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Introduction

The experience of time: neural mechanisms and the interplay of emotion, cognition and embodiment

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Time research has been a neglected topic in the cognitive neurosciences of the last decades: how do humans perceive time? How and where in the brain is time processed? This introductory paper provides an overview of the empirical and theoretical papers on the psychological and neural basis of time perception collected in this theme issue. Contributors from the fields of cognitive psychology, psychiatry, neurology and neuroanatomy tackle this complex question with a variety of techniques ranging from psychophysical and behavioural experiments to pharmacological interventions and functional neuroimaging. Several (and some new) models of *how* and *where* in the brain time is processed are presented in this unique collection of recent research that covers experienced time intervals from milliseconds to minutes. We hope this volume to be conducive in developing a better understanding of the sense of time as part of complex set of brain–body factors that include cognitive, emotional and body states.

Keywords: time perception; temporal processing; interval timing; cognition; emotion; embodiment

1. INTRODUCTION

Among our senses, the 'sense of time' is peculiar. First, time is intangible. One cannot point the finger at a 'duration object' as one could at a table or a sound source, yet time can be experienced when one waits for something to happen or to end, but also, in more subtle ways, when one performs or listens to music. Time is ubiquitous in our experiential world and yet nowhere to be found in the physical one. Second, there exists no sense organ for time perception and, as such, all sensory modalities are possible entries at the interface of physical time with perceptual time. Third, perceptual time is not 'isomorphic' to physical time and many factors including attention, memory, arousal and emotional states are all potential modulators of time perception. The accuracy and precision of time estimation in the seconds-to-minutes range, which may or may not depend on a neural clock, is under the influence of these cognitive and emotional factors.

We thus depart from the notion that time is a mental construct, and that the brain must actively derive estimates of time from multiple sources of information both outside and inside the boundary of the mental and material self. Insofar as the experience of time is tied to the mental status of the beholder, it reflects one's cognitive state and emotional well-being. Regarding the sense of time in relation to seconds, minutes and hours, our subjective well-being strongly influences how time is being experienced: time flies during pleasant activities but drags during periods of mental distress (Flaherty 1999; Bschor *et al.* 2004; Wittmann *et al.* 2006*b*). Despite this intuitive notion, empirical work over the last decades in time perception research has mainly focused on classic 'internal clock models', a metaphoric view of time-keeping mechanisms in the brain that has led to tremendous progress (Church 1984; Zakay & Block 1997). Nevertheless, the neurobiological basis for such an internal clock that would represent the passage of time and duration has not been found. Such a biological mechanism exists as the circadian clock (with a periodicity of approx. 24 hours) that regulates the daily rhythms in fundamental aspects of physiology and behaviour (Roenneberg *et al.* 2003; Wittmann *et al.* 2006*a*). Despite all efforts, however, a similar clock has not been identified for the time sense that relates to fractions of a second to multiple minutes.

In recent years, new ideas have emerged regarding the neurobiological mechanisms underlying the experience of time. In particular, major progress has been made with the realization that time perception may engage distinct brain mechanisms (and areas) depending on the time scale at which events occur (Gibbon *et al.* 1997; Pöppel 1997; Rammsayer 1999; Lewis & Miall 2003). Moreover, with the emergence of empirical data showing how emotion and bodily

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

sensations shape the perception of time, new models are evolving, which partly extend, but also challenge the classic internal clock models for the time range of seconds to minutes. Regarding the milliseconds range, whether a central mechanism explicitly encodes time or whether neural populations within each region intrinsically encode the temporal characteristics of sensory events through time-dependent neural changes is in debate (Ivry & Schlerf 2008; van Wassenhove *et al.* 2008; Ulbrich *et al.* 2009). In the latter case, time would be an emergent property of the underlying neural dynamics and not dependent on a dedicated timing mechanism (Mauk & Buonomano 2004). Hence, models of time perception have developed different strategies based on the time scale under scrutiny. As such, the two main questions have to be tackled: *how* and *where* in the brain is time processed? It will become clear that the field is far from reaching a consensus on these two questions, but this theme issue will provide an overview of recent psychological and neurobiological models of time perception at different time scales. Yet, it is not exhaustive. Many models and ideas remain outside the scope of this volume; an indication of how diverse and complex the topic of time perception is.

