lies in its ability to describe timing behaviours that are more than just an expression of an internal clock. As numerous studies have shown, higher-end cognitive processes, such as attention, memory, and decision processes have critical roles in timing behaviour (e.g., Brown & West, 1990; Macar et al., 1994; Wearden, 2004). TIP incorporates these elements of timing behaviour; however, there is much flexibility in fitting data, and as pointed out by TIP proponents (e.g., Wearden, 1999), there is often difficulty in isolating tripartite clock-memory-decision model components for understanding the role of lower-end or physiological processes associated with pacemaker-accumulator clock functions and higher-end or cognitive processes across timing tasks.

Some researchers have argued that the brain has two timing systems: one for shorter durations on the order of one second or less, and one for longer durations on the order of one second or more (e.g., Buonomano & Karmarkar, 2002; Madison, 2001; Mangels et al., 1998; Rammsayer, 1999). Although the shorter-duration timing system is not well understood, it is believed to be a complex system, accounting for timing behaviours associated with coordination and movement, conditioned reflexes, and rhythm production (see Buonomano & Karmarkar, 2002, for a review). Researchers refer to this system using terms such as "bottom-up processing," "fast, parallel processing," or, "time-dependent processing." Unlike temporal processing of durations in the range of one second or more, temporal processing of brief durations is believed to be beyond cognitive control, and is based on sensory processes at the subcortical level (Michon, 1985; Rammsayer & Lima, 1991). Indeed, Mattes and Ulrich (1998) showed that performance on temporal discrimination of intervals with durations of up to 300 ms was not influenced by experimentally-induced changes in directed attention. However, because there has been little research in this area, it is unknown whether there is a clear boundary or an overlap between "bottom-up" and "top-down" timing systems.

A number of studies have suggested discontinuities in timing processes (e.g., Weber fractions, correlational data) when the duration is close to one second (e.g., discrimination of timbre: Kubovy & Howard, 1976; discrete intervals: Grondin, Meilleur-Wells, & Lachance, 1999; the last interval in a series: Halpern & Darwin, 1982; sensorimotor synchronization: Woodrow, 1932; or variability in tapping: Madison, 2001). Further, pharmacological experiments suggest there is a dissociation between ms and sec processing. Rammsayer (1997b) found that remoxipride, a dopamine antagonist selective for D2 receptors, can impair time processing on a second scale but not with 50 ms interval tasks. Also, the administration of benzodiazepines can lead to significantly worse performance on a one sec task but have no effect on a 50 or 100 ms task (Rammsayer, 1992, 1999).

A large part of the timing literature has ignored duration-specificity because other issues have been in focus. Experiments typically use one or a few different intervals within a range less than or greater than one second. However, the question of whether a timing system is scale-invariant is important. If the system works the same way, for all parameter values, as has been suggested by proponents of TIP, then it is truly a linear system. However, this is unlikely the case, as we know that biological systems are intrinsically dynamical, with a great deal of overlap and redundancy due to evolutionary selection pressures. While there have been many studies that support scalar timing and Weber's law, few studies have traversed the one second duration mark. Data reported by Wearden and McShane (1988) and Allan and Gibbon (1991) appear to be the only instances, with both studies supporting the scalar timing model and Weber's law. However, it is possible that human timing is qualitatively different for different regions of the time continuum. Further, as mentioned previously, the results of scalar timing research with humans show that human timing is less rigid and more strongly context dependent than animal timing. These findings support the idea that top-down influences, such as attention, have impact on timing performance, although the interaction of higher-end cognitive processes and neural timing mechanisms across a range of durations has not been systematically investigated. By measuring 400- and 1600-STI FLK and NFLK performances and comparing these to established cognitive tests, we did, however, attempt to examine some of these links.

Buonomano and Merzenich (1995) proposed a model for temporal processing that describes interval timing in the ms range as relying on a dynamic network that exhibits time-dependent neuronal properties such as paired-pulse facilitation (PPF) and slow inhibitory postsynaptic potentials (IPSPs). PPF refers to a form of short-term plasticity in which the second of a pair of action potentials can produce a larger postsynaptic response. Slow IPSPs refer to GABA-mediated postsynaptic currents. The time course of both paired-pulse facilitation and slow IPSPs ranges from tens to a few hundred milliseconds. The network is comprised of a large population of interconnected excitatory and inhibitory neurons in which the excitatory synapses exhibit PPF and the inhibitory synapses produce both slow and fast IPSPs. Bunonmano and Karmarkar (2002) propose that networks of neurons are intrinsically capable of decoding temporal information as a result of time-dependent changes in network state produced by short-term forms of plasticity, and that time interval discrimination is quite sensitive in this range versus seconds timing. Changes in the dynamic balance between excitation and inhibition in circuits produce neuronal response characteristics that are dependent on previous activity, thus, sensory stimulus history has impact on present temporal encoding.

While Buonomano and Merzenich's (1995) model is compatible with the idea that distinct neural mechanisms underlie ms and sec timing, it is possible that a longer-duration interval timing system builds on multiples of short intervals. In this regard, the neural network for shorter-duration timing could easily be extended to include frontal cortical connections associated with working memory and attentional processes. As discussed by Killeen and Weiss (1987), there is an advantage to segmenting an interval to be judged into subintervals. Just as tapping movements of the foot help musicians to "keep time," a consistent rhythm, such as counting, increases the reliability and accuracy of time judgments for longer durations. However, it is possible that even in the absence of conscious counting strategies, the longer-duration timing system involves a consolidation of lower-end timing processes through the use of top-down resources such as working memory. By chunking smaller intervals together, longer durations could be remembered. Increases in the sum of the variances of "chunks" or subintervals would contribute to a proportional relation between the variance of the time judgments and stimulus durations, as seems to be the case for time judgments across the less than and greater than one second range.

Neither the TIP nor Buonomano and Merzenich's (1995) model for shorter-duration timing can account for our results. TIP describes the variability of time judgments as increasing linearly, in proportion to increases in the base duration. Shorter-duration timing is described as less variable than longer-duration timing. However, we observed disproportionately greater and highly variable 400 ms thresholds within the context of a timing task that involved shifts between shorter- and longer-duration timing.

While the disparity between thresholds for 400 ms and 1600 ms was large, 400 ms and 1600 ms measures of proportion correct were less disproportionate, suggesting that the relatively extended range for 400 ms timing (1.5 time increment contrast, versus .58 for 1600 ms) might account for the discrepancy. However, observations of threshold during the preliminary study suggested that an increased time increment contrast range was required for obtaining suprathreshold measures of sensitivity across participants, while a shorter range was required for 1600 ms timing. Performances appeared to be much more variable for 400 ms, with some individuals showing rapid increases in sensitivity over relatively small time increment contrasts while others only showed increases at considerably greater time contrasts. These observations together with the fact that proportion correct over the range was significantly lower than that with 1600-STI, despite a disproportionately greater time increment contrast range and low FA rate, suggest that the disproportionately greater and highly variable 400-STI thresholds likely resulted due to the random presentation of shorter- and longer-duration timing within the same block of trials. We posit that these shifts may have led to an interaction of shorter- and longer-duration timing systems, where top-down perceptual influences such as counting or chunking interfered with short-term plasticity needed for shorter-duration timing processes.

Many participants in the present study described the 400 ms standard-test pairs as being "faster" than the 1600 ms pairs. Participants also reported that the presentation of 400-STI pairs seemed to be a single perceptual event with shorter ISI, while the presentation of 1600-STI pairs were reported to be more fragmented. While subjective in nature, these reports support the possibility that higher-end perceptual processes had impact on both 400 ms and 1600 ms timing, where attempts to use a counting strategy led to top-down chunking of both shorter- and longer-durations. Most, if not all, the participants reported that they attempted to count intervals, although they did not find this to be a useful strategy for shorter durations. It is possible that the practice of a perceptual strategy such as counting during the trials could have reduced the flexibility for shifting between timing systems, leading to the predominant use of longer-duration timing strategies with the net result of lowering resolution for short durations.

What is the Effect of an Increase in Pacemaker Speed on Time Perception, and Does this Effect Vary Across Time-sensitive and Time-insensitive Groups?

Treisman and colleagues (Treisman, Cook, Naish & MacCrone, 1994; Treisman, Faulkner, & Naish, 1992; Treisman, Faulkner, Naish, & Brogan, 1990) proposed that repetitive stimulation (auditory clicks or flicker) could increase the speed of the pacemaker for an internal clock, where the sensory information served to activate and entrain neural processes associated with timing. Recent research supports this proposal (Burle & Casini, 2001; Droit-Volet & Wearden, 2002), as time judgments reflect a subjective lengthening of duration subsequent to this experimental manipulation. TIP researchers suggest two possible explanations for this phenomenon: (1) that the repetitive stimulation induces an increase in arousal, thereby increasing the rate of the internal clock pacemaker, so that an increased number of "pulses" from the pacemaker occurs per unit time. This manipulation would lead to an increase in subjective duration; (2) that the repetitive stimulation may alter the flow of pulses between the pacemaker and accumulator by increasing the gating "on" and "off" speed of the switch, resulting in increased pulse accumulation over time. The mathematical properties of pacemaker-accumulator clocks suggest that the first of the two explanations is most plausible (Wearden & Culpin, 1998), as the effect due to repetitive stimuli has been found to increase as duration increases (e.g., Burle & Casini, 2001). As proposed by Wearden and Culpin, faster switch time would lead to a constant increase in perceived duration regardless of stimulus length.

We considered that increased pacemaker speed might increase the resolution for timing, perhaps by decreasing the variability in the number of pulses emitted over a period of time, thereby increasing the accuracy of an internal representation of time. This effect could be achieved by repetitive visual stimuli of frequency and intensity sufficient for entraining more centralized pacemakers, as was suggested by Treisman et al. (1990, 1992, 1994). Our MOCS methodology allowed a test of this hypothesis. Our results support the proposal that repetitive visual stimuli can enhance the resolution for timing; however, there was an interaction of DURATION with this effect, where the resolution for 1600-STI increased and the resolution for 400-STI timing decreased. Presenting flickering stimuli during longer-duration discrimination tasks (as compared to 1600-STI NFLK performances) showed increases in sensitivity and efficiency, as well as reduced inter-subject variability. FLK effects with 400-STI could be described as an amplification of this study's main DURATION effects. Thresholds were increased, efficiency and overall accuracy decreased, slopes increased reflecting greater uncertainty, and decision criterion tended to be more stringent. While there was significant DURATION x STIMULUS interaction, it should also be noted that the poorest and best performances were found with 400-STI FLK and 1600-STI FLK, respectively. This points to a two-system timing process. However, at the same time intra-subject THRESH and PROPC performance reliability was greater with the FLK stimuli. In this regard, flicker entrainment may have an effect on all timing processes, irrespective of duration.

As already mentioned, it is possible that implicit/explicit counting or "chunking" during blocks of trials may have led to the use of a primarily "top-down" strategy for both shorter and longer duration tasks. The interleaved, random trial method we used might easily lend itself to this kind of "top-down" influence. This strategy, however, could interfere with lower-end short-term plasticity that is normally associated with increased accuracy, resulting instead in a reduced sensitivity for short durations. If neural entrainment of central pacemakers associated with central processing occurred, we would expect an increase in "top-down" influences on shorter-duration timing. Further, this explanation could account for the observations of decreased effect of repetitive stimuli on shorter durations reported in the literature.

