

Review

The inner experience of time

Marc Wittmann*

*Department of Psychiatry, University of California San Diego, 9500 Gilman Drive,
La Jolla, CA 92093-9116A, USA*

The striking diversity of psychological and neurophysiological models of ‘time perception’ characterizes the debate on *how* and *where* in the brain time is processed. In this review, the most prominent models of time perception will be critically discussed. Some of the variation across the proposed models will be explained, namely (i) different processes and regions of the brain are involved depending on the length of the processed time interval, and (ii) different cognitive processes may be involved that are not necessarily part of a core timekeeping system but, nevertheless, influence the experience of time. These cognitive processes are distributed over the brain and are difficult to discern from timing mechanisms. Recent developments in the research on emotional influences on time perception, which succeed decades of studies on the cognition of temporal processing, will be highlighted. Empirical findings on the relationship between affect and time, together with recent conceptualizations of self- and body processes, are integrated by viewing time perception as entailing emotional and interoceptive (within the body) states. To date, specific neurophysiological mechanisms that would account for the representation of human time have not been identified. It will be argued that neural processes in the insular cortex that are related to body signals and feeling states might constitute such a neurophysiological mechanism for the encoding of duration.

Keywords: time perception; subjective duration; emotion; interoception; insula

1. INTRODUCTION

Throughout history, philosophers have been intrigued by the nature of time and how we, as humans, experience its progression. The perception of time is part of human experience; it is essential for everyday behaviour and for the survival of the individual organism (Pöppel 1997; Wittmann 1999; Buhusi & Meck 2005). Yet, and surprisingly enough, its neural basis is still unknown. Temporal intervals, lasting only seconds or spanning a lifetime, are judged according to their perceived duration—often regarded as painfully long or, the reverse, as lasting too short. Everyday decisions we make, as simple as either waiting for the elevator or taking the stairs, are based on the experienced passage of time and anticipated duration (Wittmann & Paulus 2008). The importance of our temporal experiences for daily living is strikingly documented in individual neurological cases where patients report of an accelerated progression of time and, consequently, have troubles in adequately interacting with the environment, i.e. driving a car (Binkofski & Block 1996). Although we doubtless have a time sense, our bodies are not equipped with a sensory organ for the passage of time in the same way that we have eyes and ears—and the respective sensory cortices—for detecting light and sound. Time,

ultimately, is not a material object of the world for which we could have a unique receptor system. Nevertheless, we speak of the perception of time. When we talk about time (‘an event lasted long’, ‘time flew by’), we use linguistic structures that refer to motion events and to locations and measures in space (Evans 2004); a further indication that time itself is not a property in the empirical world.

Despite a growing body of knowledge on the psychology and on the neural basis of the experience of time, the riddle for philosophers and scientists alike is still unsolved: how does the mind (or, for that matter, the brain) create time? Martin Heidegger’s paraphrase of St Augustine’s famous quotation¹ ‘In you, my spirit, I measure times; I measure myself, as I measure time’ (Heidegger 1992) reflects a theoretical approach—founded in western philosophical tradition—which states that time is a construction of the self. Perceived time, thereafter, represents the mental status of the beholder. In terms of a functional equation, one could state that time t is a function f of the self, where the self stands for all possible psychological (i.e. empirical and theoretical) properties of an individual who perceives time,

$$t = f(\text{self}). \quad (1.1)$$

Psychological research has shown that cognitive functions such as attention, working memory as well as long-term memory determine our temporal judgements (Brown 1997; Zakay & Block 2004; Taatgen *et al.* 2007). Moreover, drive states, moods and emotions (Wittmann *et al.* 2006; Droit-Volet & Meck 2007;

*wittmann@ucsd.edu

One contribution of 14 to a Theme Issue ‘The experience of time: neural mechanisms and the interplay of emotion, cognition and embodiment’.

Noulhiane *et al.* 2007a) as well as factors of personality (Rammsayer 1997) influence duration estimates. For example, time intervals are judged to be longer when we pay more attention to time and when the load of varying experiences stored in memory is higher. Our subjective well-being also strongly influences how time is experienced. Time speeds up when we are involved in pleasant activities, but it drags during periods of boredom. Thus, our sense of time is a function of the intricate interplay between specific cognitive functions and of our momentary mood states.

The aforementioned psychological factors definitely influence the processing of duration. However, a specific neural timing mechanism—influenced by the aforementioned factors—nevertheless, could account for our ability to accurately process temporal intervals. Especially for shorter durations up to a few seconds, humans can accurately synchronize their movements to regular beats (Mates *et al.* 1994), discriminate tones with different durations (Rammsayer & Lima 1991) or reproduce presented intervals (Eisler & Eisler 1994). Yet, there is no consensus as to which temporal mechanisms account for these temporal-processing abilities. Over the last decades, the most successful models for such a mechanism have been variants of a pacemaker–accumulator clock, where an oscillator (a pacemaker) produces a series of pulses (analogous to the ticks of a clock) and the number of pulses recorded over a given timespan represents experienced duration (Pöppel 1971; Church 1984; Treisman *et al.* 1990; Meck 1996; Zakay & Block 1997). However, competing models assume neuronal system properties for encoding duration not related to a simple pacemaker–accumulator system (Matell & Meck 2004; Wackermann & Ehm 2006; Karmarkar & Buonomano 2007), or they propose that memory decay processes are involved in time perception (Staddon 2005; Wackermann & Ehm 2006). Related to this unsolved issue, the question of which areas of the brain process duration has also not yet been answered definitely. Among other regions, most prominently, the cerebellum (Ivry & Spencer 2004), the right posterior parietal cortex (Buetti *et al.* 2008a), the right prefrontal cortex (Rubia & Smith 2004; Lewis & Miall 2006) as well as fronto-striatal circuits (Harrington *et al.* 2004a; Hinton & Meck 2004) have been implicated as the neural substrates of a potential timekeeping mechanism.

In summary, as this brief outline suggests, there is still considerable uncertainty on *how* (regarding psychological and neurophysiological models) and *where* in the brain time is processed. This paper has several goals that are related to the issues raised: (i) to give an answer to the question of why so many different brain regions have been assigned to the neural basis for our experience of time, i.e. to explain some of the variation found across models, and (ii) to describe recent developments in the research on time perception, which are indicative of a strong involvement of emotions and mood states. These developments could be described as an ‘emotive turn’ in this area of research, which might follow decades of focusing on cognitive aspects of time perception. (iii) Recent conceptualizations and empirical findings, which have

led to this emotive turn, might develop into a neural theory of time perception that will encompass subjective feeling and interoceptive (within the body) states. Specific neurophysiological processes in circumscribed regions of the brain, as they are related to these feeling states, might constitute a mechanism for encoding duration.

2. COGNITIVE AND NEURAL MODELS OF TIME PERCEPTION

Investigations in the fields of experimental psychology, clinical neuropsychology and neuroimaging have resulted in an extensive literature on the mechanisms and underlying neural systems of temporal processing. Over the last decades, certain cognitive and neural models have dominated time perception research, but alternative models exist and the number of potential theories has to date increased considerably. To summarize the status of the research field in general terms: there is a lot of conflicting evidence and there are several competing conceptualizations. In the following, a short review of (i) predominant cognitive models of time perception and (ii) related neural theories of interval timing is provided. These models and theories will be contrasted with alternative conceptualizations and empirical evidence in order to provide an overview of the heterogeneity of ideas concerning mechanisms of time perception.

Cognitive models distinguish two fundamental perspectives in time estimation: prospective and retrospective time estimation (James 1890; Zakay & Block 2004).² In the former, an observer judges the duration of an interval that is being presently experienced. In retrospective time estimation, by contrast, an observer estimates a timespan that has already been passed and to which he is only now paying attention. Models of prospective time estimation assume an ‘internal clock’ with a pacemaker producing a sequence of time units that are fed into an accumulator (Church 1984; Treisman *et al.* 1990). In a variant of these pacemaker–accumulator models, the attentional-gate model (Zakay & Block 1997), the time units produced are only registered when attention is directed to time. Thus, prospective timing is always a dual task since an observer has to divide attention between temporal and non-temporal processes (Grondin & Macar 1992; Taatgen *et al.* 2007). The number of units that have been recorded during a physical time period (being stored in working memory) is then compared (in a decision process) with long-term memory of stored representations of time periods, which can be verbalized as seconds or minutes (Pouthas & Perbal 2004; Wearden 2004). Thus, in addition to the pacemaker (the actual clock component), several cognitive processes such as working memory, long-term memory, attention and decisions are involved in prospective time perception.

In retrospective time estimation, the duration of a time interval that has already elapsed has to be judged. Then, an observer has to estimate a given duration in retrospect from the amount of processed and stored memory contents; that is, duration has to be reconstructed from memory (Ornstein 1970; Flaherty *et al.* 2005; Noulhiane *et al.* 2007b). The more changing

experiences we have during a certain timespan—which are stored in memory and later retrieved—the longer the duration is subjectively experienced (Bailey & Areni 2006). In retrospect, routine activity when compared with novel activity leads to the perception of shorter time intervals (Avni-Babad & Ritov 2003). Thus, the subjective impression of a long time interval depends on the activity of a person with diverse experiences and recruits the activation of areas such as the medial temporal cortex, known to be involved in episodic memory (Noulhiane *et al.* 2007b). Retrospective duration judgements are based on temporal intervals spanning a few seconds (short-term memory) to, in principle, a whole lifetime (long-term memory) (Wittmann & Lehnhoff 2005). Pure prospective duration judgements, by contrast, are only conceivable over a limited and shorter time range where an observer attends to time for a period of seconds to minutes.

