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## Review Paper

## Ticks per thought or thoughts per tick? A selective review of time perception with hints on future research

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## ABSTRACT

The last decade underwent a revival of interest in the perception of time and duration. The present short essay does not compete with the many other recent reviews and books on this topic. Instead, it is meant to emphasize the notion that humans (and most likely other animals) have at their disposal more than one time measuring device and to propose that they use these devices *jointly* to appraise the passage of time. One possible consequence of this conjecture is that the same physical duration can be judged differently depending on the reference 'clock' used in any such judgment. As this view has not yet been tested empirically, several experimental manipulations susceptible to directly test it are suggested. Before, are summarized a number of its latent precursors, namely the relativity of perceived duration, current trends in modeling time perception and its neural and pharmacological substrate, the experimental literature supporting the existence of multiple 'clocks' and a selected number of experimental manipulations known to induce time perception illusions which together with many others are putatively accountable in terms of alternative clock readings.

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"It is not we who are in space [or time], but it is space [or time] which is in us." (Lotze, 1892, p. 53)

## 1. Introduction

Just like Lotze (1892) who, in order to render space material (given his view that mental representations have an essentially non-spatial character), posited the *local sign theory*,<sup>1</sup> others (Hoagland, 1933) postulated an internal clock to make sense of our perception of (particularly short) time intervals. Of course, we measure also time by the size expansion of an approaching ball, by the passage of our thoughts, by the light of the day, by the moon cycle, by the passing seasons, by the three stages laid out in the sphinx's enigma... But all these gauges are capricious. They are alterable by, respectively, body temperature (François, 1927; Hoagland, 1933; Rammsayer, 1997a), the known/unknown size of the approaching ball (e.g. Hosking and Crassini, 2011), by the variable number of our thoughts (e.g. James, 1890), by the latitude of our location, by the clouds, by our health... So then how does the brain (or, for that matter, any device) measure time? Prior to this question, thinkers of all epochs have asked what time is or even if it exists (e.g. McTaggart, 1908; Sachs, 1996). It is certainly not the purpose of this short review to dive into such everlasting matters. Instead, it will be argued that while the relativity of time has been firmly established since Einstein (or even Aristotle), its perceptual implications have barely been studied. One central notion presently put forward is that the brain may gauge the duration of the very same event differently depending on its choice of a mutable reference 'clock'.

## 2. Relativity of perceived duration (PeDu)

All time perception models are rooted in the notion that one's reading of an internal 'clock' is equivalent to one's experience of time. However, experience of duration is in no way equivalent to its reading of a wrist watch, nor is estimation of a given physical duration necessarily unique.

### 2.1. A metaphor

Think of a boiling egg. To get it soft-boiled, one may use a clock. But if the egg comes out hard-boiled, then the clock must have been too slow. So, the state of the egg (just like the state of a neural network) could be used as a measure of the clock's fidelity. Yet, the duration needed to soft-boil the egg depends on other (inaccessible) factors such as the atmospheric pressure, and the thickness of the eggshell. Hence the boiling time cannot be used as an absolute measure of (experienced) time. Also, when introspecting on the many thoughts we could have while the egg was boiling, we may feel either that the passing of time has accelerated – if we are to gauge it by the number of our thoughts *relative to what we*

*take to be a canonical time for soft-boiling an egg* –, or that it slowed down – if we are to gauge it by the time for soft-boiling the egg *relative to what we take to be the canonical number of thoughts we usually have during such an interval*. In other words, we can gauge the passage of time in units of *ticks per thought* or of *thoughts per tick*.<sup>2</sup>

The above observations amount to saying that no clock reading is a reliable measure of time and that our experience of duration cannot be based on just one such clock reading. Both statements are but a rephrasing of Einstein's relativity theory applied to psychological time and echo thousands of years of introspection (at least since Aristotle; see Buhusi and Meck, 2009; Sachs, 1996; van Wassenhove, 2009).