Our observations and analyses suggest that flicker had a large effect on low-sensitivity timers with 1600-STI NFLK, and little effect with the shorter 400-STI NFLK. This suggests that their timing processes or central resources that contribute to timing were made more efficient with flicker. Perhaps the flicker led to an imposed "counting" strategy that increased the accuracy and consistency for chunking strategies or other perceptual processes. This is difficult to ascertain, however, given the random interleaved nature of our trial presentations. To truly discern these effects, one needs to present separated blocks of short or long standard interval trials. Of course, the reason we did not do this in the first place is because we wanted to reduce such biases as timing order, counting, or anticipatory bias. In other words, we wanted to avoid an experimentally-induced “top-down” effect which becomes almost compulsory when all trials are of the same duration in a given block. This is why methodological trade-offs need to be carefully considered in future research efforts in this area.

Processing accuracy appears to have an impact on both short and long durations, at least when the duration trials are presented randomly. With stimulus flicker, individuals who exhibited faster processing speed also showed a greater ability to balance this speed with accuracy, and this was true regardless of DURATION level. The ability to balance speed and accuracy on cognitive tasks is generally attributed to “executive” or central processes (Lezak, 1995). These “top-down” influences are usually attributed to frontal lobe activity. Frontal areas are involved with planning, maintaining information, retrieving information, executing motor behaviour, and organizing incoming sensory information.

As we explained previously, our MOCS design was an attempt to produce “naturalistic” observations of timing behaviour. In real life, timing involves attentional shifts between external stimuli and their internal representations for a large range of shorter and longer durations. Within the context of our timing task methodology, rapid shifts between shorter- and longer-duration timing systems resulted in reduced sensitivity for both shorter and longer durations with a particular detrimental effect on 400-STI . However, despite the fact that sensitivity was most greatly reduced for 400 ms timing, approximately two-thirds of individuals reported that they felt more confident about their “shorter” than their “longer” duration judgments. These subjective experiences are not in agreement with objective observations of increased uncertainty as ascertained by 400-STI transducer function slopes. Increased uncertainty for the 400-ms timing task was associated with more stringent criteria, and this varied little from individual to individual. However, short-duration sensitivity was highly variable, suggesting that a stabilized cognitive decision criteria had little influence on performance. This was true for both low- and high-sensitivity timers. This suggests that 400-ms time discriminations largely relied on clock processes other than decision, such as pacemaker pulse speed and memory. The threshold measurement appears to best reflect consistency and accuracy for creating internal representations of duration (i.e., the sensory as opposed to the motoric side of temporal processing). Our cognitive evaluation observations of individual differences in processing accuracy and working memory support this interpretation. Significantly lower thresholds were observed for individuals who obtained significantly greater processing accuracy and memory scores, with accuracy accounting for the majority of variance with 400-STI thresholds across low- and high- temporal sensitivity groups. In contrast, 1600-STI: THRESH were associated with more flexible decision processes, and showed a greater degree of association with working memory, accuracy, and processing speed scores.

What Is The Relationship Between Individual Differences In Time Perception and Performance On Standardized Cognitive Tasks?

We predicted that there would be significant relationships between temporal performance and scores on tests of cognitive performance, and proposed that these relationships would help characterize the importance of information processing speed, accuracy and working memory in timing tasks. Other researchers have conducted similar investigations (e.g., Perbal et al., 2002; Pouthas & Perbal, 2004; Wearden et al., 1997), however, they focus on identifying these relationships within groups of participants that are known to exhibit declines in cognitive performance, such as the elderly, patients with Parkinson's disease, and patients with severe traumatic brain injury. We observed significant associations between individual differences in cognitive processes and timing performances in a relatively young, healthy sample of university students, despite relatively truncated ranges for cognitive performance scores. Relationships between timing performances and cognitive performances were examined within those individuals who showed consistent timing sensitivity across DURATION.

Slower information processing speed is believed to account for age-related changes in duration judgments; however, performance on RT tasks has not been reliably linked to temporal variability in other groups (e.g., Pouthas & Perbal, 2004). As discussed previously, it is most likely the case that the influence of processing speed on timing accuracy and variability is best observed within the context of speed – accuracy tradeoffs. As RT may express overall quickness in information processing and motor response, processing ability associated with perceptual accuracy is not a factor in RT analyses. High-sensitivity timers, as determined by NFLK THRESH distributions, were closely associated with higher working memory scores, followed by greater accuracy scores. However high-sensitivity timers as determined by FLK THRESH distributions, showed greater accuracy scores, followed by faster processing speed and higher working memory scores. As suggested by the results of the data analyses that examined the effect of FLK on NFLK-defined low- and high-sensitivity groups, individuals may vary in terms of their ability to benefit from an increase in pacemaker speed. Individuals who have slower processing speeds and/or reduced ability to balance a flicker induced increase in processing speed using higher level central processor attentional resources are less likely to show significant increases in sensitivity and efficiency for timing. While no causality is implied by any of the results of the cognitive performance data analyses, they highly suggest that individual differences in working memory, processing speed, and the ability to balance speed and accuracy, have their relationships to psychophysically-determined timing performances. Similarly, a reverse argument can be made in which different timing-sensitive individuals might show different behavioral performances on a standardized cognitive test, with the performance differences having no bearing on the intended construct of the test. This is a validity issue that certainly warrants further investigation.

Summary

The present results have important implications for internal clock models and research that investigates the nature of timing mechanisms. Individuals differ in terms of their ability to discriminate durations, and these differences are manifest across tasks of shorter and longer duration. Controlling for individual differences in timing behaviour can assist investigators that seek to elucidate factors that contribute to aberrations in timing processes. Qualitative and quantitative differences in timing processes were associated with shorter and longer durations, supporting the idea that different timing systems contribute to timing in the ms to s range. The stability of individual differences across these durations and the relative increase in this stability in the flicker condition suggests that the timing system associated with higher-end "top-down" central processes interfered with lower-end timing systems, which we believe led to reduced sensitivity for time interval discriminations in the few hundred ms range. It is apparent, that future *psychophysical* research is sorely needed if we are to better understand the system, its components (if any) and the sensory/cognitive/motor processes involved with time perception.

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Appendix A

Cognitive Tasks

Seashore Rhythm Test (Reitan & Wolfson, 1985)

Participants completed the Seashore Rhythm Test, a timing task from the Halstead-Reitan Neuropsychological Test Battery (Reitan & Wolfson, 1985), used for the purpose of comparing visual timing sensitivity with an auditory timing task. Neuropsychologists consider the Seashore Rhythm Test to be a measure of non-verbal auditory discrimination that is sensitive to impairments in attention and concentration (Lezak, 1995). The test was administered by audiotaped instructions and test items that were provided by the test maker. Thirty pairs of rhythmic patterns were presented in three blocks of 10 rhythmic pairs. Participants were instructed to indicate whether the two rhythms in each pair were the same or different. The Seashore Rhythm Test is a brief test. Performances do not reflect reliable measures of auditory temporal sensitivity by time perception research standards, however, the test was readily available and easily administered, allowing a test of its utility for our research purposes.

Processing Speed and Accuracy Tasks

These tasks included the California Computerized Assessment Package (CalCAP, Miller, 1999) Simple, Choice, and Sequential Reaction Time tasks, the Stroop Neuropsychological Screening Test (Trenerry, Crosson, DeBoe, & Leber, 1989), and the Symbol Search subtest from the Wechsler Adult Intelligence Scale – Third Edition (WAIS-III, Wechlser, 1997a).

CalCAP (Miller, 1999). This battery provides measures of reaction time for tasks that place demands on selective attention, rapid visual scanning, and ability to sustain attention. The CalCAP Simple Reaction Time task provides a basal measure of reaction time. The task has very high internal consistency (.91 - .95) and very low test-retest reliability (.20 - .29), suggesting that the psychomotor skills measured by this task vary considerably depending on state variables such as motivation, fatigue, time of day, etc. The CalCAP Choice and Sequential Reaction Time measures have very high internal consistency reliability (.86 - .96), and moderate 6-month test-retest reliability (.68). The results of factor analyses suggest that these subtests load onto factors that are not strongly associated with CalCAP Simple Reaction Time tasks or auditory memory span scores (WAIS-III Digit Span).

The Stroop Neuropsychological Screening Test (Trenerry et al., 1989). This test provides a standardized version of the Stroop procedure (Stroop, 1935) which consists of Color and Color-word tasks that require test-takers to read as quickly and as accurately as possible, colour names printed in congruent ink colour (112 words listed in 4 columns on an 8.5" X 11" sheet) and then colour names that have been printed with incongruent colors (112 words listed in 4 columns). The Stroop effect is manifest as increased response latency and error when test-takers are instructed to attend to a novel versus familiar aspect of the stimuli in the colour-word incongruent condition. Although a variety of tasks have been used for examining the Stroop effect (see MacLeod, 1991, for a review), the colour and colour-word task are the most familiar. Because test-takers must maintain focused attention on the colour aspect of the stimuli and ignore the word meaning, level of performance is believed to reflect selective and sustained attention capabilities, as well as mental flexibility.

Symbol Search (WAIS-III; Wechsler, 1997a). This test is a pencil and paper task, that requires the examinee to look at two symbols and decide whether either one is present in a subsequently presented array of five symbols. Arrays of symbols are presented in 60 rows down the length of four 8.5" X 11" sheets of paper. Symbol Search is a speed test; test-takers must complete as many items as possible in two minutes. The test measures speed for visual discrimination and visuoperceptual scanning. Symbol Search is a moderately reliable subtest (r_{xx}=.77, Sattler, 2001).

Short-term/Working Memory Tasks.

These tasks included subtests taken from the Wechsler Memory Scale – Third Edition (WMS-III; Wechsler, 1997b); Digit Span Forward and Backward, Spatial Span Forward and Backward, and Letter-Number. The relatively simple Digit Span Forward task measures the storage component of short-term or working memory for auditory information, while the Digit Span Backward and Letter-Number Sequencing subtests measure ability for storage and the processing of simple and complex sequences of auditory information, respectively. The auditory stimuli in the Digit Span and Letter-Number Sequencing tasks are comprised of numbers, and letters and numbers, respectively. The Spatial Span Forward and Backward subtests measure ability for storage and processing of simple and complex sequences of visual-spatial information. The visual stimuli in the Spatial Span tasks consist of ten three-dimensional blocks that are in a fixed (glued) pattern on a small platform. The working memory subtests reflect a modality-specific conceptualization of memory, however, there is evidence that suggests that the Spatial Span backward task is closely associated with measures of immediate and delayed auditory memory (Wilde & Strauss, 2002). The WMS-III memory tasks exhibit strong test-retest stability (r_{xx} = .84 to .90; Sattler, 2001).

Appendix B

Acronyms

AGM	attentional gate model
TIP	temporal information processing model
SET	scalar expectancy theory
LI	latent inhibition
STM	short-term memory
LTM	long-term memory
SDT	signal detection theory
MOCS	method of constant stimuli
LWS	long wavelength-sensitive
MWS	medium wavelength-sensitive
NFLK	noflicker
FLK	flicker
400-STI	400 ms standard interval
1600-STI	1600 ms standard interval
THRESH	threshold
DEC	decision
PROP	proportion correct
MEM	memory
ACCUR	accuracy
ISI	interstimulus interval
TOE	time-order effect

Table 1

Psychophysical Measures of Time Perception for 400 ms and 1600 ms Standard Time Intervals, for No-flicker and Flicker Stimulus Conditions: Descriptive Statistics (N = 78)

Variables	M	SD	Range
THRESH 400-STI NFLK	.78	.29	.24 – 1.5
THRESH 400-STI FLK	.85	.29	.33 – 1.5
THRESH 1600-STI NFLK	.29	.13	.09 – .58
THRESH 1600-STI FLK	.26	.11	.08 – .58
DEC 400-STI NFLK	1.72	.26	1.00 – 2.05
DEC 400-STI FLK	1.84	.25	1.08 – 2.05
DEC 1600-STI NFLK	1.27	.60	-.10 – 2.05
DEC 1600-STI FLK	1.24	.56	.00 – 2.05
PROPC 400-STI NFLK	.59	.09	.34 – .81
PROPC 400-STI FLK	.56	.09	.32 - .82
PROPC 1600-STI NFLK	.66	.09	.40 - .82
PROPC 1600-STI FLK	.69	.09	.42 - .94
SLOPE 400-STI NFLK	2.20	1.25	.62 – 5.2
SLOPE 400-STI FLK	2.44	1.29	.52 – 5.2
SLOPE 1600-STI NFLK	2.05	1.23	.43 – 4.9
SLOPE 1600-STI FLK	1.71	.89	.57 – 4.6

Note. THRESH = Threshold (as proportion increment contrast); 400-STI = 400 ms standard time interval; 1600-STI = 1600 ms standard time interval; NFLK = No-flicker; FLK = Flicker; DEC = decision bias; PROPC = Proportion Correct; SLOPE = slope.