Prospective timing studies in animals and humans have yielded the general hypothesis that fronto-striatal circuits consisting of recurrent loops between frontal cortex (SMA), caudate–putamen, pallidum and thalamus, which are modulated by the dopamine system, are critical for the processing of duration (Hicks 1992; Harrington *et al.* 2004a). Support for the anatomical hypothesis comes from investigations in patients with brain lesions and from neuroimaging studies. For example, individuals with structural damage to the frontal lobes (Nichelli *et al.* 1995; Kagerer *et al.* 2002) or traumatic brain injury predominantly affecting frontal areas (Pouthas & Perbal 2004) show impaired estimates of temporal intervals. Neuroimaging studies with healthy volunteers find that the perception of duration is linked to activation in right prefrontal and striatal regions (Ferrandez *et al.* 2003; Nenadic *et al.* 2003; Coull *et al.* 2004). Regarding the involvement of neurotransmitter systems, D2 dopaminergic antagonists (such as haloperidol) impair duration discrimination abilities in healthy subjects (Rammsayer 1999). Moreover, studies with animals and humans indicate that both dopaminergic agonists, e.g. methamphetamine, and antagonists influence timing processes, presumably by increasing and decreasing clock speed, respectively (Mohs *et al.* 1980; Buhusi & Meck 2002; Cevik 2003). Individuals dependent on cocaine and methamphetamine, who have abnormal brain metabolism and structural changes involving dopaminergic target areas such as the striatum and the frontal cortex, exhibit impaired time processing on several timing tasks (Wittmann *et al.* 2007b). Additional evidence for the involvement of the dopamine system in time perception comes from patients with Parkinson's disease who have decreased dopaminergic function in the basal ganglia and show deficits discriminating and reproducing temporal intervals (Hellstrom *et al.* 1997; Harrington *et al.* 1998). Further evidence comes from a study in which subthalamic deep brain stimulation in patients with Parkinson's disease levelled temporal reproduction performance to that of control subjects (Koch *et al.* 2004). Thus, intact dopamine neurotransmission within striatal and frontal areas of the brain is an important prerequisite for accurate temporal-processing abilities.

However, some neuroimaging studies, revealing areas of activity while subjects estimate durations or time their movements, suggest that a core temporal-processing mechanism is located in the right prefrontal cortex (dorsolateral and ventrolateral areas) for both sub- and supra-second intervals (Rubia *et al.* 1998; Brunia *et al.* 2000; Lewis & Miall 2003a; Smith *et al.* 2003). In these (and other) studies, the basal ganglia did not show activation, thus leading to the conclusion that dopamine modulation in right prefrontal areas might be the basis for a primary timekeeping mechanism (Lewis & Miall 2006). Furthermore, and pointing to yet another different brain region, since patients with cerebellar dysfunctions are impaired in the precise timing of movements (Ivry *et al.* 1988) as well as in the sensory discrimination of duration (Ivry & Keele 1989), the cerebellum seemingly plays an important role in the processing of time. It has been speculated that separate, i.e. non-overlapping, neural elements in the cerebellum that have different delay properties could potentially encode duration (Ivry & Spencer 2004). Last but not least, the right posterior–inferior parietal cortex has been implicated (i) in integrating duration information as represented in the sensory modalities and (ii) as an interface between the perception of duration and timed actions (Buetti *et al.* 2008a,c). Repetitive transcranial magnetic stimulation (rTMS) selectively disrupts duration discrimination in the visual and auditory modality if the respective sensory cortices are affected, but stimulation of the right parietal cortex disrupts timing in both the visual and auditory domains (Buetti *et al.* 2008a,b). Buetti and colleagues thus support the idea of distributed, modality-specific, timekeeping processes that converge in the parietal cortex. Neurophysiological studies in monkeys complement these findings by showing that specific increasing (ramp-like) neuronal activity in the posterior parietal cortex encodes duration (Leon & Shadlen 2003). However, similar neural activity in the monkey brain and related to the timing of events has been recorded in the premotor and motor cortex as well (Lebedev *et al.* 2008).

One difficulty in deciding on which regions are the primary target areas for a suspected timekeeping mechanism comes from neuroimaging studies where, typically, multiple brain regions show activation during time perception tasks (Lewis & Miall 2003b). The involvement of all these brain areas is probably due to different cognitive processes not subtracted out in the contrasts between primary time perception and control tasks, the principal method used in functional magnetic resonance imaging (fMRI). Many active areas are not primarily related to the encoding of duration (i.e. an internal clock) but, nevertheless, take part in a complex timing system representing attention, working memory and decision-making processes (Rubia & Smith 2004; Livesey *et al.* 2007). A consequence of the complex architecture of an assumed timekeeping system is that disruptions in any component can result in timing impairments. That could explain why so many different patient groups with damage to the brain, i.e. lesions or degenerative processes in the basal ganglia, cerebellum or right parietal, as well as frontal cortex, can be impaired

(Wittmann 1999). Likewise, it cannot be clearly decided whether experimental disruptions with rTMS are due to the transient impairment of a neural clock or of other processing components. For example, rTMS applied to the dorsolateral prefrontal cortex reliably impairs temporal reproductions of a few seconds as well as multiple second intervals, but it is unclear whether this accounts for the disruption of a neural clock or of working memory (Koch *et al.* 2003, 2007; Jones *et al.* 2004). rTMS applied to the cerebellum transiently impairs the temporal reproduction of intervals with durations of approximately half a second (but not approx. 2 s), a finding that could be interpreted by the disruption of either a millisecond timer or of a motor programme involved in millisecond timing (Koch *et al.* 2007).

Two further complicating factors in this discussion arise from neuropsychological studies with brain-injured patients. First, some studies report negative findings in which patients do not differ in their timing abilities from control subjects. Second, timing deficits, if registered, although significant from a statistical point of view, are not necessarily dramatic. For example, and contrasting earlier findings, patients with cerebellum lesions following a stroke were not impaired in a duration discrimination task and only mildly impaired in a motor-timing task (Harrington *et al.* 2004b). Patients with focal basal ganglia lesions, although impaired in performing with maximum tapping frequency, were as accurate in motor timing as were controls (Aparicio *et al.* 2005). Moreover, although these patient groups, as shown in several studies, on average, and according to the inferential statistics, differed from the performance of control subjects, the deviations were often minimal (Ivry & Keele 1989; Harrington *et al.* 1998; Kagerer *et al.* 2002; Wittmann *et al.* 2007b).

One suggested solution to the problem of not being able to pin down specific regions of the brain as representing a clock-type timing mechanism is to assume distributed neural networks where neural populations within each region would encode duration (Mauk & Buonomano 2004). If several neural units would possess intrinsic temporal-processing properties, many different brain areas could contribute to the perception of time depending on the modality and the type of task. These network or state-dependent models do not incorporate a dedicated timing system (with a centralized clock) but rather time-dependent neural changes, such as short-term synaptic plasticity (Karmarkar & Buonomano 2007). However, such intrinsic mechanisms would be limited to short time intervals up to several hundred milliseconds. Time perception in the range of seconds would still require additional processes (Ivry & Schlerf 2008). Similarly, it is conceivable that temporal-processing functions are embedded in several specialized and interacting neural circuits, where the timing function would not be the primary process in those brain regions (through a dedicated mechanism for temporal processes) but, for example, motor systems would implicitly be involved in the temporal processing of intervals (Nobre & O'Reilly 2004). Alternatively, an idea that has been very recently stated suggests that the effort made when we perceive and act might determine experienced duration

(Marchetti 2009). An intuitive example fitting this idea is the phenomenon that novel experiences seem to last longer than routine events, which can be explained by the greater demand of mental activities involved in performing a task or analysing a situation for the first time. The idea of mental effort as a determinant of time experience is compatible with the notion of 'fluency', the subjective experience of ease or difficulty of a mental task (Oppenheimer 2008). The experience of time, according to this view, would not rely on clock processes but would be an epiphenomenon evolving from cognitive and emotional responses during a time interval, where a cognitively demanding task (a filled interval) and doing nothing (an empty interval, i.e. when sitting in the doctor's waiting room) would likewise lead to the impression of a slow passage of time (the act of waiting without any distraction can be filled with painful emotions) (Flaherty 1999).

Further conceptualizations, which argue against the idea of dedicated timing systems, add to the diversity of time perception models. Just as is argued for the retrospective perspective on duration, prospective timing could be governed by memory processes, where the decreasing memory strength over time, specifically modelled using leaky integrators, leads to the impression of passing time and, eventually, of duration (Staddon 2005). In a different model, the 'dual klepsydra' model, inflow and outflow processes of a leaky accumulator form properties of a timekeeping mechanism (Wackermann & Ehm 2006). Subjective duration is defined by the state of a leaky integrator that depends on inflow units (accumulation over time during the encoding of stimulus duration) and outflow units (loss over time). Parameters of that model fit well to individual temporal reproduction responses as well as to changes in the timing of behaviour induced by experimental manipulations (Wackermann *et al.* 2008).

In summary, a multitude of incompatible conceptualizations exists on how time is processed. Furthermore, there is no agreement on which brain areas or brain systems—dedicated to time or not—might underlie our perception of duration. The important conclusion so far is that different processing components are involved when we perceive duration or time our movements, which are not related to an internal clock. Nevertheless, through experimental manipulation or in certain patient populations, changes in these processes can affect perception and behaviour related to the time domain. In the following, one further factor will be discussed that may explain some of the variation found in studies on time perception, i.e. why so many different brain regions have been assigned with a central timekeeping function. The main point will be that different neural systems are involved in temporal processes (and related experiences) depending on the duration of the processed interval.