Contextual perceived duration (PeDu) effects have been quantified since Wundt (see James, 1890; Fraisse, 1963, 1984). With very few exceptions (e.g. Buhusi and Meck, 2009), they have been exclusively documented for sequential rather than concurrent temporal intervals.<sup>3</sup> Sequential relativity can be accounted for by just one 'central' (e.g. Coull et al., 2010; Eagleman, 2008; James, 1890), or 'local' clock (e.g. Ivry and Schlerf, 2008; Johnston et al., 2006). Instead, *instantaneous relativity* requires the existence of more than one clock as implied by the fact that a given time interval is registered differently in the context of other simultaneously running time intervals than in their absence (Buhusi and Meck, 2009). The interpretation of such results has been however based on the notion that each of such intervals is appraised by a different clock. What if, in the absence of any *explicit* context (including concurrent tasks), any time interval is measured by more than one clock (as in the boiled egg example)? On this conjecture, the PeDu of a given interval should depend on which of the *n* clocks is read out. As this choice is a priori arbitrary, one should perceive a given time interval *within the same context* as either longer or shorter or, perhaps, simultaneously longer *and* shorter than some reference. Introspection seems to provide a positive answer to the question of whether such contradictory duration appraisals do actually occur.<sup>4</sup> Nonetheless, this possibility has never been addressed experimentally or even stated.

As a first step toward the founding of the instantaneous PeDu relativity hypothesis, the multiplicity of internal clocks must be established. Before that will be briefly summarized the main conceptual modeling trends in the time perception literature (typically neutral as to the one vs. multi-clock debate) and the neural and

<sup>2</sup> What does one mean when saying "I didn't see time go by"? That the given *known* physical interval (such as the one needed to soft-boil an egg) appeared to be short vis-à-vis the time *normally* needed to string the many thoughts one had during that interval. Equivalently, it means that the time in this person's "dreaming away world" (measured by the number of thoughts) was long vis-à-vis the given *known* physical interval. This is the same logic as the one most frequently used to account for the *moon illusion*. According to this logic, the horizon moon appears larger *precisely* because its angular size is the same as that of the zenith moon, while the horizon (presumably) appears to be further away than the zenith. If the horizon moon is further away, then it should appear smaller; however, since its angular size is (more or less) constant, it *must be that it is actually larger* (Cleomedes, around AD 200/Ross, 2000). Equivalently, a perceived duration depends on the "world" one is considering (the "thoughts world" or the "boiling egg world") with reference to the "world" that this one uses as yardstick. In this view time is measured as a ratio (ticks/thought or thoughts/tick) with the nominator and denominator referring respectively to what subjects use as 'focal' (attended) and 'background' (non-attended) worlds.

<sup>3</sup> "Our sense of time, like other senses, seems subject to the law of contrast. It appeared pretty plainly in Estel's observations that an interval sounded shorter if a long one had immediately preceded it, and longer when the opposite was the case." (in Wundt, 1883 cited by James, 1890).

<sup>4</sup> "In general, a time filled with varied and interesting experiences seems short in passing, but long as we look back. On the other hand, a tract of time empty of experiences seems long in passing, but in retrospect short." (James, 1890, p. 624).

<sup>1</sup> 'Local sign' is defined as an inherent qualitative factor by means of which one visual or tactile sensation can be distinguished from others in respect to its position in space (Wolman, 1973). Equivalently, 'local sign' can be regarded as a specific character assumed to be *inherent* in the sensory experience aroused by a single receptor or by a single afferent neuron so that it differs for each receptor or for each afferent neuron (basically the *specific nerve energy* theory of Müller (1844); see also Barlow, 1972; Gorea, 1991). It is so called because it furnishes a cue to the position of the receptor-unit stimulated and hence to the *absolute* location of a stimulus *within the sensory space* (Warren, 1934).

pharmacological substrate of time-perception as revealed mainly by fMRI studies (globally sustaining a single ‘meta-clock’ view) and by dopaminergic manipulations.