Table 2

Psychophysical Measures of Time Perception for 400 ms and 1600 ms Standard Time Intervals, for No-flicker and Flicker Stimulus Conditions: Correlations (N = 78)

Variables	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1. THRESH 400-STI NFLK	–															
2. THRESH 400-STI FLK	.62***	–														
3. THRESH 1600-STI NFLK	.55***	.46***	–													
4. THRESH 1600-STI FLK	.63***	.70***	.51***	–												
5. DEC 400-STI NFLK	-.30**	-.08	-.26*	-.16	–											
6. DEC 400-STI FLK	-.17	.36**	-.31**	-.24*	.25*	–										
7. DEC 1600-STI NFLK	-.40***	-.22	-.55***	-.29*	.43***	.24*	–									
8. DEC 1600-STI FLK	-.53***	-.41***	-.35**	-.58***	.36**	.28*	.67***	–								
9. PROPC 400-STI NFLK	-.84***	-.58***	-.40***	-.52***	-.11	.00	.24*	.38**	–							
10. PROPC 400-STI FLK	-.58***	-.85***	-.33**	-.60***	-.09	-.01	.08	.30**	.67***	–						
11. PROPC 1600-STI NFLK	-.27*	-.41***	-.59***	-.40***	-.21	.09	-.22	-.14	.37**	.47***	–					
12. PROPC 1600-STI FLK	-.28*	-.46***	-.34**	-.62***	-.08	.00	-.25*	-.14	.31**	.52***	.67***	–				
13. SLOPE 400-STI NFLK	.35**	.08	.01	-.06	-.03	.11	.06	-.05	-.47***	-.12	-.03	.11	–			
14. SLOPE 400-STI FLK	-.08	.14	-.01	-.08	.29*	-.02	.29*	.31**	-.05	-.35**	-.36**	-.21	-.05	–		
15. SLOPE 1600-STI NFLK	.04	.11	.40***	.02	.02	-.01	-.24*	-.02	-.03	-.15	-.35**	.08	-.04	.08	–	
16. SLOPE 1600-STI FLK	.14	.05	.13	.06	-.04	-.06	.09	.07	-.20	-.03	-.25*	.25*	.15	.03	.05	–

Note. THRESH = Threshold; 400-STI = 400 ms standard time interval; 1600-STI = 1600 ms standard time interval; NFLK = No-flicker; FLK = Flicker; DEC = decision bias; PROPC = Proportion Correct; SLOPE = estimated slope from Weibull fit.
*$p < .05$. **$p < .01$,. ***$p < .001$, . (2-tailed).

Figure Caption

Figure 1. Temporal information processing model (TIP, adapted from the scalar timing model, Gibbon, Church, & Meck, 1984). The TIP model consists of three, interrelated information processing stages – clock, memory, and decision – which are associated with timing, storage, and responding, respectively. The clock (second rectangle down on the left) is responsible for transforming objective time into subjective time, and its processes consist of a pacemaker (first oval to the right of "clock process") that emits pulses at some mean rate (determined by level of general arousal), to a switch (second oval to the right of "clock process") that is controlled by a timing signal, and then to an accumulator (right-most oval at level of "clock process") that sums the pulses. The content (i.e., number of pulses) of the accumulator increases as a linear function of real time (i.e., power function with an exponent of 1.0). Memory processes, including working memory and reference memory, are associated with the storage of clock information. The contents of the accumulator are loaded to working memory, and this information serves as an extended buffer for temporal information from the current trial. Reference memory stores critical temporal information from past trials. The most recent representation in working memory and the reference representation in memory are compared at the decision level (diamond at "decision process" level). The comparator determines a response on the basis of a decision rule which involves a ratio comparison of current time stored in working memory with remembered time sampled from reference memory. The exact decision rule depends upon the timing task (e.g., generalization task requires one comparison, bisection task requires two comparisons). Each component of the model represents a potential independent source of variability.

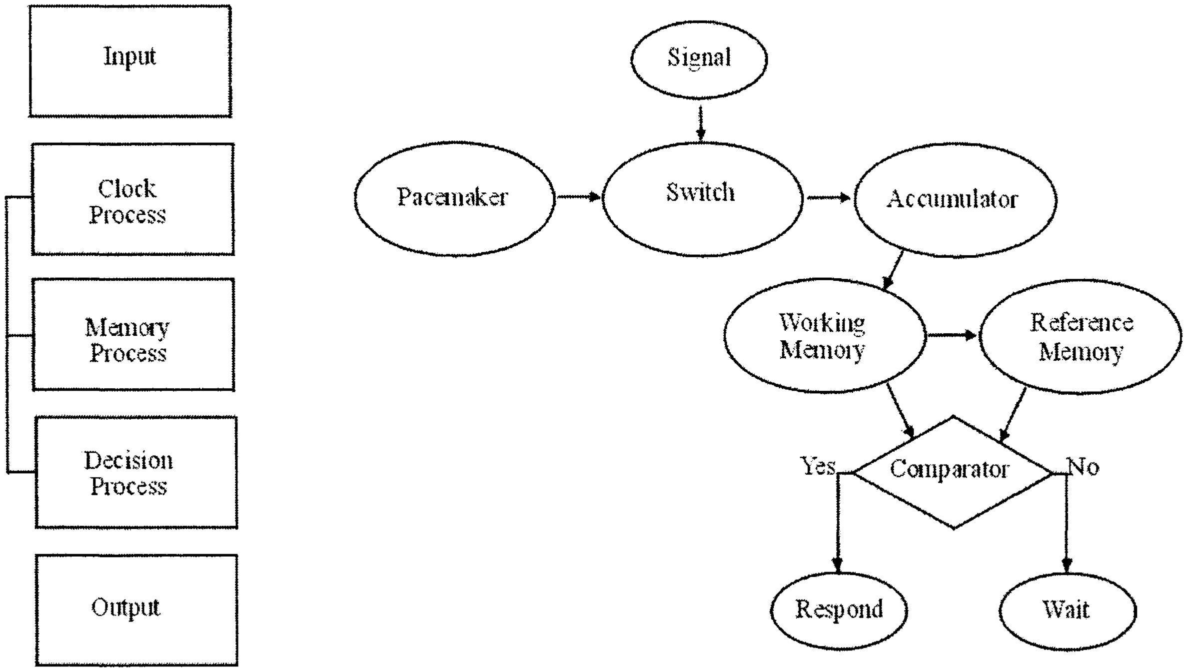

Input
Clock Process
Memory Process
Decision Process
Output
Signal
Pacemaker
Switch
Accumulator
Working Memory
Reference Memory
Yes
Comparator
No
Respond
Wait

Figure Caption

Figure 2. The attentional gate model (AGM), adapted from Zakay and Block (1996). A major element of this model is the attentional gate (second oval from the left), a cognitive mechanism controlled by the allocation of attention to time. As an individual allocates more attention to time, the gate opens wider or more frequently. In this model, duration judgments involve counting the total pulses accumulated in the cognitive counter, a process that also may require attentional resources. The AGM consists of a pacemaker (left-most oval), a gate, a switch, a cognitive counter, and cognitive component processes, including memory and a comparison mechanism. The pacemaker produces pulses at a rate influenced by both general (e.g., circadian) arousal and specific (e.g., stimulus-induced) arousal. Greater arousal is associated with increased pulse rate. A greater number of pulses may pass through the gate if attention is preferentially allocated to time (as opposed to external stimulus events). If duration estimates occur under retrospective conditions, the gate narrows, allowing fewer pulses to pass through it. When a stimulus signaling the beginning of a relevant interval is perceived, a switch (third oval from the left) opens the pathway, the cognitive counter is set to zero, and the flow of pulses begins to be accumulated. The switch operates in an all-or-none fashion according to the temporal meaning of stimuli. The switch closes the pathway when a signal indicating the termination of a relevant interval is perceived, thereby preventing additional pulses from entering the counter. When an estimation or other response is needed, the count is transferred to short-term memory. The count is transferred to reference memory. However, humans, unlike other species, may not depend on reference memory for producing temporally based responses, and may compare two pulse counts for recent presentations in short-term memory (i.e., standard and test interval). When the total pulse counts in STM match, cognitive comparison processes (lower right-most oval) elicit a

response that indicates that the time period has ended. If the number of pulses does not yet match that in reference memory, then individuals will wait or judge the interval as shorter than that in memory (response mechanism, lower-most oval).