3. TIME SCALES IN THE PERCEPTION OF TIME

It is intuitively most unlikely that one mechanism or one neural system would be responsible for all possible durations that an organism has to process. Different temporal processing mechanisms must be involved on

different time scales (Trevarthen 1999; Wittmann 1999; Mauk & Buonomano 2004; Buhusi & Meck 2005). Experimental interventions have repeatedly shown duration-specific effects of psychopharmacological agents on interval timing. For example, the dopamine receptor antagonist haloperidol as well as the benzodiazepine midazolam impair duration discrimination of intervals ranging approximately 1 s, whereas processing of 50 ms intervals is affected by haloperidol only (Rammsayer 1999). According to these results, any pharmacological treatment that affects working memory capacity (e.g. midazolam) would interfere with temporal processing of intervals above 1 s. However, intervals with a length of up to a few hundred milliseconds (such as the 50 ms interval) are supposed to be processed based on brain mechanisms outside of motor and cognitive control and reflect pure timing processes (thus, not being influenced by midazolam). According to this view, additional processes such as attention and working memory, not related to time *per se*, come into play with intervals exceeding several hundred milliseconds in length and complementing dopamine-driven processes, which are involved both in shorter and longer time intervals (Rammsayer *et al.* 2001). A similar theoretical proposal, derived from a meta-analysis on neuroimaging data, suggests two distinct neural timing systems: (i) an automatic timing system for shorter intervals up to approximately 1 s, which recruits motor systems of the brain (SMA, basal ganglia and cerebellum) and (ii) a cognitively controlled timing system for supra-second intervals connected mainly to right prefrontal and parietal cortical areas (Lewis & Miall 2003b). This separation of time perception systems is to some extent mirrored by findings in motor-timing studies, where qualitative changes in tapping performance occur with inter-tap intervals of approximately 1 and 1.5 s duration (Madison 2001). Time ranges between 0.45 and 1.5 s seem to be automatically processed, i.e. not strongly affected by attentional demands, whereas attention and working memory processes (stimulated by secondary tasks) affect intervals in the range between 1.8 and 3.6 s (Miyake *et al.* 2004).

The notion that perception and motor behaviour are processed in discrete windows or processing epochs has been conceptualized for some time (White 1963; Pöppel 1970; Dehaene 1993; VanRullen & Koch 2003; Fingelkurts & Fingelkurts 2006). These temporal integration units fuse successive events into a unitary experience, ‘snapshots of experience’ or ‘psychological presents’ (Blumenthal 1977), which are characterized by co-temporality, meaning that events within this time zone have no temporal relationship (Ruhnau 1995). For example, the perception of temporal order of short stimuli in different modalities is only possible if the individual events are separated by at least 20–60 ms (Exner 1875; Hirsh & Sherrick 1961; Kanabus *et al.* 2002; Fink *et al.* 2006). If the two events are separated by smaller intervals, an observer is not able to tell which of the two appeared first. Moreover, since stimulus properties of speech stimuli are perceptually segmented into these sequential processing units, temporal information

within a segment of a speech sound may not be relevant for decoding (Kiss *et al.* 2008). A longer time frame of approximately 200 ms determines the integration of auditory–visual input in speech processing (van Wassenhove *et al.* 2007). Fusion percepts were reported if the onset of lip movements and heard syllables did not exceed this time lag. Threshold values of approximately 250–300 ms have long been suggested to represent a specific integration process in perception (Münsterberg 1889; White 1963). A minimum stimulus duration (or minimum inter-onset interval) of 200–300 ms is necessary for detecting the temporal sequence of four acoustic events (Warren & Obusek 1972; Shrivastav *et al.* 2008) and for optimal effects in an oddball task that leads to the subjective expansion of duration (Tse *et al.* 2004). Temporal integration mechanisms in a time frame of approximately 250 ms also seem to be involved in sensorimotor processing, distinguishing maximum tapping speed from a personal, controlled motor speed (Peters 1989; Wittmann *et al.* 2001).

On a different time scale, a perceptual mechanism seems to exist that integrates separate successive events into a unit or perceptual *gestalt* (see Pöppel 2009). We do not just perceive individual events in isolation, but automatically integrate them into perceptual units with a duration of approximately 2–3 s (Fraisse 1984; Pöppel 1997). For example, while listening to a metronome at a moderate speed, we do not hear a train of individual beats, but automatically form perceptual units, such as 1–2–3, 1–2–3, etc. These are mental constructs—physically speaking, they do not exist. The duration of this temporal integration mechanism, referred to as the subjective present, seems to be limited to 2–3 s (Szelag *et al.* 1996; Wittmann & Pöppel 2000). Phenomenological approaches have revealed that temporal intervals shorter than 2 s are perceived qualitatively as different from longer intervals (Benussi 1913; Nakajima *et al.* 1980). Typically, intervals up to 2–3 s are reproduced accurately, whereas longer intervals tend to be underestimated (Ulbrich *et al.* 2007; Noulhiane *et al.* 2008). In one study measuring event-related potentials (ERPs) during the reproduction of visual stimuli ranging in duration between 1 and 8 s, accurate reproductions up to 3 s were accompanied by a contingent negative variation-like slow negative shift in the ERP signal. This shift was reduced or absent when durations exceeded 3 s (Elbert *et al.* 1991). Duration discrimination thresholds with base durations up to 2 s show constant Weber fractions ($\Delta t/t$, where Δt is the difference between the base duration t and the length of the comparison interval at which a duration difference is just noticeable), but with longer durations, Weber fractions rise rapidly³ (Getty 1975). Subjects can accurately synchronize their motor actions to a sequence of tones presented with a frequency of approximately 1–2 Hz. The ability to synchronize these tones becomes more difficult with increasing inter-tone intervals and finally breaks down when intervals exceed durations of approximately 2–3 s (Mates *et al.* 1994; Miyake *et al.* 2004). With respect to even longer intervals, it is also conceivable that distinct processes are involved for different durations. For example, the estimation of a 1 h interval seems to be related to the duration of wake

time of an individual, whereas the estimation of seconds and minutes is related to body temperature (Aschoff 1998).

Experimental interventions selectively affect intervals of specific time ranges, i.e. the psychopharmacological substance psilocybin has an effect on duration longer than 2 s (Wittmann *et al.* 2007a), rTMS of the cerebellum affects solely millisecond timing and rTMS of the right dorsolateral frontal cortex only affects timing in the seconds range (Jones *et al.* 2004; Koch *et al.* 2007). Nevertheless, a reliable correlation between time scales and neural systems has not been accomplished so far. Also, individual neuroimaging studies often find similar brain areas activated in time perception tasks employing different durations (Pouthas *et al.* 2005; Jahanshahi *et al.* 2006).

To summarize §§ 2 and 3, several factors contribute to the diversity of different models on the question of how (which mechanism) and where (which neural system) in the brain duration is processed. First, there are several cognitive processes that are entangled with our perception of time (independent of a potential internal clock), which require the integrative processing of multiple modules distributed across the brain. Experimental manipulations of task load (in attention and working memory, for example), clinical studies with selected patients with dysfunctions in different brain areas (i.e. cerebellum, basal ganglia, frontal and parietal cortex) as well as neuroimaging studies show that many parts of the brain and multiple cognitive processes contribute to the perception of duration. Moreover, there is no single area of the brain on which functioning our temporal experiences would completely rely on; that is, patients with damage to the brain may be affected in the processing of duration but their performance hardly ever breaks down completely. Second, different neural mechanisms are most probably responsible for temporal processes and time experiences depending on the duration involved.

4. THE EMOTIONAL EXPERIENCE OF TIME

Time does not pass with a steady-paced flow. Perceptual time is not isomorphic to physical time, meaning that the subjective passage of time and estimates of duration vary considerably. In uneventful or unpleasant situations, such as when nervously waiting for something to happen, we experience a slower passage of time and overestimate its duration. By contrast, if we are entertained and focus on rewarding activities, time seems to pass more quickly and duration is more likely to be underestimated. These examples of time judgements are inherently emotional. They point to an aspect of time perception, although part of everyday experience, which has been neglected in research over the past few decades. Only very recently, a body of evidence has accumulated which is indicative of the intricate interplay between mood states and perceived duration. In most cases, the influence of emotions (often leading to longer time estimate) is explained by the standard cognitive model of prospective time perception in which emotions affect the degree of attention to time or increased physiological arousal levels lead to a higher pacemaker rate

(Droit-Volet & Meck 2007; Wittmann & Paulus 2008). Both increased attention to time and a higher pacemaker rate of an assumed internal clock would lead to the accumulation of more temporal units during a given timespan.

Regarding durations of multiple seconds to minutes, it has been shown that patients with depression (Bschor *et al.* 2004) and cancer patients with high levels of anxiety (Wittmann *et al.* 2006) report a slowing down of the pace of time and overestimate temporal intervals. It would appear that the psychological distress these individuals suffer from directs attention away from meaningful thoughts and actions to the passage of time. Also, boredom-prone individuals estimate time intervals to last longer than persons with low levels of boredom (Danckert & Allman 2005). Similarly, subjects who were socially rejected in a psychological experiment overestimated intervals of multiple seconds, a finding that was interpreted as stemming from a state of reactive emotional and cognitive deconstruction, which in turn resulted in a stronger attentional focus on the present (Twenge *et al.* 2003).

Positive correlations of general anxiety levels with duration estimates of multiple seconds have been reported in undergraduate students (Siegman 1962) and in patients with psychiatric diagnoses (Melges & Fougousse 1966). Spiderphobics who had to look at spiders for 45 s also overestimated this exposure time when compared with controls (Watts & Sharrock 1984). These overestimations were interpreted as resulting from an arousal-induced increase in an internal pacemaker. Moreover, emotional stress such as the anticipation of a mild electric shock (Falk & Bindra 1954), when compared with control conditions, led to an overestimation of duration.

Generally speaking, time distortions are stress related as they are often experienced during dangerous or life-threatening situations such as road accidents or encountered violence (Hancock & Weaver 2005). In movies, scenes depicting combat are sometimes shown in slow motion to portray what the involved protagonist subjectively experiences. To date, two studies experimentally tested this phenomenon. Novice skydivers, for example, who reported a stronger fear during their first tandem jump, also experienced its duration (subjective estimates approx. 30 min) as lasting longer than did less fearful novice skydivers (Campbell & Bryant 2007). A similar time dilation effect was also seen on a shorter time scale. Subjects who experienced a free fall of 31 m before they landed safely in a net overestimated retrospectively the duration of that fall when compared with when watching others fall (Stetson *et al.* 2007). However, a slow-motion effect was not detected when probed with a special chronometer that had to be watched during the fall. Even in more conventional and less frightening experimental situations, subjects overestimate the duration of high arousing pictures with emotional valence (depicting angry faces or accidents), which last only several hundred milliseconds to a few seconds (Angrilli *et al.* 1997; Droit-Volet *et al.* 2004; Gil *et al.* 2007). These effects seem to be strongly tied to the embodiment of emotions. Participants seem to overestimate emotional faces only when they are able to

spontaneously imitate the perceived emotions on the faces which they have to judge, thus showing that affect is embodied (Effron *et al.* 2006). To be more precise, however, paradoxical effects can occur in the way that emotional stimuli can cause over—as well as underestimations of time. For example, in one study (Angrilli *et al.* 1997), low-arousing and emotionally negative pictures led to an underestimation of duration (interpreted as resulting from the subjects' distraction from time and attention to the emotional content of the stimuli), whereas high-arousing emotional pictures led to an overestimation of duration (interpreted as resulting from an increased pacemaker). In another study (Noulhiane *et al.* 2007a), unpleasant sounds (e.g. sobs, a crying woman) were judged to last longer than pleasant (e.g. laughs) or neutral stimuli. This finding was again interpreted through an increase in pacemaker rate. Furthermore, and contrasting with the reported findings above, high-arousing sounds were judged to be shorter than low-arousing sounds (interpreted as resulting from the distraction from time).