2. OVERVIEW OF THE THEME ISSUE

The first contribution (van Wassenhove 2009) starts the debate by highlighting several theoretical difficulties in understanding the mapping between physical, neural and psychological time in a thorough review of the literature on time perception in the millisecond range and across sensory modalities. In discussing the question of potential discrete time quanta in the brain (one of the main topics of this theme issue), it is argued that although neural temporal processing may operate with certain temporal windows of integration, this resolution does not entail the conscious perception of time units, namely discrete *implicit* temporal processing does not equate discrete *explicit* temporal representations. For example, fine temporal processing is necessary for pitch perception and source localization, although the conscious percept is not that of time but of a tone or a spatial source. Even when speaking of temporal order or duration percept, the possible discrete processes underlying the subjective time percept do not map onto each other. van Wassenhove (2009) summarizes evidence and develops the idea that automatic processes of the brain that have specific temporal properties (and *per se* do not lead to conscious perception of time) are read out as (or mapped onto) abstract representations of time during a second attention-driven step.

This critical account of time perception in the short time range is followed by the presentation of ‘A theory of magnitude’ (Bueti & Walsh 2009). In this theory, the perception of time is not treated as a separate faculty (to be studied as other separate categories in cognitive neuroscience), but as part of a generalized magnitude processing system for space, time and number involving the right inferior parietal cortex. In developing their theory, the authors discuss converging evidence on (i) how non-temporal features (e.g. brightness and size) influence our time percepts, namely, how different magnitudes interfere with behavioural performance, (ii) how lesions to the right inferior parietal cortex cause perceptual disturbances across several magnitudes, and (iii) neuroimaging and transcranial magnetic stimulation (TMS) studies pointing to the crucial role of this area in the brain for quantifying duration as well as the spatial representation of number.

The next contribution proposes a different model related to coding efficiency (Eagleman & Pariyadath 2009). The paper extends the notion of non-identity of physical and subjective time highlighted by numerous temporal illusions. Experiments with repeating stimuli clearly show that the amount of energy required to process a cue is proportionally related to perceived duration. Repeated exposure to the same stimulus, leading to high predictability of its occurrence and content, shortens subjective duration; conversely, an unexpected cue or an oddball in a series of identical stimuli leads to an overestimation of duration when compared with the standard stimuli. The authors draw the hypothesis that the amount of energy committed to processing environmental stimuli in the short time range (milliseconds to a few seconds) accounts for the perception of duration. Repeated stimulation results in more coding efficiency and, in turn, leads to shorter subjective duration. A new stimulus, by contrast, necessitates more consumption of neural energy.

Two papers (Buonomano *et al.* 2009; Spencer *et al.* 2009) follow, which empirically address the recently developed idea of a state-dependent network (SDN) model (Karmarkar & Buonomano 2007). One open question in the current debate on temporal-processing mechanisms is whether stimulus durations in the sub-second range are processed by a dedicated system or whether neural populations within different regions of the brain intrinsically encode duration as a result of time-dependent neural changes; in the latter case, referred to as SDN model, temporal processing may be dedicated to spatial attributes of a scene, but time would nevertheless be intrinsically coded (and could, for example, be retrieved as an emergent property). In two experiments conducted by Spencer *et al.* (2009), the randomized occurrence of an irrelevant distracter interval in a duration estimation task was introduced to test predictions of the SDN model. According to the SDN model, contextual influences of stimuli with similar attributes to stimuli, which have to be judged for their duration, are to be expected since the representation of duration will depend on the initial state of the network. The results partly support the SDN model for time intervals shorter than 300 ms. However, the authors also find support for an alternative model in which attentional mechanisms account for their findings. Buonomano *et al.* (2009) show in accordance with their predictions of contextual influences that the interference decreased when the duration of stimuli that had to be judged had different frequencies (as opposed to when the same frequencies were used) or when the stimuli were separated with interstimulus intervals longer than 250 ms. The latter finding is corroborated by Spencer *et al.* (2009) who show that interference effects diminished with intervals of 300 ms. Both contributions offer challenging data providing empirical means for the reader to evaluate the plausibility of the SDN model.