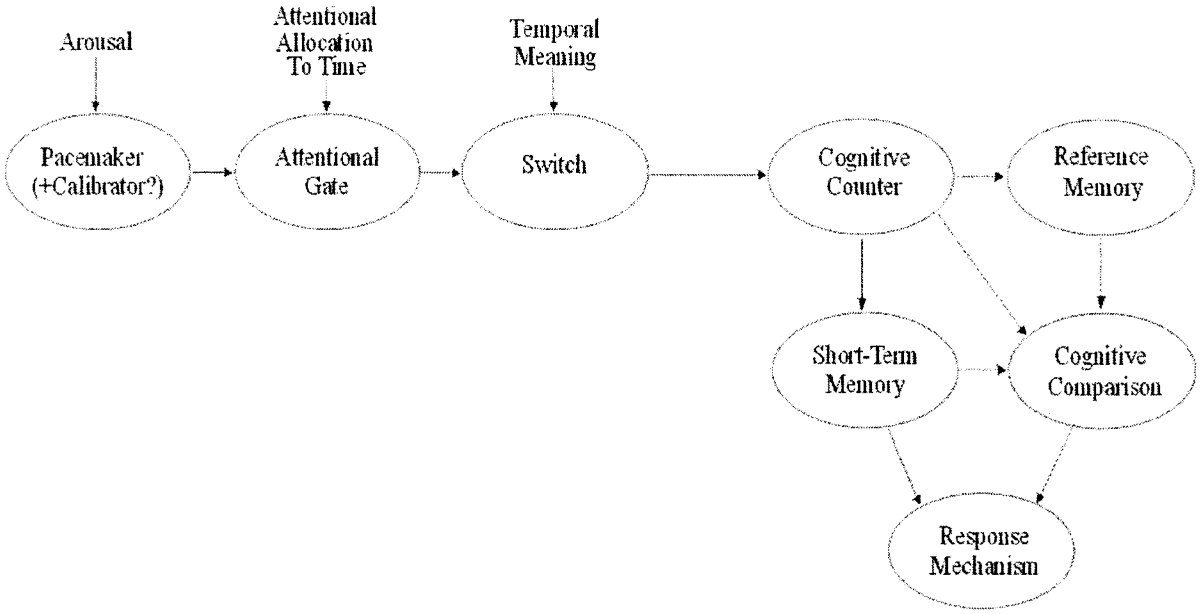
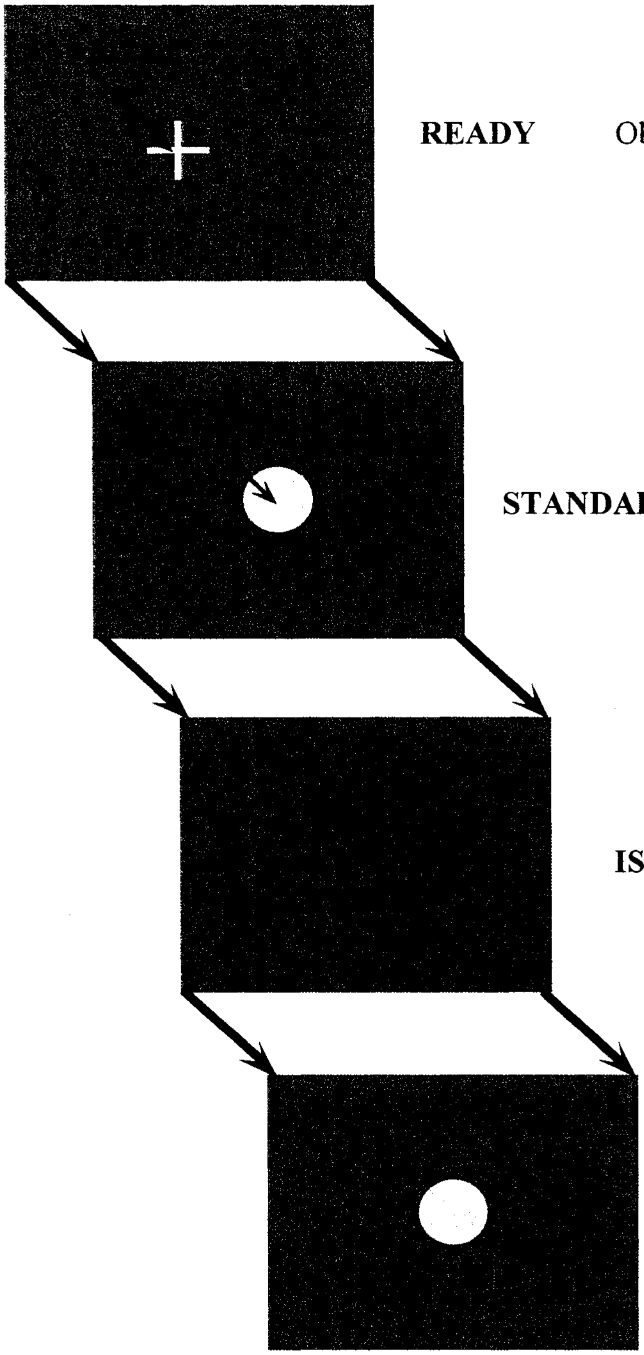

Arousal
Attentional Allocation To Time
Temporal Meaning
Pacemaker (+Calibrator?)
Attentional Gate
Switch
Cognitive Counter
Reference Memory
Short-Term Memory
Cognitive Comparison
Response Mechanism

Figure Caption

Figure 3. A schematic of the spatial and temporal arrangements of the stimuli and trial intervals are shown.



READY Observer initiates trial

STANDARD
400 ms (**400-STI**)
1600 ms (**1600-STI**)

ISI 900 ms

TEST INTERVAL - 5 increments plus 2 “blanks” (same as standard). These intervals minus the Standard = “*Time Increment Contrast*”

Figure Caption

Figure 4. Average 400 ms no-flicker timing data plotted as *d*' versus time increment contrast (solid points). Not surprisingly, discriminability or sensitivity to differences between standard and test intervals increases with increasing time increment contrast. The gray vertical and horizontal lines depict the time increment contrast (x) threshold where $d'=1.5$ (y). The continuous transducer function is a Weibull curve fit to the data. Error bars represent the standard error of the mean. See text for details.

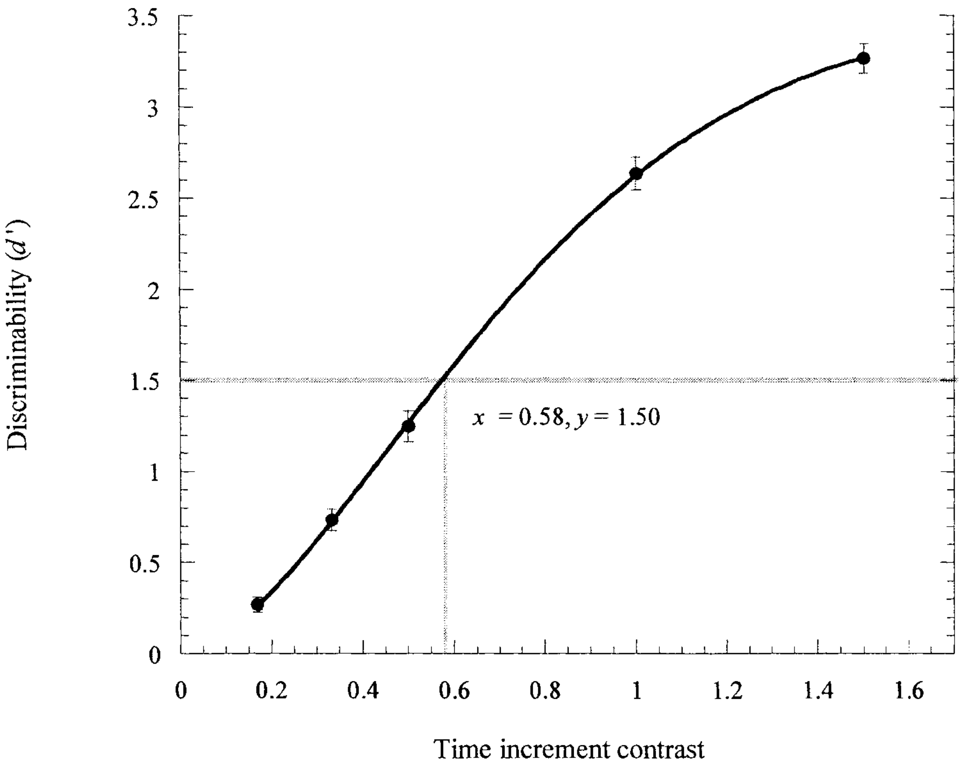

3.5
3
2.5
2
1.5
1
0.5
0
Discriminability (d')
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
Time increment contrast
x = 0.58, y = 1.50

Figure Caption

Figure 5. Average 1600-ms timing data plotted as *d'* versus time increment contrast (solid points). Discriminability between standard and test intervals increases with increasing time increment contrast. The gray horizontal line depicts the threshold in time increment contrast (*x*) values where *d'*=1.5 (*y*). As in Figure 3, the continuous transducer function is a Weibull fit to the data. Error bars represent the standard error of the mean.

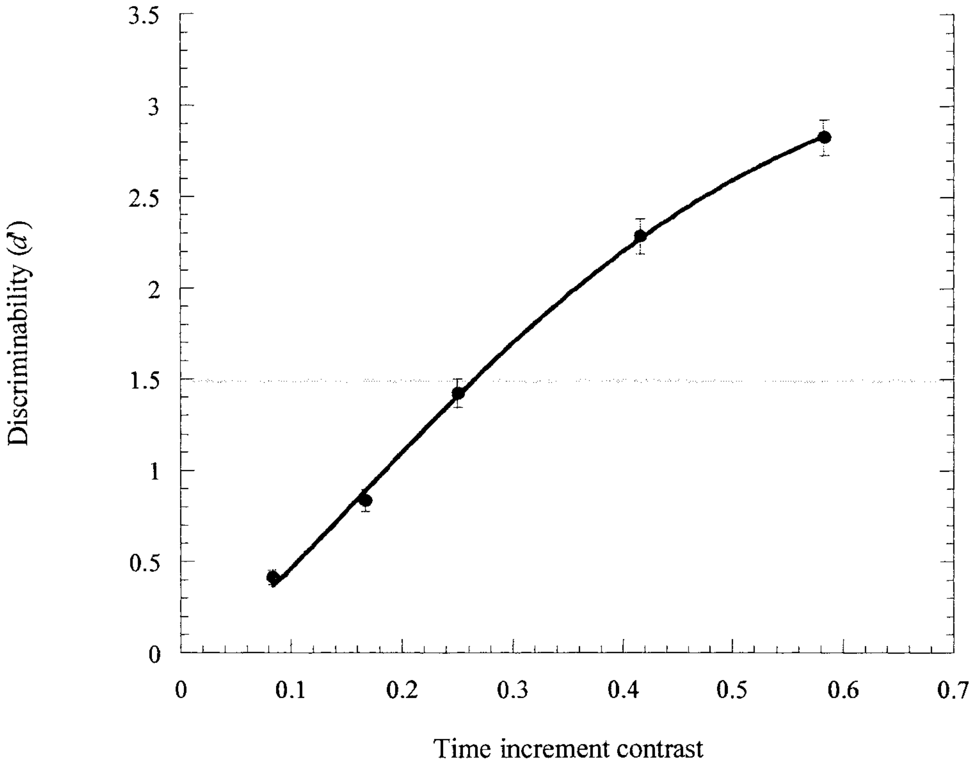

3.5
3
2.5
2
1.5
1
0.5
0
Discriminability (d')
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Time increment contrast

Figure Caption

Figure 6. Significant main effect of DURATION and the two factor (DURATION X STIMULUS) interaction effect on threshold.

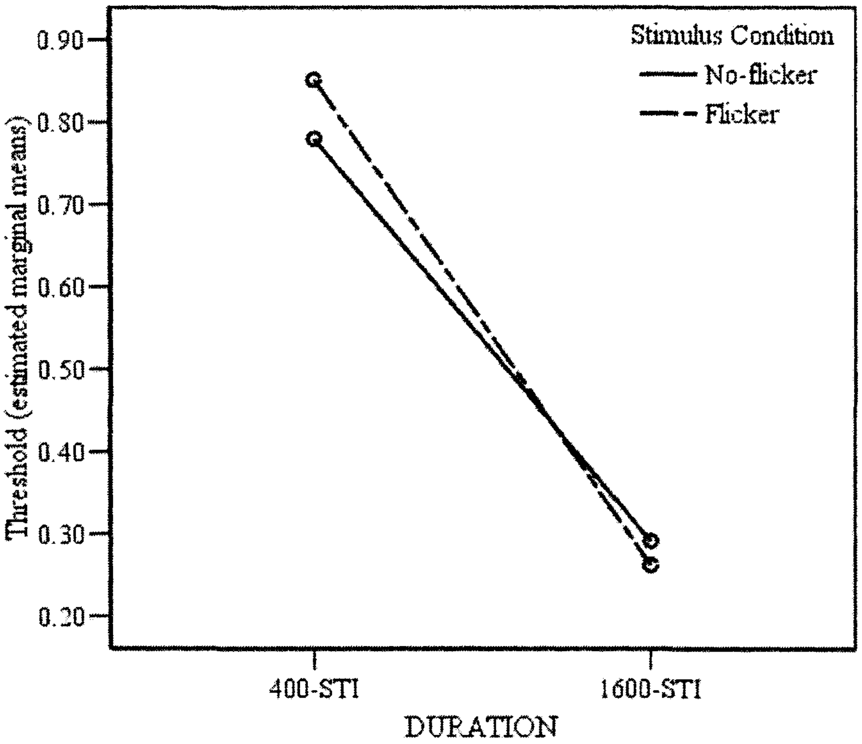

Threshold (estimated marginal means)
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
Stimulus Condition
No-flicker
Flicker
400-STI
1600-STI
DURATION

Figure Caption

Figure 7. Distributions for threshold (THRESH) across DURATION and STIMULUS levels are presented. Boxplots show the median and interquartile range. Both no-flicker (NFLK) and flicker (FLK) 1600 ms thresholds are significantly reduced relative to 400 ms thresholds, and they show reduced inter-subject variability.