In summary, increased attention to time (such as in waiting situations) and an increase in physiological arousal (such as under stress) can lead to longer time estimates when judging intervals in the range of milliseconds to seconds and minutes. However, paradoxical effects of an underestimation of duration in emotional situations can occur, which are discussed as stemming from a distraction from time. It is difficult to decide which mechanism, attention related or activation induced, actually affects the sense of time (and in which direction). Physiological measurements would have to complement the employed time perception measures. For example, in one study, acute marijuana effects in healthy subjects corresponded with underproductions of time intervals (interpreted as acceleration of a pacemaker) and an increase in heart rate, indicative of an increase in physiological arousal (Tinklenberg *et al.* 1976). The two proposed mechanisms influencing time experience are not necessarily exclusive but could contribute in an additive way (Burle & Casini 2001). For example, overestimations of time intervals of approximately 1 min in duration as detected in many impulsive patient groups could be due to an increase in physiological arousal as well as caused by an increase in attention to time (Berlin & Rolls 2004; Wittmann *et al.* 2007b).

The impact of our emotional states on the experience of time is usually discussed in the framework of the standard cognitive model of prospective time perception, which proposes a pacemaker-accumulator that is embedded in a system of cognitive components. However, on reviewing the empirical evidence and as argued above, the basic questions of how our sense of time is created are still unresolved. The recent upsurge in empirical investigations on the relationship between emotions and time, perhaps signifying an emotive turn, might result in a new psychological and neural theory of time perception. So far, emotions and physiological states, similar to cognitive functions such as attention and working memory, have been treated as modulators of an assumed neural clock. What if mood processes and the representation of body

sensations themselves function as a timekeeper? Since emotions and physiological states seem so fundamental to the experience of time, it is tempting to assign a pivotal role to these processes related to a core time-keeping system.

Since the late nineteenth century, based on the theory by James and Lange, it has been argued that affective states as well as experienced emotions are inseparable from autonomic responses (e.g. cardiovascular activity, abdominal sensations and breathing patterns; Saper 2002; Pollatos *et al.* 2005). According to this notion, bodily signals, visceral and somatosensory feedback from the peripheral nervous system, enact emotions (Damasio 1999; Wiens 2005). For example, people's heartbeat detection ability is positively related to subjective ratings of emotional pictures as more arousing (Pollatos *et al.* 2007a). Interoceptive awareness, as tested with heart rate detection tasks, is predicted (among other regions) by right anterior insula activity (Critchley *et al.* 2004; Pollatos *et al.* 2007b). The insular cortex of primates, structurally embedded in the extended limbic system, is considered as the primary receptive area for visceral input, i.e. for physiological states of the body (Craig 2002; Saper 2002). The capacity for the awareness of emotions is probably built on the anatomical organization and a progressive integration of information in the insula (Craig 2003). A posterior-to-anterior progression of representations in the human insular cortex is the basis for the sequential integration of body states and internal autonomic responses with cognitive and motivational conditions, the latter being instantiated by distributed neural processes across the brain. This progression culminates in the anterior insula and leads to the conscious awareness of complex feeling states. A direct link between the perception of time and physiological processes has been proposed by Craig (2008), who claims that our experience of time relates to emotional and visceral processes because they share a common underlying neural system, the insular cortex and the interoceptive system. He suggests that the insula, through the temporal integration of signals from within the body, produces a series of 'emotional moments' in time. The perception of duration thereafter would be defined by these successive moments of self-realization, formed by information originating within the body (see also Craig 2009).

Several attempts have been made to directly relate rhythms of the body to temporal processes in perception and action. For example, Münsterberg (1889), being his own subject, reported that when the onset and the offset of temporal intervals to be reproduced and ranging in duration between 6 and 60 s coincided with him starting to inhale, his temporal reproductions were more accurate than when temporal intervals started at other points in time not systematically related to his breathing cycle. Münsterberg, who did not count in his experiments, concluded that the sense of time relied on the sensation of tension in different organs which are caused by muscle contractions. Fraisse (1982) highlights findings showing that the periodicities of the heart, of walking, of the preferred tapping tempo as well as of preferred acoustical rates are of the same order of magnitude of 500–700 ms. However,

he concludes that ‘we cannot assume that one phenomenon can be explained by the other. There is only a narrow range of frequencies of natural or voluntary rhythms and of preferred tempo’ (p. 154). Despite this conclusion, however, one study showed that participants’ preferred tempo of successive tones was in a harmonic relation (with a ratio of 1, 1.5 and 2) to individual heart rates as measured during the presentation of the tone sequences (Iwanaga 1995).

Other studies, which attempted to relate heart rate (in some cases also breathing rate) to time estimates in the range of several seconds to minutes, some testing subjects before and after physical exercise, found no relationship (Schaefer & Gilliland 1938; Bell & Provins 1963) or associations that were weak or difficult to interpret (Ledietz & Tong 1972; Osato *et al.* 1995). One study, nevertheless, employing shorter intervals with duration up to 4 s, found that drugs, which either stimulate or inhibit the central or peripheral sympathetic nerve system, lead to an increase or decrease in heart rate and breathing rate and an accompanying relative under- or overproduction of intervals, respectively (Hawkes *et al.* 1962). A relative underproduction of intervals can be interpreted as resulting from an increase in clock speed. Although this latter result points to the role of cardiac and respiratory cycle rates in the judgement of duration, one has to keep in mind that proponents of the standard cognitive models of time perception could still argue that it is not the heart rate *per se* that functions as an internal clock but that generally increased arousal levels affect the pacemaker of an internal clock in the brain (Wittmann & Paulus 2008). Especially regarding the short durations tested in the study by Hawkes *et al.* (1962) of just a few seconds, a heart rate cycle of typically approximately 700 ms could not accurately represent different temporal intervals.

Although hardly any convincing evidence exists that would show how specific physiological cycles function as an internal clock for judging time, body states as a whole could, nevertheless, form the building blocks of a timekeeping mechanism. Ultimately, interoceptive processes as registered in the insula encompass the physiological status of all body tissues and organs such as the skin, muscles and the viscera (Craig 2008). It has been shown that the self-regulation of emotions (Vohs & Schmeichel 2003) and of autonomic parameters in biofeedback procedures (Cohen 1981) lead to longer time percepts. One attempt to explain these and other findings is that the insular cortex, which integrates body signals, is the anatomical basis for the creation of emotions and the sense of time (Craig 2008). Being more strongly aware of one’s own emotions and body processes would, at the same time, lead to a prolongation of subjective duration. When individuals are experimentally deprived of sensory stimuli (auditory–tactual–visual) their overall sense of duration over several days gets strongly impaired. However, these subjects, who have to rely solely on their inner sense, report that time passes painfully slowly (Schulman *et al.* 1967). Experienced practitioners of mindfulness meditation who concentrated ‘on the self across time and the present moment’ in an fMRI study showed stronger activity in a

right lateralized network including the insula and somatosensory cortex (Farb *et al.* 2007).

An explicit assignment to a functional role for the insula in temporal processing was made by Ackermann *et al.* (2001), who showed in an fMRI study that a linear increase in left anterior insula activity was a function of presented click train rates (increasing up to 6 Hz). By contrast, a linear increase in right anterior insula activity was recorded when click rates slowed down to 2 Hz. This and other findings have led to the idea that the insula is an essential component in the sequencing of sounds and the perception of rhythm in music (Bamiou *et al.* 2003). Moreover, an involvement of the insular cortex has repeatedly been shown in neuroimaging studies on duration processing with different timing tasks (Brunia *et al.* 2000; Rao *et al.* 2001; Lewis & Miall 2003b; Pouthas *et al.* 2005; Livesey *et al.* 2007; Stevens *et al.* 2007); however, the significance of insula activation in the context of time perception is seldom discussed. Recently, however, evidence of neurophysiological activity in the posterior insula of the human brain has shown to be involved in the encoding of multiple-second durations. Time–activity curves of neural activation derived from event-related fMRI during a time reproduction task showed activation in bilateral posterior insula that linearly built up when subjects were presented with 9 and 18 s tone intervals (Wittmann *et al.* 2008). This build-up of neuronal activation peaked at the end of the respective intervals. Related to the functional role of the dorsal posterior insula, this finding of accumulator-type activity was, therefore, interpreted as representing the registration of physiological changes over time that eventually leads to the representation of duration. The flow of time, thereafter, corresponds to the flow of interoceptive signalling from the body as sensed in the dorsal posterior insula.

A shift in attention to emotional processes and insular cortex activity in the search for the underlying mechanisms of time perception has only recently started. The greatest obstacle to a sound theory on the neural bases of time perception has been the lack of evidence for a neurobiological mechanism. The finding on accumulator-type activity during the processing of multiple second intervals represents such a potential mechanism. This finding is also compatible with the pacemaker–accumulator model of time perception where pulses emitted by a pacemaker are transiently stored in an accumulator and the number of pulses defines duration (Pfeuty *et al.* 2005). In line with this conceptualization, it is conceivable that the number and rate of body signals accumulated in the posterior insula over a given timespan creates our perception of duration. To disclose mechanisms on different time scales, i.e. milliseconds and a few seconds, will be the challenge for future research. Interval processing over different time ranges may be controlled by different neurobiological mechanisms.