### 3. Brief overview of PeDu modeling

Originally, the concept of an ‘internal clock’ was meant as an absolute time-base or pacemaker (coupled with an accumulator) against which all other temporal events are gauged (Creelman, 1962; Gibbon, 1977; Treisman, 1963; but before them Hoagland, 1933). It remains until today without any neurophysiological support. To account for behavioral data, such clock should tick within the 200 Hz range and its coupled accumulator should not skip a beat. These are implausible physiological properties (see Matell and Meck, 2000, 2004; Mauk and Buonomano, 2004). At least five other conceptualizations of a time measuring device have been proposed.

#### 3.1. Oscillators

An extension of the pacemaker view is that of multiple oscillators (Church and Broadbent, 1991; Miall, 1989) whereby a large variety of oscillation periods are initiated at signal onset and time is coded by the combination of phase readouts across the ensemble of oscillators (see Salinas and Sejnowski, 2001). Longer durations are primarily coded by longer oscillation periods. A version of this approach (referred to as ‘spectral models’) consists in coding time by the period of coincidentally firing neurons at the criterion time (Gluck et al., 1990; Miall, 1989). The existence of long period oscillations needed to gauge long time intervals has been questioned but beat periods of up to 60 s have been observed in the Basal Ganglia (Ruskin et al., 1999; see also Section 4). To date, this approach seems to be the most biologically plausible. It is not clear at all how it should be enriched to account for a large class of time illusions (see Sections 6 and 7).

#### 3.2. Memory trace

Timing based on the memory trace decay has been proposed, amongst others, by Grossberg and Schmajuk (1989) and by Stadon and Higa (1999), but well before them by Augustin (1993) and by Herbart (1812). How such time and stimulus intensity dependent decay rates can be disentangled and how memory decay applies to empty intervals remains problematic. Memory trace decay has not been found in the neural network supposed to sustain time estimation (see Section 4).

#### 3.3. Neural response energy

Recently, Pariyadath and Eagleman (2007) and Terao et al. (2008) proposed that time could be measured in units of neural response energy or, equivalently, by the number of activated neurons (an idea already alluded to by Ward, 1880) that in itself may depend on subject’s attentional state, expectation/surprise and/or habituation. The proposal is meant to account for a number of known temporal illusions related to such factors (Eagleman and Pariyadath, 2009; see Section 7). In addition to not being able to disentangle internal response energy dependent on stimulus energy itself from the internal response decay over time, this view encounters problems, among others, with empty interval estimations. Also, and despite these authors’ claims, internal response energy is little, if at all, dependent on stimulus speed within a range known to induce perceived duration dilation/contraction effects.

#### 3.4. State dependent networks

It has also been proposed that the passage of time is directly coded by the evolving pattern of activity in a neural network (a multi-neuron response trajectory in a neural manifold) activated by a timing onset event (Buonomano, 2000; Buonomano and Mauk, 1994; Buonomano and Merzenich, 1995; Maass et al., 2002). This conceptual view (referred to as ‘state dependent networks’, SDN) is difficult if not impossible to test. The SDN resistance to noise and its account of a number of PeDu illusions remain undocumented.

#### 3.5. Priors of temporal statistics of real world events

Recently, Ahrens and Sahani (2011) proposed that time estimation is based on individuals’ innate and/or learned statistics of (in their case, visual) changes in the world (of the  $1/f^2$  type<sup>5</sup>) and hence on individuals’ expectations of such changes. The model has nonetheless problems with the implementation of the priors as well as with predicting PeDu distortions larger than a few percentages.

In principle, any of the above model classes could be enriched to account for the relativity of perceptual timing.<sup>6</sup> Curiously, no such extension has been formally considered. Perceived time modeling has also ignored putative inter-clock interactions. Given that the issue of biological time measurement remains unsettled, in the present review the term ‘clock’ is used generically to refer to any of the above time measuring schemes.