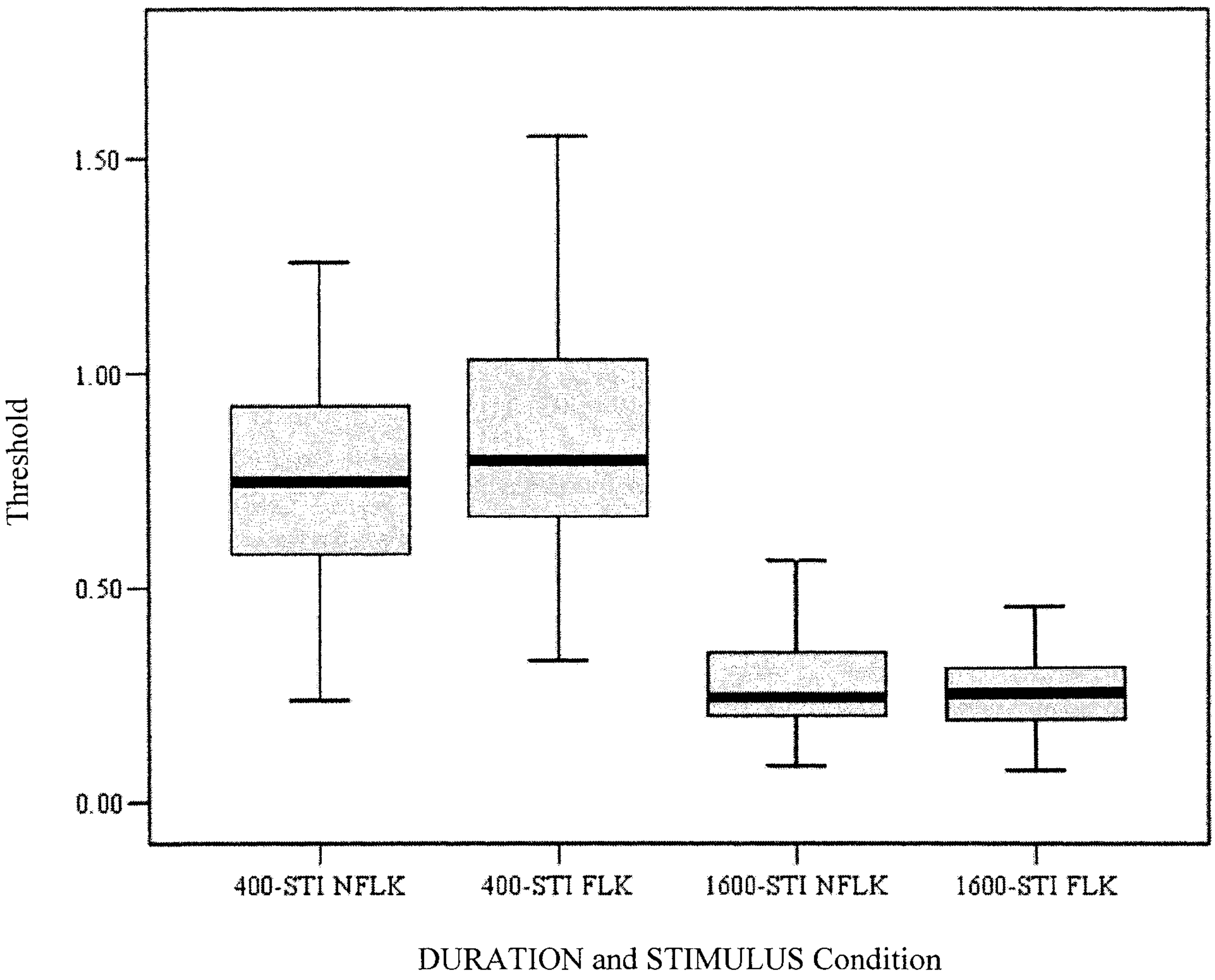

Threshold
1.50
1.00
0.50
0.00
400-STI NFLK
400-STI FLK
1600-STI NFLK
1600-STI FLK
DURATION and STIMULUS Condition

Figure Caption

Figure 8. Mean discriminability as a function of time increment contrast for 400-STI (dashed line fit) and 1600-STI NFLK (continuous line fit) durations. Thresholds (*d*'=1.5) are larger for 400-STI as can be seen in the rightward shift of the dashed psychometric function. Error bars represent the standard error of the mean.

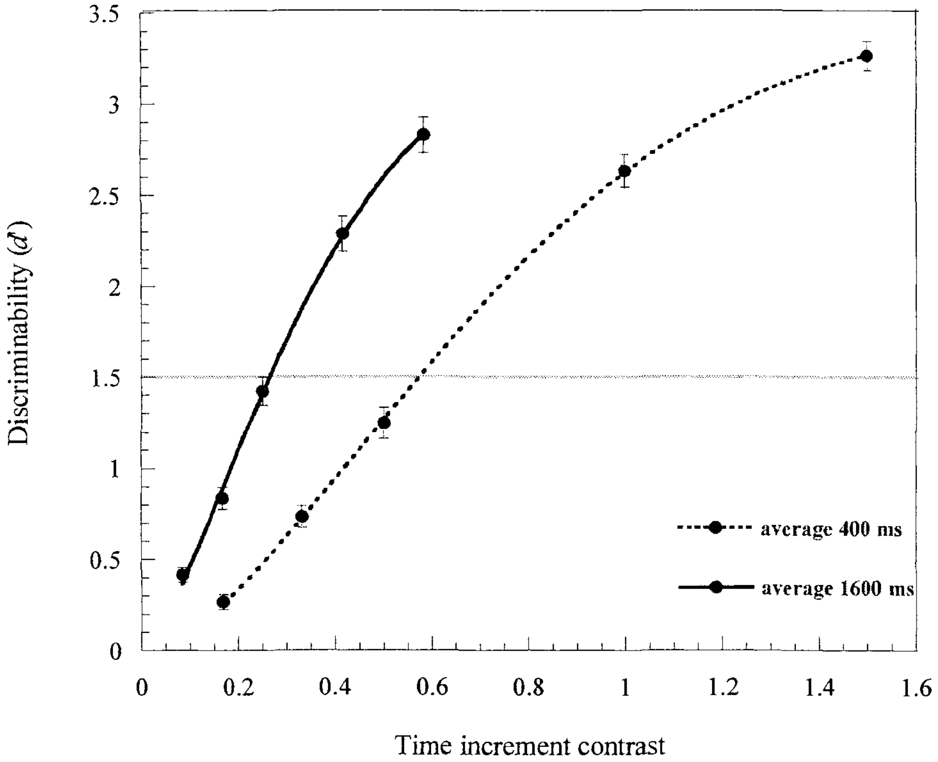
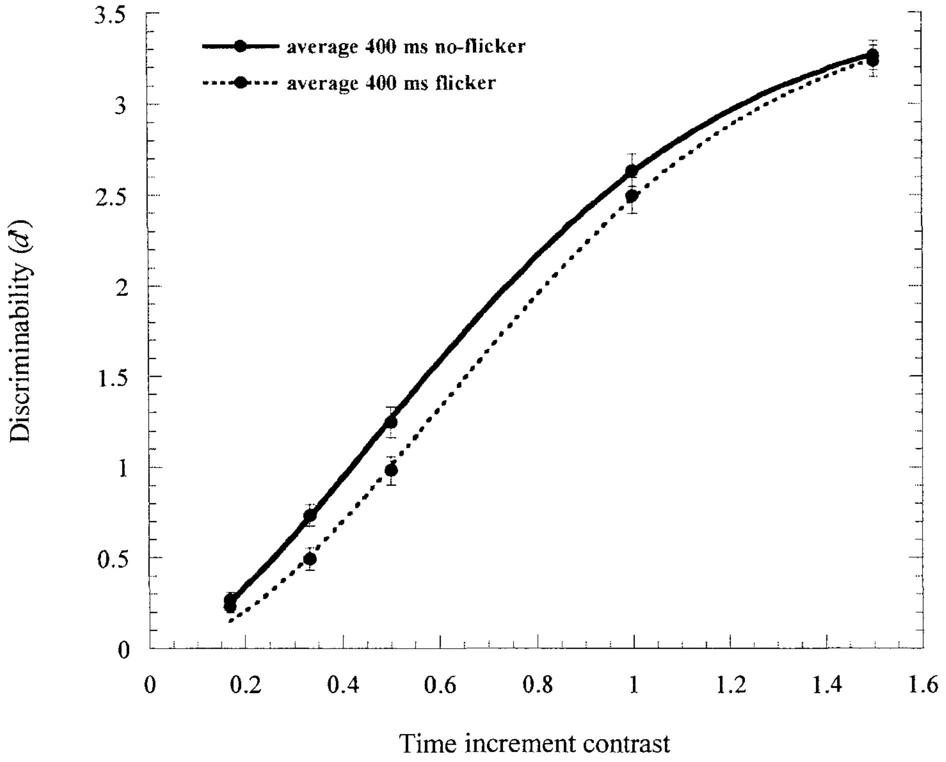

Discriminability (d')
3.5
3
2.5
2
1.5
1
0.5
0
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
Time increment contrast
average 400 ms
average 1600 ms

Figure Caption

Figure 9. Average transducer functions for 400 ms no-flicker and flicker stimuli. 400 ms flicker thresholds were significantly greater than the 400-ms no-flicker thresholds, reflecting reduced time discrimination sensitivity for 400-ms flicker timing. The effect of flicker on average measures of discriminability is greatest over the sub-threshold and threshold range. The effect progressively decreases over the supra-threshold range. Error bars represent the standard error of the mean.



average 400 ms no-flicker
average 400 ms flicker
Discriminability (d')
0
0.5
1
1.5
2
2.5
3
3.5
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
Time increment contrast

Figure Caption

Figure 10. Average transducer functions for1600 ms no-flicker and flicker stimuli. 1600 ms flicker thresholds were significantly lower than the1600 ms no-flicker thresholds, reflecting greater time discrimination sensitivity for 1600 ms flicker timing. The effect of flicker on average measures of discriminability is greatest over threshold and supra-threshold range. Error bars represent the standard error of the mean.