5. CONCLUSION

Despite the fact that time is an essential factor for understanding complex behaviour, the processes underlying the experience of time and the timing of

action are incompletely understood. Too many contradictory theories exist—in psychology and neuroscience alike—that aim at explaining how we judge duration. One could argue that the conceptualization presented here of relating body processes to the experience of time represents yet another alternative approach among so many others. Only future empirical evidence, based on strong theoretical grounds, will tell whether a dedicated neural system actually exists for the representation of time and which neurobiological mechanism causes the experience of time.

One argument of plausibility as to why our inner sense, our body awareness, might be related to the sense of time should be mentioned here. The recent proposal of an intimate relationship between time and the awareness of an emotional and visceral self (see Craig 2008 2009) seems to be in line with a western philosophical tradition proposing that time is a creation of the self. ‘Inner time or duration is virtually indistinguishable from the awareness of the self, the experience of the self as an enduring, unitary entity that is constantly becoming’ (Hartocollis 1983, p. 17). Thereafter, the experience of our self is only possible as an entity across time. One attribute of the self is time, or differently expressed, the self is defined by its extension over time, a succession of moments that constitutes duration.⁴ This idea is probably most explicitly expressed by Henri Bergson who noted that ‘psychic states [...] unfold in time and constitute duration’ (Bergson 1913). According to his view, the phenomenal self creates the sense of duration.

In neurobiological terms, we perceive signals from the body which create a ‘material me’ that has subjective feelings and is self-aware (‘I feel it’s me!’; Craig 2002). Since the ascending pathways to the insular cortex inform us about the ongoing status of the body, a pacemaker-type signal (accumulating successive states of the material self) would be continuously present that could be employed in a timekeeping system. An accumulation of physiological states over time would be registered in the insula. This sketch of a processing model is, of course, borrowed from the cognitive models with a pacemaker–accumulator unit and is, to date, speculative. To summarize the main lines of argument put forward in this review:

- (i) Although the perception of time is an essential and inextricable component of everyday experience, no conclusive answers to the questions of *which* neural substrates and *what kind* of neurophysiological processes could account for the experience of duration have been established. That is, several areas of the brain have been identified as potential contributors to timekeeping (e.g. cerebellum, frontal cortices and basal ganglia), but none have been specifically implicated for this process and there is no consensus as to the precise neural mechanisms accounting for our sense of time.
- (ii) Philosophical wisdom beginning in antiquity has related the experience of time to the feeling of a self. The body self and emotional self in modern biological terms is based on insular cortex activity. The signalling of body states, which define the material me and contribute to the ‘feeling me’, is a

permanent and ongoing process over time and, thus, could function as an inner measure of duration by matching external temporal intervals with the duration of physiological changes.

- (iii) The strong relationship between effect and time is not only an everyday experience of everyone but it is also well documented by many empirical studies. Since affective states are entangled with body states, insular cortex activity (the primary sensory area for visceral signals) may, therefore, cause the experience of the passage of time.

ENDNOTES

¹Book 11 of St Augustine’s Confessions: *In te, animus meus, tempora metior [...] ipsam metior, cum tempora metior* (electronic edition: <http://ccat.sas.upenn.edu/jod/augustine/>).

²A vivid description of our experience of time from the prospective and retrospective perspectives can be found in Thomas Mann’s novel *The magic mountain*. In his chapter entitled *Excursus on the sense of time*, Thomas Mann narrates some of the basic mechanisms of time perception as described in the psychological sciences of today.

³From the beginning of psychophysical investigations following Fechner’s pioneering work, it has been known that, across the time range between milliseconds and several seconds, the auditory time sense does not follow the Weber–Fechner law, i.e. $\Delta t/t$ is not a constant (Mach 1865). Mach discovered that, in auditory duration, discrimination, the highest acuity is achieved with base durations approximately 300–400 ms.

⁴In this context, Borges (1999), hinting at the existential aspect of time, formulated: ‘Time is the substance of which I am made. Time is a river that sweeps me along, but I am the river; it is a tiger that mangles me, but I am the tiger; it is a fire that consumes me, but I am the fire’ (p. 332).

REFERENCES

- Ackermann, H., Riecker, A., Mathiak, K., Erb, M., Grodd, W. & Wildgruber, D. 2001 Rate-dependent activation of a prefrontal–insular–cerebellar network during passive listening to trains of click stimuli: an fMRI study. *Neuroreport* **12**, 4087–4092. (doi:10.1097/00001756-200112210-00045)
- Angrilli, A., Cherubini, P., Pavese, A. & Manfredini, S. 1997 The influence of affective factors on time perception. *Percept. Psychophys.* **59**, 972–982.
- Aparicio, P., Diedrichsen, J. & Ivry, R. B. 2005 Effects of focal basal ganglia lesions on timing and force control. *Brain Cogn.* **58**, 62–74. (doi:10.1016/j.bandc.2004.09.009)
- Aschoff, J. 1998 Human perception of short and long time intervals: its correlation with body temperature and the duration of wake time. *J. Biol. Rhythms* **13**, 437–442. (doi:10.1177/074873098129000264)
- Avni-Babad, D. & Ritov, I. 2003 Routine and the perception of time. *J. Exp. Psychol. Gen.* **132**, 543–550. (doi:10.1037/0096-3445.132.4.543)
- Bailey, N. & Areni, C. S. 2006 Background music as a quasi clock in retrospective duration judgments. *Percept. Mot. Skills* **102**, 435–444. (doi:10.2466/PMS.102.2.435-444)
- Bamiou, D. E., Musiek, F. E. & Luxon, L. M. 2003 The insula (Island of Reil) and its role in auditory processing. Literature review. *Brain Res. Rev.* **42**, 143–154. (doi:10.1016/S0165-0173(03)00172-3)
- Bell, C. R. & Provins, K. A. 1963 Relation between physiological responses to environmental heat and time judgments. *J. Exp. Psychol.* **66**, 572–579. (doi:10.1037/h0048993)
- Benussi, V. 1913 *Psychologie der Zeitauffassung*. Heidelberg, Germany: Carl Winters Universitätsbuchhandlung.