In the time range of seconds, there is some consensus that a centralized clock-type mechanism could exist for duration estimation. In internal clock models, similar to a stop watch, a pacemaker produces a series of pulses and the number of pulses recorded over a given time span represents subjective duration (Church 1984; Treisman *et al.* 1990; Zakay & Block 1997). Testing a variant of these model types with rats and using a specific task (the peak interval procedure), Buhusi & Meck (2009) show the importance of allocating attention to time as opposed to the situation when subjects are distracted from time. The authors do note that the cognitive time sharing hypothesis finding empirical support in their experiments can be applied to any neuronal model of time perception. In the presented peak interval procedure, rats are trained to press a lever after a certain time interval has passed. When attention is distracted from time (distracter intervals are presented during the interval to be timed), accuracy of the timed performance deteriorates. However, the authors add a new feature to their model: given that the relative duration of the distracter influences timing performance, a working memory decay component is added to the model, which complements earlier models.

One of the assumptions of the internal clock models is that precision in timing across the typically assessed time scales (between milliseconds to multiple seconds) should not change dramatically, since one centralized time keeper is governing these estimates. However, alternative concepts favour the idea of duration-dependent timing processes (Fraisse 1984; Szelag *et al.* 2002). Based on psychophysical and behavioural observations as well as neurophysiological studies, Pöppel (2009) proposes a temporal segmentation model on two different time scales. One segmentation mechanism derives from neural oscillations with periods of approximately 20–40 ms, which are necessary for the temporal binding of spatially distributed brain activities, and accounts for detection thresholds of temporal order perception. A different temporal integration mechanism is proposed to function with a range of approximately 2–3 s, and potentially forms a temporal platform for conscious awareness. Both processes form necessary constraints for cognitive processing, i.e. they are prerequisites for temporally structuring perception and action, and essential for interacting with others and the environment.

In a rare attempt to test subjects' timing abilities across a broad range of durations—ranging from fractions of seconds to many minutes—Lewis & Miall (2009) empirically address a basic assumption of the standard internal clock model, namely the scalar timing property. The scalar timing property is related to the coefficient of variation, as a measure of the stability of timing behaviour, which should remain constant across different durations. In their analysis of the coefficient of variation, the authors detect a constant logarithmic decrease in values with increasing interval lengths, a clear violation of the assumption. However, the data does not support the hypothesis of multiple timer models. In fitting their data, a simple logarithmic regression accounted significantly for the detected slope. The authors discuss the possibility of the existence of multiple timers, which could overlap so strongly that outward performance would make it difficult to detect break points. In addition, they discuss the possibility of such a break point at an interval of 3–4 s as corresponding to a two-part logarithmic regression that also fits the data well. This contribution provides crucial empirical ground for anyone interested in tackling the question of multiple timers for different durations.

The contribution by Koch *et al.* (2009) provides an overview of neurological studies that examined timing behaviour in patients with different cortical and subcortical dysfunctions (e.g. patients with Parkinson's disease and lesions in different locations of the brain) as well as using TMS in healthy volunteers. The overall take in this contribution is that timing functions can hardly be circumscribed to specific areas of the brain, and the authors suggest that time perception relies on the intricate interplay of several brain structures. Additionally, they tentatively make more specific claims: for instance, the cerebellum may be more involved in the processing of shorter time intervals (sub-second range), whereas circuits connecting the basal ganglia and fronto-parietal areas of the cortex would be engaged in longer time intervals (supra-second range), and in the processing of more complex tasks involving other cognitive functions.