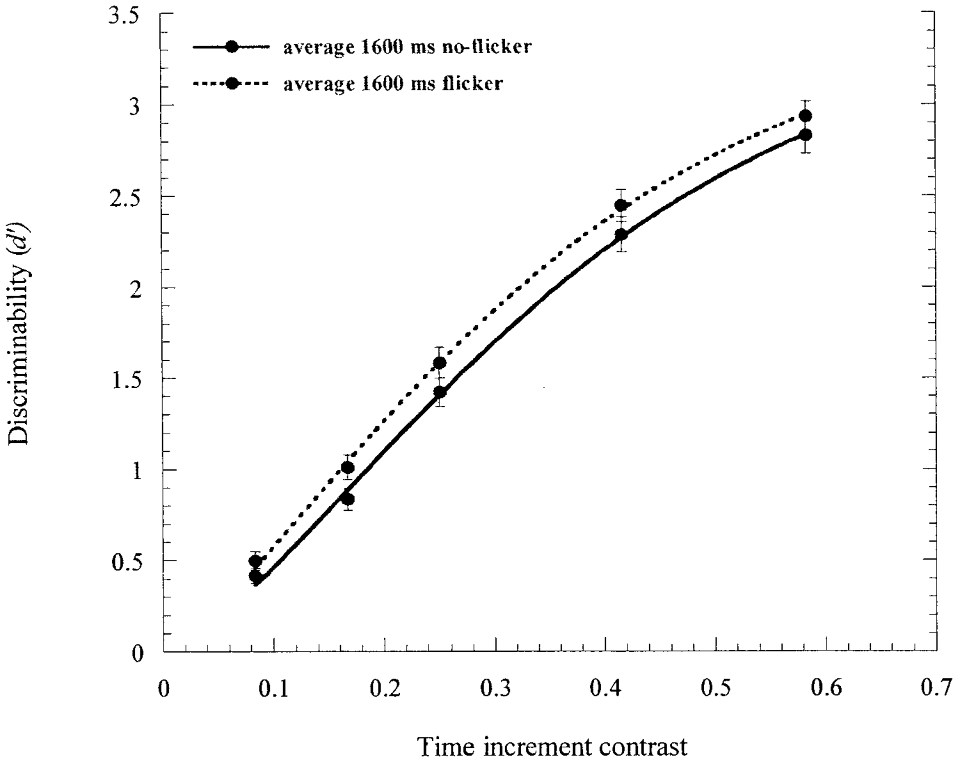

average 1600 ms no-flicker
average 1600 ms flicker
Discriminability (*d'*)
Time increment contrast
3.5
3
2.5
2
1.5
1
0.5
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7

Figure Caption

Figure 11. The significant main effect of DURATION on decision bias. No main significant main effect of STIMULUS or interaction of DURATION and STIMULUS was detected.

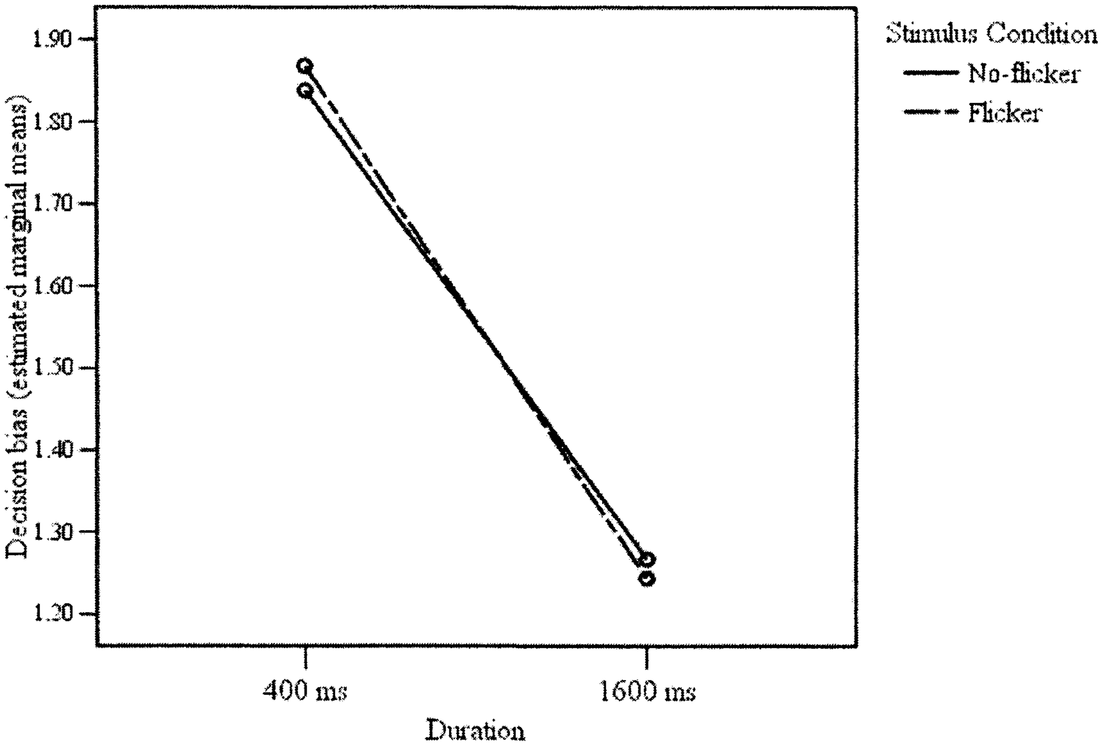

Decision bias (estimated marginal means)
1.90
1.80
1.70
1.60
1.50
1.40
1.30
1.20
400 ms
1600 ms
Duration
Stimulus Condition
No-flicker
Flicker

Figure Caption

Figure 12. Decision bias (*c*) distributions for 400- and 1600-STI. Boxplots show the median and interquartile range. Measures of decision bias (c) are based on the proportion of correct responses on blank trial presentations.

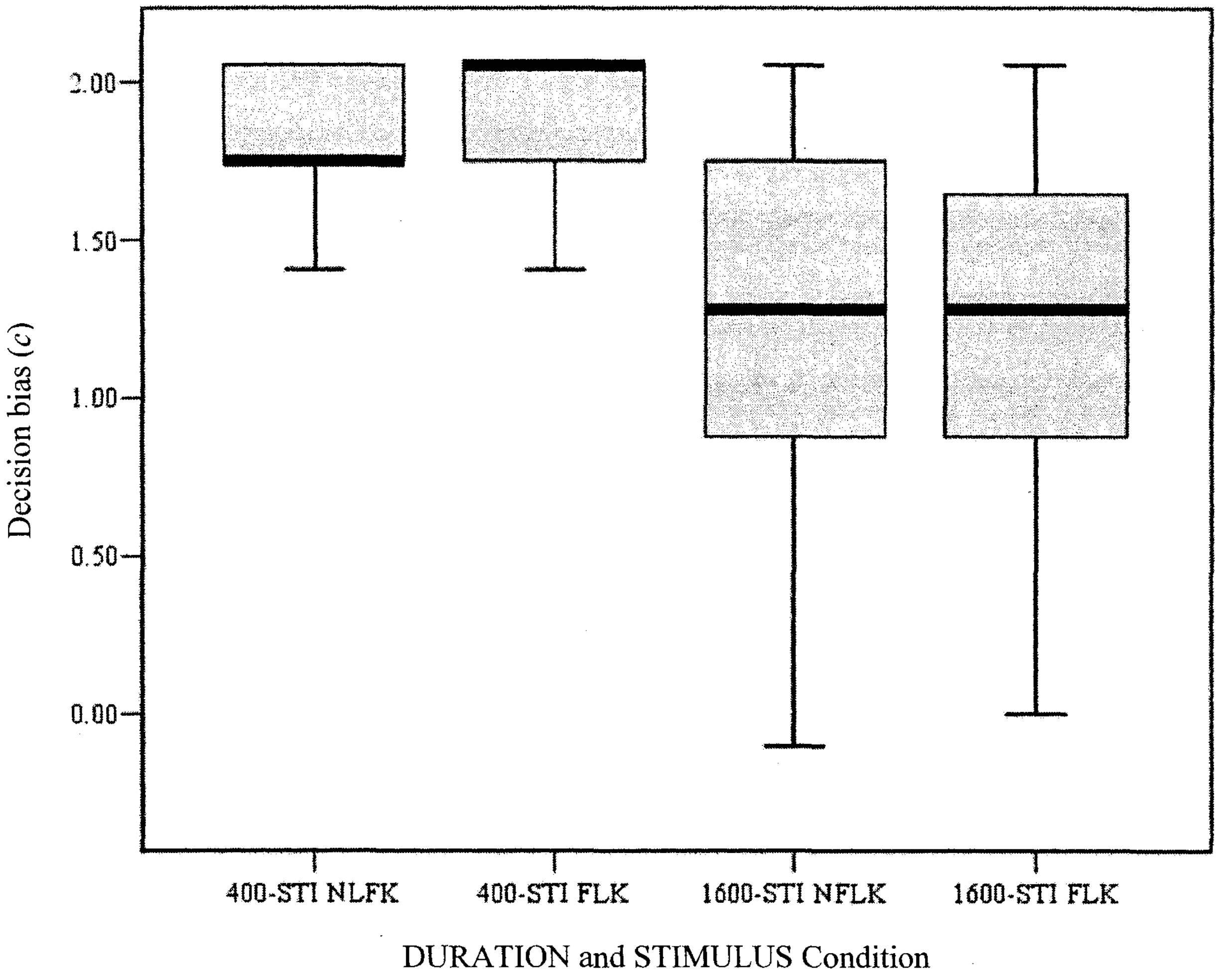

2.00
1.50
1.00
0.50
0.00
Decision bias (*c*)
400-STI NLFK
400-STI FLK
1600-STI NFLK
1600-STI FLK
DURATION and STIMULUS Condition

Figure Caption

Figure 13. Significant main effects of DURATION and STIMULUS and the two factor interaction effect (DURATION and STIMULUS) on proportion correct.

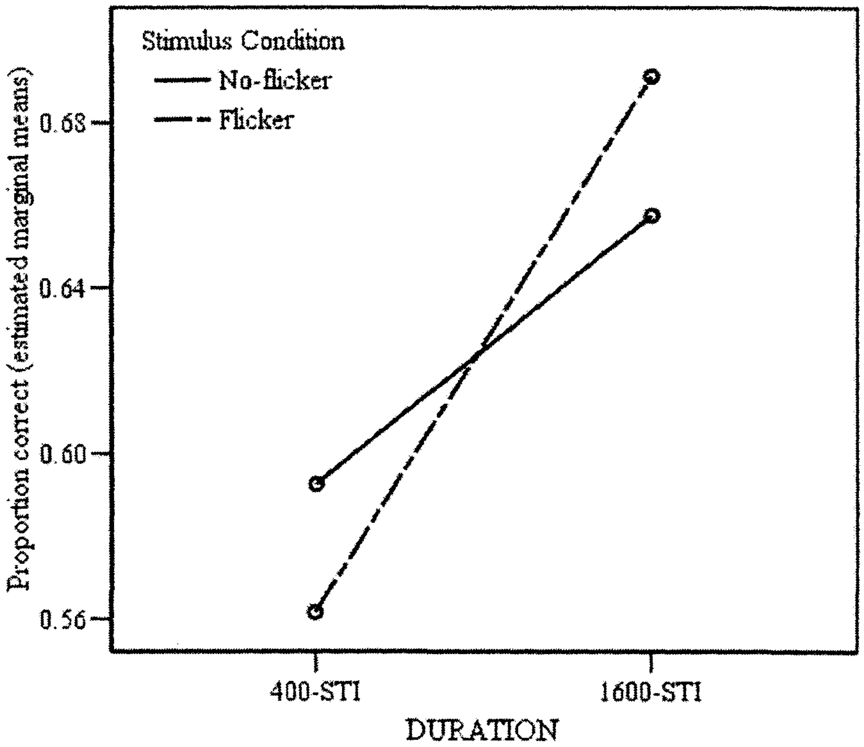

Stimulus Condition
No-flicker
Flicker
Proportion correct (estimated marginal means)
0.68
0.64
0.60
0.56
400-STI
1600-STI
DURATION

Figure Caption

Figure 14. Distributions for proportion correct (PROPC) across levels of DURATION and STIMULUS. Boxplots show the median and interquartile range. 1600-STI PROPC averages are significantly greater than the 400-STI averages. Also note that the 400-STI NFLK measures are greater than the 400-STI FLK measures, and the1600-STI NFLK measures are less than the1600-STI FLK measures.