- Bergson, H. 1913 *Time and free will*. London, UK: George Allen, Company, Ltd.
- Berlin, H. A. & Rolls, E. T. 2004 Time perception, impulsivity, emotionality, and personality in self-harming borderline personality disorder patients. *J. Pers. Disord.* **18**, 358–378. (doi:10.1521/pedi.2004.18.4.358)
- Binkofski, F. & Block, R. A. 1996 Accelerated time experience after left frontal cortex lesion. *Neurocase* **2**, 485–493. (doi:10.1080/13554799608402424)
- Blumenthal, A. L. 1977 *The process of cognition*. Englewood Cliffs, NJ: Prentice-Hall.
- Borges, J. L. 1999 In *Selected non-fictions* (ed. E. Weinberger), New York, NY: Viking.
- Brown, S. W. 1997 Attentional resources in timing: interference effects in concurrent temporal and nontemporal working memory tasks. *Percept. Psychophys.* **59**, 1118–1140.
- Brunia, C. H. M., de Jong, B. M., van den Berg-Lenssen, M. & Paans, A. M. J. 2000 Visual feedback about time estimation is related to a right hemisphere activation measured by PET. *Exp. Brain Res.* **130**, 328–337. (doi:10.1007/s002219900293)
- Bschor, T., Ising, M., Bauer, M., Lewitzka, U., Skerstubeit, M., Muller-Oerlinghausen, B. & Baethge, C. 2004 Time experience and time judgment in major depression, mania and healthy subjects. A controlled study of 93 subjects. *Acta Psychiatr. Scand.* **109**, 222–229. (doi:10.1046/j.0001-690X.2003.00244.x)
- Bueti, D., Bahrami, B. & Walsh, V. 2008a The sensory and association cortex in time perception. *J. Cogn. Neurosci.* **20**, 1054–1062. (doi:10.1162/jocn.2008.20060)
- Bueti, D., van Dongen, E. V. & Walsh, V. 2008b The role of superior temporal cortex in auditory timing. *PLoS ONE* **3**, e2481. (doi:10.1371/journal.pone.0002481)
- Bueti, D., Walsh, V., Frith, C. & Rees, G. 2008c Different brain circuits underlie motor and perceptual representations of temporal intervals. *J. Cogn. Neurosci.* **20**, 204–214. (doi:10.1162/jocn.2008.20017)
- Buhusi, C. V. & Meck, W. H. 2002 Differential effects of methamphetamine and haloperidol on the control of an internal clock. *Behav. Neurosci.* **116**, 291–297. (doi:10.1037/0735-7044.116.2.291)
- Buhusi, C. V. & Meck, W. H. 2005 What makes us tick? Functional and neural mechanisms of interval timing. *Nat. Rev. Neurosci.* **6**, 755–765. (doi:10.1038/nrn1764)
- Burle, B. & Casini, L. 2001 Dissociation between activation and attention effects in time estimation: implications for internal clock models. *J. Exp. Psychol. Hum. Percept. Perform.* **27**, 195–205. (doi:10.1037/0096-1523.27.1.195)
- Campbell, L. A. & Bryant, R. A. 2007 How time flies: a study of novice skydivers. *Behav. Res. Ther.* **45**, 1389–1392. (doi:10.1016/j.brat.2006.05.011)
- Cevik, M. O. 2003 Effects of methamphetamine on duration discrimination. *Behav. Neurosci.* **117**, 774–784. (doi:10.1037/0735-7044.117.4.774)
- Church, R. M. 1984 Properties of the internal clock. In *Timing and time perception*, vol. 423 (eds J. Gibbon & L. Allan), pp. 566–582. New York, NY: New York Academy of Sciences.
- Cohen, J. 1981 A preliminary investigation on time perception and autonomic self-regulation. *Biofeedback Self Regul.* **6**, 289–293. (doi:10.1007/BF01000654)
- Coull, J. T., Vidal, F., Nazarian, B. & Macar, F. 2004 Functional anatomy of the attentional modulation of time estimation. *Science* **303**, 1506–1508. (doi:10.1126/science.1091573)
- Craig, A. D. 2002 How do you feel? Interoception: the sense of the physiological condition of the body. *Nat. Rev. Neurosci.* **3**, 655–666.
- Craig, A. D. 2003 Interoception: the sense of the physiological condition of the body. *Curr. Opin. Neurobiol.* **13**, 500–505. (doi:10.1016/S0959-4388(03)00090-4)
- Craig, A. D. 2008 Interoception and emotion: a neuroanatomical perspective. In *Handbook of emotion* (eds M. Lewis, J. M. Haviland-Jones & L. F. Barrett), pp. 272–288. 3rd edn. New York, NY: Guilford.
- Craig, A. D. (Bud) 2009 Emotional moments across time: a possible neural basis for time perception in the anterior insula. *Phil. Trans. R. Soc. B* **364**, 1933–1942. (doi:10.1098/rstb.2009.0008)
- Critchley, H. D., Wiens, S., Rotshtein, P., Öhman, A. & Dolan, R. J. 2004 Neural systems supporting interoceptive awareness. *Nat. Neurosci.* **7**, 189–195. (doi:10.1038/nrn1176)
- Damasio, A. 1999 *The feeling of what happens: body and emotion in the making of consciousness*. San Diego, CA: Harcourt, Inc.
- Danckert, J. A. & Allman, A. A. A. 2005 Time flies when you're having fun: temporal estimation and the experience of boredom. *Brain Cogn.* **59**, 236–245. (doi:10.1016/j.bandc.2005.07.002)
- Dehaene, S. 1993 Temporal oscillations in human perception. *Psychol. Sci.* **4**, 264–270. (doi:10.1111/j.1467-9280.1993.tb00273.x)
- Droit-Volet, S. & Meck, W. H. 2007 How emotions colour our perception of time. *Trends Cogn. Sci.* **11**, 504–513. (doi:10.1016/j.tics.2007.09.008)
- Droit-Volet, S., Brunot, S. & Niedenthal, P. M. 2004 Perception of the duration of emotional events. *Cogn. Emot.* **18**, 849–858. (doi:10.1080/02699930341000194)
- Effron, D. A., Niedenthal, P. M., Gil, S. & Droit-Volet, S. 2006 Embodied temporal perception of emotion. *Emotion* **6**, 1–9. (doi:10.1037/1528-3542.6.1.1)
- Eisler, A. D. & Eisler, H. 1994 Subjective time scaling: influence of age, gender, and type A and type B behavior. *Chronobiologia* **21**, 185–200.
- Elbert, T., Ulrich, R., Rockstroh, B. & Lutzenberger, W. 1991 The processing of temporal intervals reflected by CNV-like brain potentials. *Psychophysiology* **28**, 648–655. (doi:10.1111/j.1469-8986.1991.tb01009.x)
- Evans, V. 2004 *The structure of time*. Amsterdam, The Netherlands; Philadelphia, PA: John Benjamins.
- Exner, S. 1875 Experimentelle Untersuchung der einfachsten psychischen Prozesse. III. Abhandlung. *Pflügers Arch. Gesamte Physiol.* **11**, 403–432. (doi:10.1007/BF01659311)
- Falk, J. L. & Bindra, D. 1954 Judgment of time as a function of serial position and stress. *J. Exp. Psychol.* **47**, 279–282. (doi:10.1037/h0061946)
- Farb, N. A. S., Segal, Z. V., Mayberg, H., Bean, J., McKeon, D., Fatima, Z. & Anderson, A. K. 2007 Attending to the present: mindfulness meditation reveals distinct neural modes of self-reference. *Soc. Cogn. Affect. Neurosci.* **2**, 313–322. (doi:10.1093/scan/nsm030)
- Ferrandez, A. M., Hugueville, L., Lehericy, S., Poline, J. B., Marsault, C. & Pouthas, V. 2003 Basal ganglia and supplementary motor area subsecond duration perception: an fMRI study. *Neuroimage* **19**, 1532–1544. (doi:10.1016/S1053-8119(03)00159-9)
- Fingelkurts, A. A. & Fingelkurts, A. A. 2006 Timing in cognition and EEG brain dynamics: discreteness versus continuity. *Cogn. Process.* **7**, 135–162. (doi:10.1007/s10339-006-0035-0)
- Fink, M., Ulbrich, P., Churan, J. & Wittmann, M. 2006 Stimulus-dependent processing of temporal order. *Behav. Process.* **71**, 344–352. (doi:10.1016/j.beproc.2005.12.007)
- Flaherty, M. G. 1999 *A watched pot: how we experience time*. New York, NY: New York University Press.
- Flaherty, M. G., Freidin, B. & Sautu, R. 2005 Variation in the perceived passage of time: a cross-national study. *Soc. Psychol. Q.* **68**, 400–410.

- Fraisse, P. 1982 Rhythm and tempo. In *The psychology of music* (ed. D. Deutsch), pp. 149–180. New York, NY: Academic Press.
- Fraisse, P. 1984 Perception and estimation of time. *Annu. Rev. Psychol.* **35**, 1–36. (doi:10.1146/annurev.ps.35.020184.000245)
- Getty, D. J. 1975 Discrimination of short temporal intervals: a comparison of two models. *Percept. Psychophys.* **18**, 1–8.
- Gil, S., Niedenthal, P. M. & Droit-Volet, S. 2007 Anger and time perception in children. *Emotion* **7**, 219–225. (doi:10.1037/1528-3542.7.1.219)
- Grondin, S. & Macar, F. 1992 Dividing attention between temporal and nontemporal tasks: a performance operating characteristics—POC—analysis. In *Time, action and cognition. Towards bridging the gap* (eds F. Macar, V. Pouthas & W. J. Friedman), pp. 119–128. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Hancock, P. A. & Weaver, J. L. 2005 On time distortion under stress. *Theor. Issues Ergon. Sci.* **6**, 193–211. (doi:10.1080/14639220512331325747)
- Harrington, D. L., Haaland, K. Y. & Hermanowicz, N. 1998 Temporal processing in the basal ganglia. *Neuropsychologia* **12**, 3–12. (doi:10.1037/0894-4105.12.1.3)
- Harrington, D. L., Boyd, L. A., Mayer, A. R., Sheltraw, D. M., Lee, R. R., Huang, M. & Rao, S. M. 2004a Neural representation of interval encoding and decision making. *Brain Res. Cogn. Brain Res.* **21**, 193–205. (doi:10.1016/j.cogbrainres.2004.01.010)
- Harrington, D. L., Lee, R. R., Boyd, L. A., Rapcsak, S. Z. & Knight, R. T. 2004b Does the representation of time depend on the cerebellum? Effect of cerebellar stroke. *Brain* **127**, 561–574. (doi:10.1093/brain/awh065)
- Hartocollis, P. 1983 *Time and timelessness or the varieties of temporal experience*. New York, NY: International Universities Press.
- Hawkes, G., Joy, R. & Evan, W. O. 1962 Autonomic effects on estimates of time: evidence for a physiological correlate of temporal experience. *J. Psychol.* **53**, 183–191.
- Heidegger, M. 1992 *The concept of time*. Oxford, UK; Cambridge, UK: Blackwell Publishers.
- Hellstrom, A., Lang, H., Portin, R. & Rinne, J. 1997 Tone duration discrimination in Parkinson's disease. *Neuropsychologia* **35**, 737–740. (doi:10.1016/S0028-3932(96)00122-4)
- Hicks, R. E. 1992 Prospective and retrospective judgments of time: a neurobehavioural analysis. In *Time, action and cognition. Towards bridging the gap* (eds F. Macar, V. Pouthas & W. J. Friedman), pp. 97–108. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Hinton, S. C. & Meck, W. H. 2004 Frontal–striatal circuitry activated by human peak-interval timing in the supra-seconds range. *Brain Res. Cogn. Brain Res.* **21**, 171–182. (doi:10.1016/j.cogbrainres.2004.08.005)
- Hirsh, I. J. & Sherrick, C. E. 1961 Perceived order in different sense modalities. *J. Exp. Psychol.* **62**, 423–432. (doi:10.1037/h0045283)
- Ivry, R. B. & Keele, S. W. 1989 Timing functions of the cerebellum. *J. Cogn. Neurosci.* **1**, 136–152. (doi:10.1162/jocn.1989.1.2.136)
- Ivry, R. B. & Schlerf, J. E. 2008 Dedicated and intrinsic models of time perception. *Trends Cogn. Sci.* **12**, 273–280. (doi:10.1016/j.tics.2008.04.002)
- Ivry, R. B. & Spencer, R. M. 2004 The neural representation of time. *Curr. Opin. Neurobiol.* **14**, 225–232. (doi:10.1016/j.conb.2004.03.013)
- Ivry, R. B., Keele, S. W. & Diener, H. C. 1988 Dissociation of the lateral and medial cerebellum in movement timing and movement execution. *Exp. Brain Res.* **73**, 167–180. (doi:10.1007/BF00279670)
- Iwanaga, M. 1995 Harmonic relationship between preferred tempi and heart rate. *Percept. Mot. Skills* **81**, 67–71.
- Jahanshahi, M., Jones, C. R. G., Dürnbacher, G. & Frith, C. D. 2006 The substantia nigra pars compacta and temporal processing. *J. Neurosci.* **26**, 12 266–12 273. (doi:10.1523/JNEUROSCI.2540-06.2006)
- James, W. 1890 *The principles of psychology*. London, UK: MacMillan.
- Jones, C. R. G., Rosenkranz, K., Rothwell, J. C. & Jahanshahi, M. 2004 The right dorsolateral prefrontal cortex is essential in time reproduction: an investigation with repetitive transcranial magnetic stimulation. *Exp. Brain Res.* **158**, 366–372. (doi:10.1007/s00221-004-1912-3)
- Kagerer, F. A., Wittmann, M., Szélag, E. & von Steinbüchel, N. 2002 Cortical involvement in temporal reproduction: evidence for differential roles of the hemispheres. *Neuropsychologia* **40**, 357–366. (doi:10.1016/S0028-3932(01)00111-7)
- Kanabus, M., Szélag, E., Rojek, E. & Pöppel, E. 2002 Temporal order judgement for auditory and visual stimuli. *Acta Neurobiol. Exp.* **62**, 263–270.
- Karmarkar, U. R. & Buonomano, D. V. 2007 Timing in the absence of clocks: encoding time in neural network states. *Neuron* **53**, 427–438. (doi:10.1016/j.neuron.2007.01.006)
- Kiss, M., Cristescu, T., Fink, M. & Wittmann, M. 2008 Auditory language comprehension of temporally reversed speech signals in native and non-native speakers. *Acta Neurobiol. Exp.* **68**, 204–213.
- Koch, G., Oliveri, M., Torriero, S. & Caltagirone, C. 2003 Underestimation of time perception after repetitive transcranial magnetic stimulation. *Neurology* **60**, 1844–1846.
- Koch, G., Brusa, L., Caltagirone, C., Oliveri, M., Peppe, A., Tiraboschi, P. & Stanzione, P. 2004 Subthalamic deep brain stimulation improves time perception in Parkinson's disease. *Neuroreport* **15**, 1071–1073. (doi:10.1097/00001756-200404290-00028)
- Koch, G., Oliveri, M., Torriero, S., Salerno, S., Gerfo, E. L. & Caltagirone, C. 2007 Repetitive TMS of cerebellum interferes with millisecond time processing. *Exp. Brain Res.* **179**, 291–299. (doi:10.1007/s00221-006-0791-1)
- Lebedev, M. A., O'Doherty, J. E. & Nicolelis, M. A. L. 2008 Decoding of temporal intervals from cortical ensemble activity. *J. Neurophysiol.* **99**, 166–186. (doi:10.1152/jn.00734.2007)
- Lediect, V. & Tong, J. E. 1972 Effects of heart-rate increase on temporal discrimination and time judgment by two groups of delinquents. *Percept. Mot. Skills* **34**, 759–764.
- Leon, M. I. & Shadlen, M. N. 2003 Representation of time by neurons in the posterior parietal cortex of the macaque. *Neuron* **38**, 317–327. (doi:10.1016/S0896-6273(03)00185-5)
- Lewis, P. A. & Miall, R. C. 2003a Brain activation patterns during measurement of sub- and supra-second intervals. *Neuropsychologia* **41**, 1583–1592. (doi:10.1016/S0028-3932(03)00118-0)
- Lewis, P. A. & Miall, R. C. 2003b Distinct systems for automatic and cognitively controlled time measurement: evidence from neuroimaging. *Curr. Opin. Neurobiol.* **13**, 250–255. (doi:10.1016/S0959-4388(03)00036-9)
- Lewis, P. A. & Miall, R. C. 2006 A right hemispheric prefrontal system for cognitive time measurement. *Behav. Process.* **71**, 226–234. (doi:10.1016/j.beproc.2005.12.009)
- Livesey, A. C., Wall, M. B. & Smith, A. T. 2007 Time perception: manipulation of task difficulty dissociates clock functions from other cognitive demands. *Neuropsychologia* **45**, 321–331. (doi:10.1016/j.neuropsychologia.2006.06.033)
- Mach, E. 1865 Untersuchungen über den Zeitsinn des Ohres. *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften Wien* **51**, 133–150.