In the context of psychiatry research, Rubia *et al.* (2009) postulate that altered time perception and timing functions underlie complex dysfunctional behaviour as seen in individuals with increased impulsivity. For one, their neuroimaging studies in children with attention deficit hyperactivity disorder point to a dysfunctional network of brain areas involved in the processing of time on different time scales and tasks. For instance, in accordance with the well-established involvement of the dopamine system in time perception, the dopamine agonist methylphenidate has a normalization effect on brain activation. Possible positive effects on timing behaviour did not reach significance, thus showing that brain activation changes in psychopharmacological intervention are more readily detectable. While the outcome of the intervention study contributes to the dopamine hypothesis of time perception, these findings also show how brain activation related to a timing disturbance can be pharmacologically modified.

The next contribution provides a fresh look at the neural bases of time perception: Craig (2009) proposes that our experience of time emerges from emotional and visceral states processed in the insular cortex. The insula is part of the extended limbic system. It is specifically implicated as the basic receptive area for physiological states of the body (interoception) and is strongly involved in subjective feeling states. In his structural model, the anterior insular cortex integrates signals from within the body across time and, thereby, produces a series of emotional moments, which, in turn, constitute the perception of duration. Craig bases part of his argumentation on the many neuroimaging studies in the literature reporting insular cortex activation, but which repeatedly fail to discuss the significance of such findings. Within this new framework, research findings on the neural basis of time perception should be discussed and understood differently.

The impact of emotions on the perception of duration is highlighted by Droit-Volet & Gil (2009). In their series of studies, subjects tended to overestimate the duration of pictures depicting arousing emotional faces (expressing anger and fear) when compared with more neutral faces. Additionally, developmental studies show that socially relevant emotions in childhood such as a sad face (a potential signal of distress from the mother) lead to a stronger overestimation of duration in children than in adults. The authors discuss their findings within the framework of the internal clock model in which arousal increases the clock rate which, in turn, leads to longer estimations of duration. However, they also point to the weakness of assuming one centralized clock in face of so many different aspects of time perception and relevant time scales. Eventually, the authors frame their findings in the context of embodiment: sensorimotor knowledge and body predisposition act in social settings where they have to synchronize activities, namely, time their interactions with others. The influence of emotional context on subjective time could thus be seen as a process of interpersonal adjustment and synchronization.

The final contribution by Wittmann (2009) gives a critical appraisal of the state of the art in time perception research. The variety of psychological and neural models and the lack of consensus among time researchers are explained by the fact that different neural systems may be involved in the processing of different durations. Moreover, different cognitive faculties, whose neural basis is distributed over the brain and not necessarily part of a neural clock *per se* do contribute to the experience of time. Thus, it is difficult to discern a clock component (if it exists at all) from these other contributing functions. It becomes clear that specific neurophysiological mechanisms for the perception of time on different time scales have not yet been identified. Recent conceptual advances on the relationship between body states and time perception, and the empirical findings on the impact of emotions on our sense of time are summarized. In accordance with a strong philosophical tradition, the author proposes that the signalling of body states and the awareness of related emotions is a permanent process over time, which could function as a measure of duration.

As the field of time research is undergoing noteworthy transformations, we are very enthusiastic to gather in a single theme issue leading researchers who present their most recent ideas and findings in time perception and temporal processes research. With this volume, we aim to provide our audience with the current empirical evidence and theoretical arguments in time perception research within a cognitive neuroscience framework, which reaches beyond the classic boundaries of the sub-disciplines of this field. We wish to show that the experience of time depends on a complex set of brain–body factors that include cognitive, emotional and body states. By grouping different areas of inquiry into a single volume of this journal, we provide a comprehensive approach to the neuropsychology of time.

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