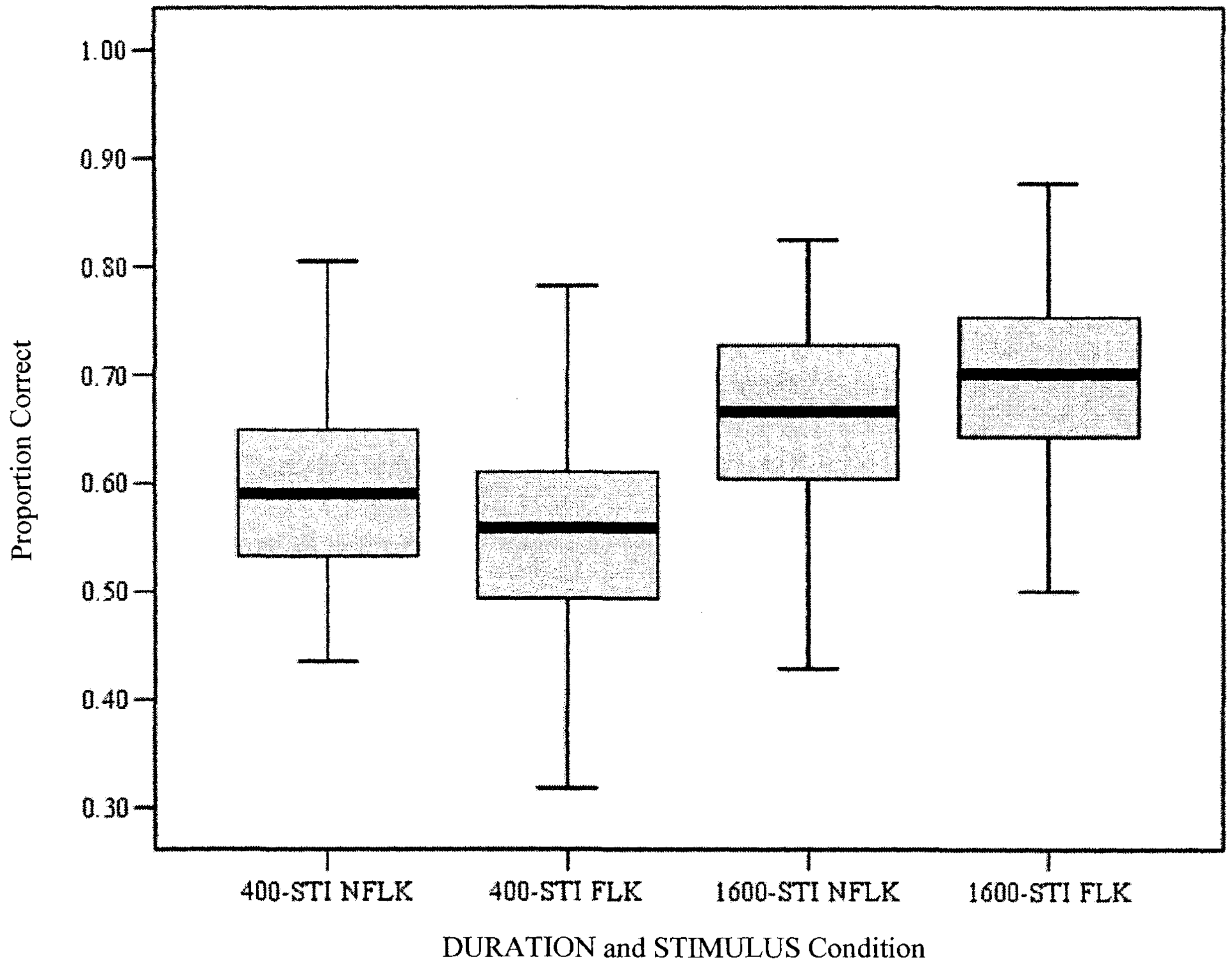

Proportion Correct
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
400-STI NFLK
400-STI FLK
1600-STI NFLK
1600-STI FLK
DURATION and STIMULUS Condition

Figure Caption

Figure 15. Comparison of two psychometric functions for 400 ms no-flicker timing. Proportion response data are fitted with a stippled Weibull function and references the right ordinate. Transducer data are fitted with a continuous Weibull function and references the left ordinate. Sub- and supra-threshold ranges lie below and above *d'*=1.5, respectively. There is relatively little functional shift along the x-axis due to the low FA rate. The functional convergence at time increment contrast value of 1.0 and the subsequent departure between 1.0 and 1.5 is an artifact of the *d'* averaging process. Error bars represent the standard error of the mean.

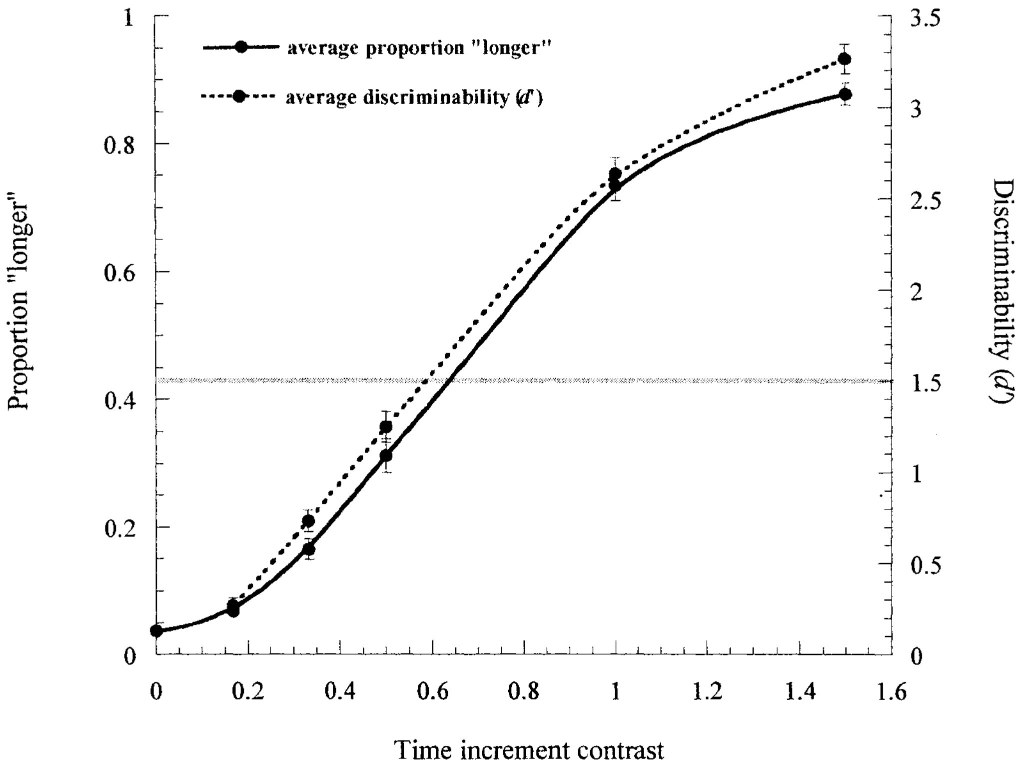

average proportion "longer"
average discriminability (d')
Proportion "longer"
Discriminability (d')
Time increment contrast
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
0
0.2
0.4
0.6
0.8
1
0
0.5
1
1.5
2
2.5
3
3.5

Figure Caption

Figure 16. Comparison of two psychometric functions for 1600 ms no-flicker timing. Proportion response data are fitted with a stippled Weibull function and references the right ordinate. Transducer data are fitted with a continuous Weibull function and references the left ordinate. Sub- and supra-threshold ranges lie below and above *d*'=1.5, respectively. The substantial shift along the x-axis is due to the FA rate which was greater than that for 400 ms no-flicker timing. The *d*' averaging process accounts for functional convergence and departure across the time increment contrast range. Error bars represent the standard error of the mean.

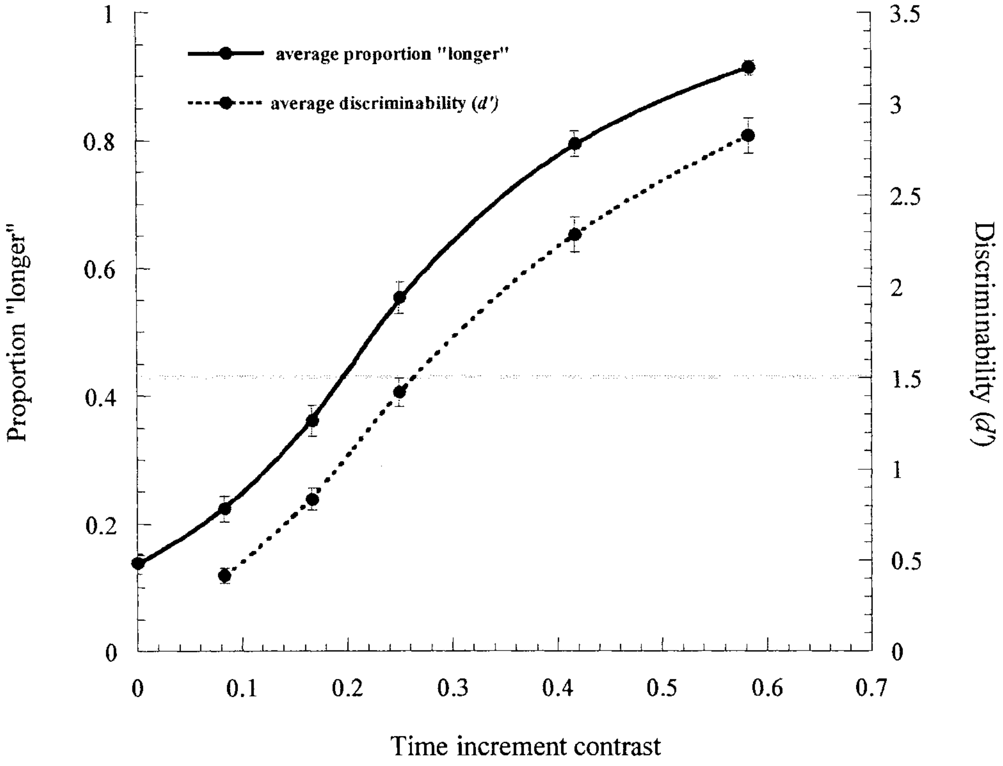

average proportion "longer"
average discriminability (d')
Proportion "longer"
Discriminability (d')
Time increment contrast
0
0.2
0.4
0.6
0.8
1
0
0.5
1
1.5
2
2.5
3
3.5
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7

Figure Caption

Figure 17. Significant SLOPE effects of DURATION and STIMULUS. The difference between mean slopes for 400 ms no-flicker and flicker timing and the difference between mean SLOPE with the 400-STI NFLK and FLK conditions, and between the 400- and 1600-STI NFLK conditions failed to reach significance.