- Madison, G. 2001 Variability in isochronous tapping: higher order dependencies as a function of intertap interval. *J. Exp. Psychol. Hum. Percept. Perform.* **27**, 411–422. (doi:10.1037/0096-1523.27.2.411)
- Marchetti, G. 2009 Studies on time: a proposal on how to get out of circularity. *Cog. Process.* **10**, 7–40. (doi:10.1007/s10339-008-0215-1)
- Matell, M. S. & Meck, W. H. 2004 Cortico-striatal circuits and interval timing: coincidence detection of oscillatory processes. *Brain Res. Cogn. Brain Res.* **21**, 139–170. (doi:10.1016/j.cogbrainres.2004.06.012)
- Mates, J., Muller, U., Radil, T. & Pöppel, E. 1994 Temporal integration in sensorimotor synchronization. *J. Cogn. Neurosci.* **6**, 332–340. (doi:10.1162/jocn.1994.6.4.332)
- Mauk, M. D. & Buonomano, D. V. 2004 The neural basis of temporal processing. *Annu. Rev. Neurosci.* **27**, 307–340. (doi:10.1146/annurev.neuro.27.070203.144247)
- Meck, W. H. 1996 Neuropharmacology of timing and time perception. *Brain Res. Cogn. Brain Res.* **3**, 227–242. (doi:10.1016/0926-6410(96)00009-2)
- Melges, F. T. & Fougousse, C. E. 1966 Time sense, emotions, and acute mental illness. *J. Psychiatr. Res.* **4**, 127–139. (doi:10.1016/0022-3956(66)90025-2)
- Miyake, Y., Onishi, Y. & Pöppel, E. 2004 Two types of anticipation in synchronization tapping. *Acta Neurobiol. Exp.* **64**, 415–426.
- Mohs, R. C., Tinklenberg, J. R., Roth, W. T. & Kopell, B. S. 1980 Sensitivity of some human cognitive functions to effects of methamphetamine and secobarbital. *Drug Alcohol Depend.* **5**, 145–150. (doi:10.1016/0376-8716(80)90191-X)
- Münsterberg, H. 1889 *Beiträge zur experimentellen Psychologie, Heft 1*. Freiburg, Germany: J. C. B. Mohr.
- Nakajima, Y., Shimojo, S. & Sugita, Y. 1980 On the perception of two successive sound bursts. *Psychol. Res.* **41**, 335–344. (doi:10.1007/BF00308878)
- Nenadic, I., Gaser, C., Volz, H. P., Rammsayer, T., Häger, F. & Sauer, H. 2003 Processing of temporal information and the basal ganglia: new evidence from fMRI. *Exp. Brain Res.* **148**, 238–246.
- Nichelli, P., Clark, K., Hollnagel, C. & Grafman, J. 1995 Duration processing after frontal lobe lesions. *Ann. NY Acad. Sci.* **769**, 183–190. (doi:10.1111/j.1749-6632.1995.tb38139.x)
- Nobre, A. C. & O'Reilly, J. 2004 Time is of the essence. *Trends Cogn. Sci.* **8**, 387–389. (doi:10.1016/j.tics.2004.07.005)
- Noulhiane, M., Mella, N., Samson, S., Ragot, R. & Pouthas, V. 2007a How emotional auditory stimuli modulate time perception. *Emotion* **7**, 697–704. (doi:10.1037/1528-3542.7.4.697)
- Noulhiane, M., Pouthas, V., Hasboun, D., Baulac, M. & Samson, S. 2007b Role of the medial temporal lobe in time estimation in the range of minutes. *Neuroreport* **18**, 1035–1038. (doi:10.1097/WNR.0b013e3281668be1)
- Noulhiane, M., Pouthas, V. & Samson, S. 2008 Is time reproduction sensitive to sensory modalities? *Eur. J. Cogn. Psychol.* **21**, 18–34. (doi:10.1080/09541440701825981)
- Oppenheimer, D. M. 2008 The secret life of fluency. *Trends Cogn. Sci.* **12**, 237–241. (doi:10.1016/j.tics.2008.02.014)
- Ornstein, R. E. 1970 *On the experience of time*. Baltimore, MD: Penguin Books.
- Osato, E., Ogawa, N. & Takaoka, N. 1995 Relations among heart rate, immediate memory, and time estimation under two different instructions. *Percept. Mot. Skills* **80**, 831–842.
- Peters, M. 1989 The relationship between variability of intertap intervals and interval duration. *Psychol. Res.* **51**, 38–42. (doi:10.1007/BF00309274)
- Pfeuty, M., Ragot, R. & Pouthas, V. 2005 Relationship between CNV and timing of an upcoming event. *Neurosci. Lett.* **382**, 106–111. (doi:10.1016/j.neulet.2005.02.067)
- Pollatos, O., Kirsch, W. & Schandry, R. 2005 On the relationship between interoceptive awareness, emotional experience, and brain processes. *Brain Res. Cogn. Brain Res.* **25**, 948–962. (doi:10.1016/j.cogbrainres.2005.09.019)
- Pollatos, O., Herbert, B. M., Matthias, E. & Schandry, R. 2007a Heart rate response after emotional picture presentation is modulated by interoceptive awareness. *Int. J. Psychophys.* **63**, 117–124. (doi:10.1016/j.ijpsycho.2006.09.003)
- Pollatos, O., Schandry, R., Auer, D. P. & Kaufmann, C. 2007b Brain structures mediating cardiovascular arousal and interoceptive awareness. *Brain Res.* **1141**, 178–187. (doi:10.1016/j.brainres.2007.01.026)
- Pöppel, E. 1970 Excitability cycles in central intermittency. *Psychol. Res.* **34**, 1–9. (doi:10.1007/BF00422860)
- Pöppel, E. 1971 Oscillations as possible basis for time perception. *Stud. Gen.* **24**, 85–107.
- Pöppel, E. 1997 A hierarchical model of temporal perception. *Trends Cogn. Sci.* **1**, 56–61. (doi:10.1016/S1364-6613(97)01008-5)
- Pöppel, E. 2009 Pre-semantically defined temporal windows for cognitive processing. *Phil. Trans. R. Soc. B* **364**, 1887–1896. (doi:10.1098/rstb.2009.0015)
- Pouthas, V. & Perbal, S. 2004 Time perception does not only depend on accurate clock mechanisms but also on unimpaired attention and memory processes. *Acta Neurobiol. Exp.* **64**, 367–385.
- Pouthas, V. *et al.* 2005 Neural network involved in time perception: an fMRI study comparing long and short interval estimation. *Hum. Brain Mapp.* **25**, 433–441. (doi:10.1002/hbm.20126)
- Rammsayer, T. H. 1997 On the relationship between personality and time estimation. *Pers. Individ. Dif.* **23**, 739–744. (doi:10.1016/S0191-8869(97)00117-7)
- Rammsayer, T. H. 1999 Neuropharmacological evidence for different timing mechanisms in humans. *Q. J. Exp. Psychol. B* **52**, 273–286. (doi:10.1080/027249899391070)
- Rammsayer, T. H. & Lima, S. D. 1991 Duration discrimination of filled and empty auditory intervals: cognitive and perceptual factors. *Percept. Psychophys.* **50**, 565–574.
- Rammsayer, T. H., Hennig, J., Haag, A. & Lange, N. 2001 Effects of noradrenergic activity on temporal information processing in humans. *Q. J. Exp. Psychol. B* **54**, 247–258. (doi:10.1080/02724990143000036)
- Rao, S. M., Mayer, A. R. & Harrington, D. L. 2001 The evolution of brain activation during temporal processing. *Nat. Neurosci.* **4**, 317–323. (doi:10.1038/85191)
- Rubia, K. & Smith, A. 2004 The neural correlates of cognitive time management: a review. *Acta Neurobiol. Exp.* **64**, 329–340.
- Rubia, K., Overmeyer, S., Taylor, E., Brammer, M., Williams, S., Simmons, A., Andrew, C. & Bullmore, E. 1998 Prefrontal involvement in temporal bridging and timing movement. *Neuropsychologia* **36**, 1283–1293. (doi:10.1016/S0028-3932(98)00038-4)
- Ruhnau, E. 1995 Time-gestalt and the observer. In *Conscious experience* (ed. T. Metzinger), pp. 165–184. Paderborn, Germany: Ferdinand Schöningh.
- Saper, C. B. 2002 The central autonomic nervous system: conscious visceral perception and autonomic pattern generation. *Annu. Rev. Neurosci.* **25**, 433–469. (doi:10.1146/annurev.neuro.25.032502.111311)
- Schaefer, V. G. & Gilliland, A. R. 1938 The relation of time estimation to certain physiological changes. *J. Exp. Psychol.* **23**, 545–552. (doi:10.1037/h0061414)
- Schulman, C. A., Richlin, M. & Weinstein, S. 1967 Hallucinations and disturbances of affect, cognition, and physical state as a function of sensory deprivation. *Percept. Mot. Skills* **25**, 1001–1024.