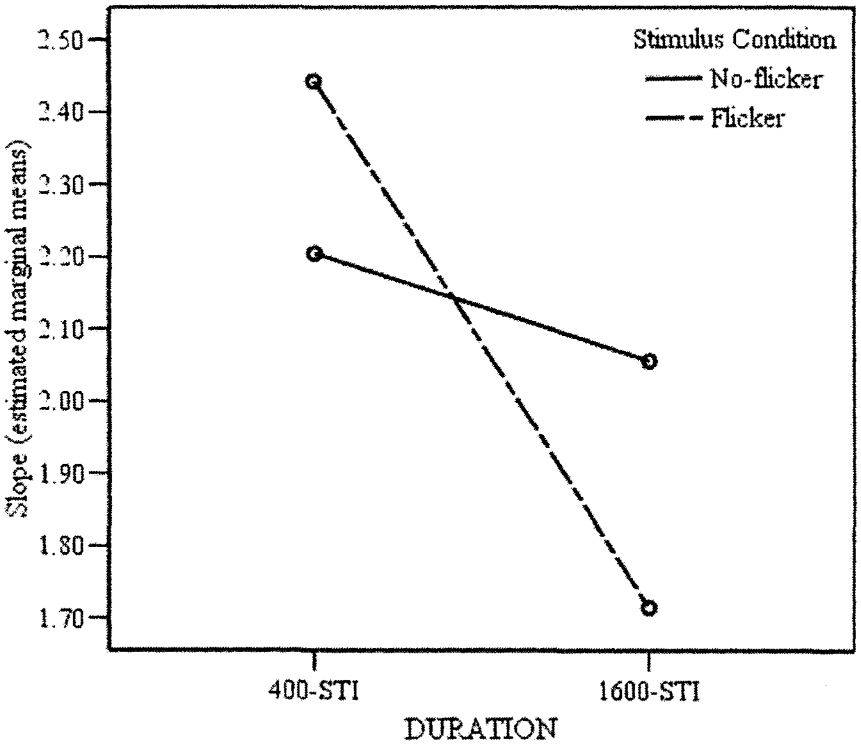
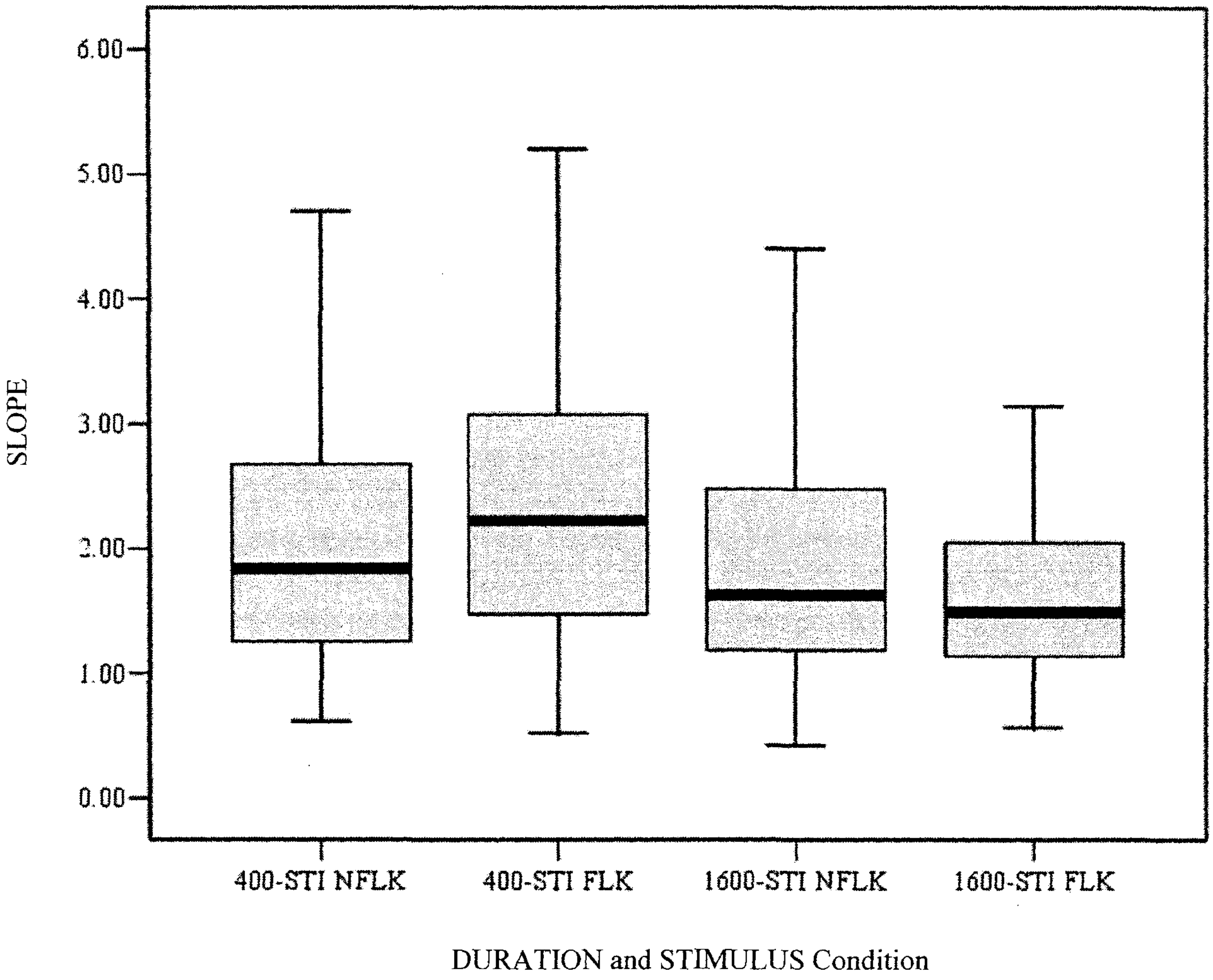

Stimulus Condition
No-flicker
Flicker
Slope (estimated marginal means)
2.50
2.40
2.30
2.20
2.10
2.00
1.90
1.80
1.70
400-STI
1600-STI
DURATION

Figure Caption

Figure 18. SLOPE distributions for 400 ms and 1600 ms timing. Boxplots show the median and interquartile range. 1600-ms flicker SLOPE are significantly reduced relative to all other measures, and as can be seen from Table 1 and this plot, there is less inter-subject variability associated with these measures.



6.00
5.00
4.00
3.00
2.00
1.00
0.00
SLOPE
400-STI NFLK
400-STI FLK
1600-STI NFLK
1600-STI FLK
DURATION and STIMULUS Condition

Figure Caption

*Figure 19.*The plot depicts the effect of flicker on mean threshold for low and high temporal sensitivity groups with 400-STI (*N* = 78). High sensitivity timers obtained lower no-flicker and flicker thresholds, and showed a significant increase in thresholds on flicker. However, thresholds for low sensitivity timers were reduced with FLK compared to NFLK conditions. Error bars denote the 95% confidence interval for the mean.

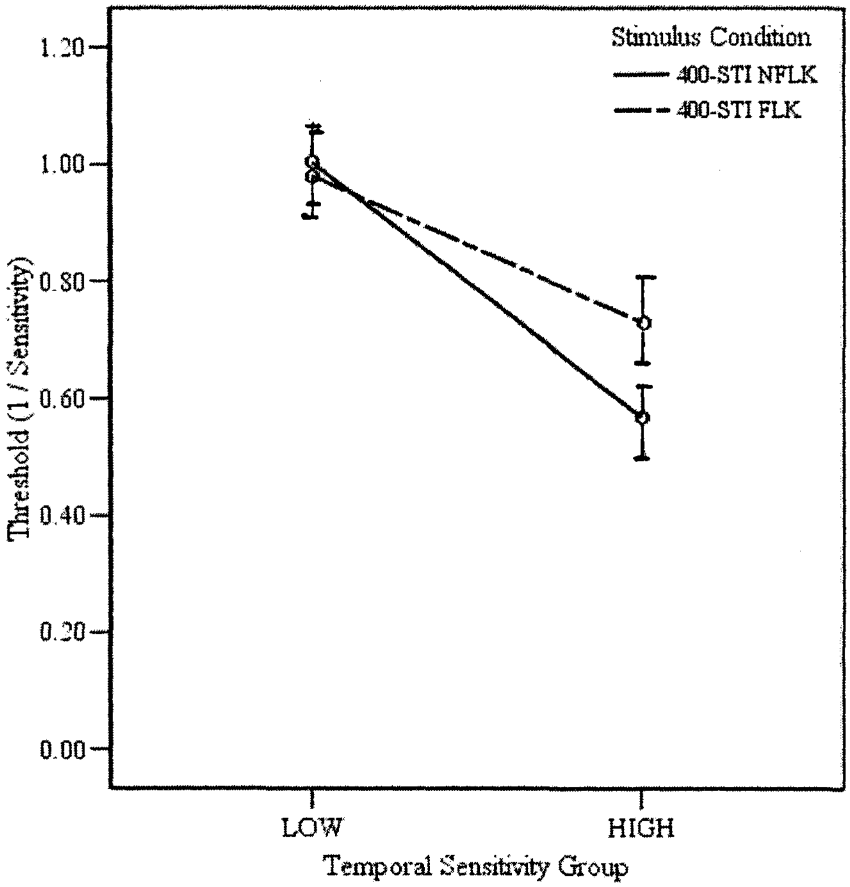
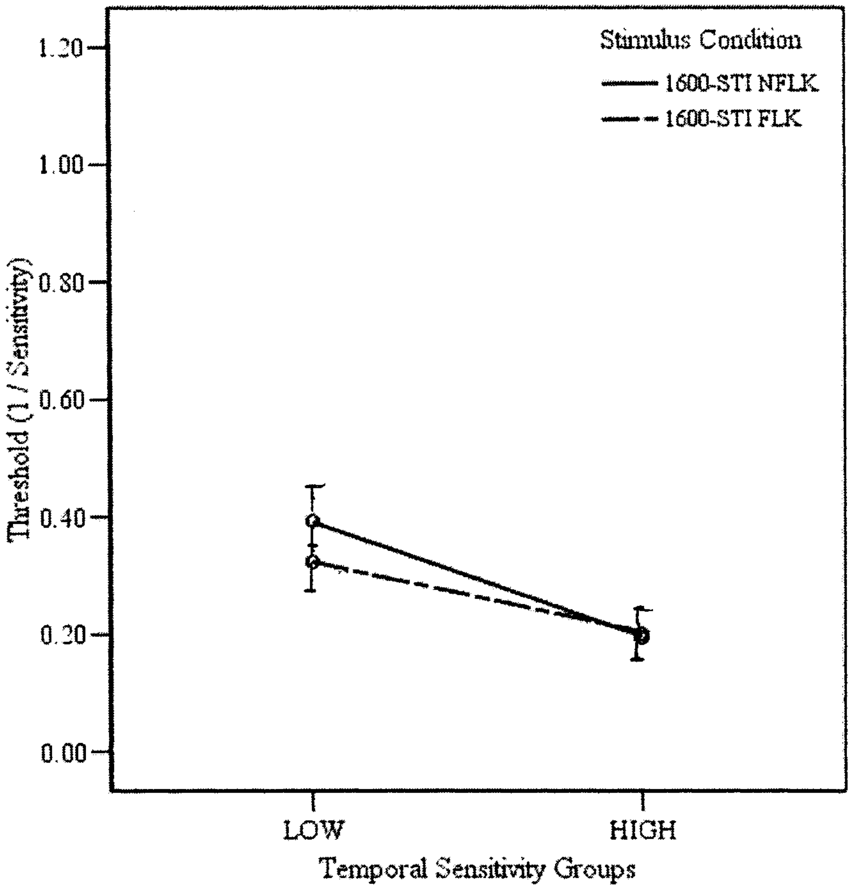

Stimulus Condition
400-STI NFLK
400-STI FLK
Threshold (1 / Sensitivity)
1.20
1.00
0.80
0.60
0.40
0.20
0.00
LOW
HIGH
Temporal Sensitivity Group

Figure Caption

Figure 20. The plot depicts the effect of flicker on mean threshold for low and high temporal sensitivity groups with 1600-STI (*N* = 78). High sensitivity timers obtained lower no-flicker and flicker thresholds, and showed a slight trend for increased thresholds with flicker. Thresholds for low sensitivity timers were higher, but the effect of flicker was greater, as can be seen by the lower mean THRES with 1600-STI FLK. Error bars denote the 95% confidence interval for the mean.



Stimulus Condition
1600-STI NFLK
1600-STI FLK
1.20
1.00
0.80
0.60
0.40
0.20
0.00
Threshold (1 / Sensitivity)
LOW
HIGH
Temporal Sensitivity Groups