- Shrivastav, M. N., Humes, L. E. & Aylsworth, L. 2008 Temporal order discrimination of tonal sequences by younger and older adults: the role of duration and rate. *J. Acoust. Soc. Am.* **124**, 462–471. (doi:10.1121/1.2932089)
- Siegmán, A. W. 1962 Anxiety, impulse control, intelligence, and the estimation of time. *J. Clin. Psychol.* **18**, 103–105. (doi:10.1002/1097-4679(196201)18:1<103::AID-JCLP2270180134>3.0.CO;2-K)
- Smith, A., Taylor, E., Lidzba, K. & Rubia, K. 2003 A right hemispheric frontocerebellar network for time discrimination of several hundreds of milliseconds. *Neuroimage* **20**, 344–350. (doi:10.1016/S1053-8119(03)00337-9)
- Staddon, J. E. R. 2005 Interval timing: memory, not a clock. *Trends Cogn. Sci.* **9**, 312–314. (doi:10.1016/j.tics.2005.05.013)
- Stetson, C., Fiesta, M. P. & Eagleman, D. M. 2007 Does time really slow down during a frightening event. *PLoS ONE* **2**, e1295. (doi:10.1371/journal.pone.0001295)
- Stevens, M. C., Kiehl, K. A., Pearlson, G. & Calhoun, V. D. 2007 Functional neural circuits for mental timekeeping. *Hum. Brain Mapp.* **28**, 394–408. (doi:10.1002/hbm.20285)
- Szelag, E., von Steinbüchel, N., Reiser, M., Gilles de Langen, E. & Pöppel, E. 1996 Temporal constraints in processing of nonverbal rhythmic patterns. *Acta Neurobiol. Exp.* **56**, 215–225.
- Taatgen, N. A., van Rijn, H. & Anderson, J. R. 2007 An integrated theory of prospective time interval estimation: the role of cognition, attention and learning. *Psychol. Rev.* **114**, 577–598. (doi:10.1037/0033-295X.114.3.577)
- Tinklenberg, J. R., Roth, W. T. & Kopell, B. S. 1976 Marijuana and ethanol: differential effects on time perception, heart rate, and subjective response. *Psychopharmacology* **49**, 275–279. (doi:10.1007/BF00426830)
- Treisman, M., Faulkner, A., Naish, P. L. N. & Brogan, D. 1990 The internal clock: evidence for a temporal oscillator underlying time perception with some estimates of its characteristic frequency. *Perception* **19**, 705–743. (doi:10.1068/p190705)
- Trevarthen, C. 1999 Musicality and the intrinsic motive pulse: evidence from human psychobiology and infant communication. *Musicae Scientiae 1999–2000* (Special Issue), 155–215.
- Tse, P. U., Intriligator, J., Rivest, J. & Cavanagh, P. 2004 Attention and the subjective expansion of time. *Percept. Psychophys.* **66**, 1171–1189.
- Twenge, J. M., Catanese, K. R. & Baumeister, R. F. 2003 Social exclusion and the deconstructed state: time perception, meaninglessness, lethargy, lack of emotion, and self-awareness. *J. Pers. Soc. Psychol.* **85**, 409–423. (doi:10.1037/0022-3514.85.3.409)
- Ulbrich, P., Churan, J., Fink, M. & Wittmann, M. 2007 Temporal reproduction: further evidence for two processes. *Acta Psychol.* **125**, 51–65. (doi:10.1016/j.actpsy.2006.06.004)
- VanRullen, R. & Koch, C. 2003 Is perception discrete or continuous? *Trends Cogn. Sci.* **7**, 207–213. (doi:10.1016/S1364-6613(03)00095-0)
- van Wassenhove, V., Grant, K. W. & Poeppel, D. 2007 Temporal window of integration in auditory–visual speech perception. *Neuropsychologia* **45**, 598–607. (doi:10.1016/j.neuropsychologia.2006.01.001)
- Vohs, K. D. & Schmeichel, B. J. 2003 Self-regulation and the extended now: controlling the self alters the subjective experience of time. *J. Pers. Soc. Psychol.* **85**, 217–230. (doi:10.1037/0022-3514.85.2.217)
- Wackermann, J. & Ehm, W. 2006 The dual klepsydra model of internal time representation and time reproduction. *J. Theor. Biol.* **239**, 482–493. (doi:10.1016/j.jtbi.2005.08.024)
- Wackermann, J., Wittmann, M., Hasler, F. & Vollenweider, F. X. 2008 Effects of varied doses of psilocybin on time interval reproduction in human subjects. *Neurosci. Lett.* **435**, 51–55. (doi:10.1016/j.neulet.2008.02.006)
- Warren, R. M. & Obusek, C. J. 1972 Identification of temporal order within auditory sequences. *Percept. Psychophys.* **12**, 86–90.
- Watts, F. N. & Sharrock, R. 1984 Fear and time estimation. *Percept. Mot. Skills* **59**, 597–598.
- Wearden, J. H. 2004 Decision processes in models of timing. *Acta Neurobiol. Exp.* **64**, 303–317.
- White, C. T. 1963 Temporal numerosity and the psychological unit of duration. *Psychol. Monogr.* **77**, 1–37.
- Wiens, S. 2005 Interoception in emotional experience. *Curr. Opin. Neurol.* **18**, 442–447. (doi:10.1097/01.wco.0000168079.92106.99)
- Wittmann, M. 1999 Time perception and temporal processing levels of the brain. *Chronobiol. Int.* **16**, 17–32. (doi:10.3109/07420529908998709)
- Wittmann, M. & Lehnhoff, S. 2005 Age effects in perception of time. *Psychol. Rep.* **97**, 921–935. (doi:10.2466/PRO.97.7.921-935)
- Wittmann, M. & Paulus, M. P. 2008 Decision making, impulsivity and time perception. *Trends Cogn. Sci.* **12**, 7–12. (doi:10.1016/j.tics.2007.10.004)
- Wittmann, M. & Pöppel, E. 2000 Temporal mechanisms of the brain as fundamentals of communication—with special reference to music perception and performance. *Musicae Scientiae 1999–2000* (Special Issue), 13–28.
- Wittmann, M., von Steinbüchel, N. & Szelag, E. 2001 Hemispheric specialisation for self-paced motor sequences. *Brain Res. Cogn. Brain Res.* **10**, 341–344. (doi:10.1016/S0926-6410(00)00052-5)
- Wittmann, M., Vollmer, T., Schweiger, C. & Hiddemann, W. 2006 The relation between the experience of time and psychological distress in patients with hematological malignancies. *Palliat. Support. Care* **4**, 357–363. (doi:10.1017/S1478951506060469)
- Wittmann, M., Carter, O., Hasler, F., Cahn, B. R., Grimberg, U., Spring, P., Hell, D., Flohr, H. & Vollenweider, F. X. 2007a Effects of psilocybin on time perception and temporal control of behaviour in humans. *J. Psychopharmacol.* **21**, 50–64. (doi:10.1177/0269881106065859)
- Wittmann, M., Leland, D. S., Churan, J. & Paulus, M. P. 2007b Impaired time perception and motor timing in stimulant-dependent subjects. *Drug Alcohol Depend.* **90**, 183–192. (doi:10.1016/j.drugalcdep.2007.03.005)
- Wittmann, M., Simmons, A. N., Aron, J. L. & Paulus, M. P. 2008 Accumulation of neural activity in the posterior insula encodes the passage of time. *Nature Precedings*. See <http://hdl.handle.net/10101/npre.2008.2062.1>.
- Zakay, D. & Block, R. A. 1997 Temporal cognition. *Curr. Dir. Psychol. Sci.* **6**, 12–16. (doi:10.1111/1467-8721.ep11512604)
- Zakay, D. & Block, R. A. 2004 Prospective and retrospective duration judgments: an executive-control perspective. *Acta Neurobiol. Exp.* **64**, 319–328.