## 4. Digest of the neural and pharmacological substrate of time perception

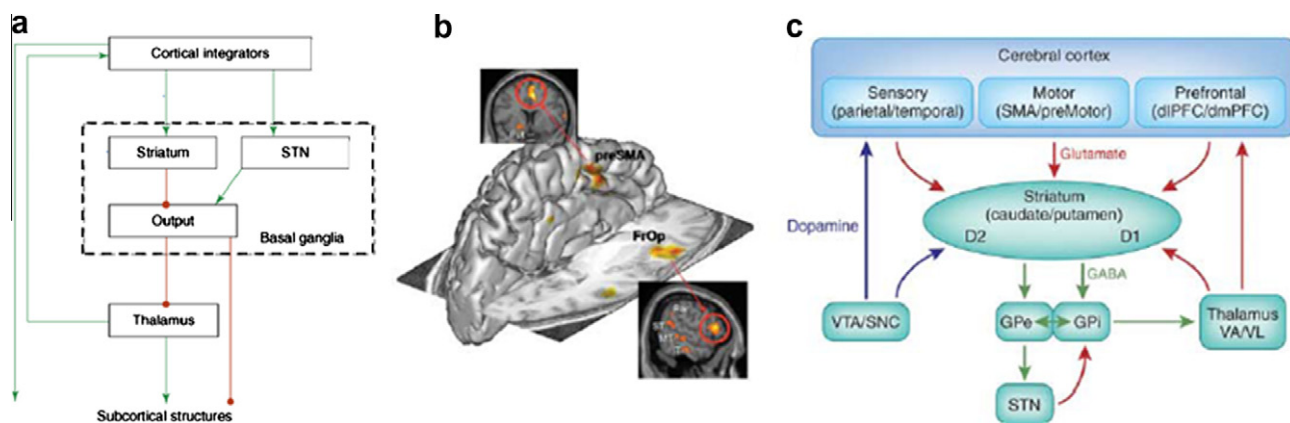
Globally speaking, this literature converges on the notion of an extended but unitary neural network subserving a unitary perception of time. This view may have also emerged because of the duration estimation tasks used in all these studies. To the current state of knowledge, no fMRI study has as yet investigated how or if the blood-oxygen-level dependence (BOLD) signal changes with PeDu modulations by contextual factors.

#### 4.1. Neuroimaging studies

fMRI techniques allow the investigation of the entire brain volume at once. This offers the potential to demonstrate the existence of multiple, anatomically discrete, modality-specific clocks within the same experimental paradigm. Yet, fMRI studies of motor (Bengtsson et al., 2005; Jäncke et al., 2000; Jantzen et al., 2007), or perceptual (Pastor et al., 2006; Pouthas et al., 2005; Shih et al., 2009) timing have consistently failed to provide evidence for multiple clocks in modality-specific processing areas. Instead, these studies have identified a centralized cortico-striatal timing network encompassing the Basal Ganglia (BG), the Supplementary Motor Area (SMA), and the right Prefrontal Cortex (rPC) (see Fig. 1) that is commonly activated across different sensory modalities or motor contexts (for reviews see Coull, 2004, 2009; Coull and Nobre, 1998, 2008; Coull et al., 2010; Wiener et al., 2010). This fMRI literature has mainly focused on the BOLD activity related to performing a time estimation task and to its modulation by the amount of attention allotted to the timing (relative to some other) task and by expectation.

<sup>5</sup>  $f$  Stands for temporal frequency. It has been shown that temporal changes in natural scenes display such a  $1/f^2$  power-law statistics (Dong and Atick, 1995).

<sup>6</sup> By considering concurrent clocks and/or memory decaying traces, modulating the number of relevant ‘oscillators’ or the size of the state dependent network according to the number of relevant contextual factors.



**Fig. 1.** Corticostriatal circuits for interval timing. (a) Schematic representation of the cortico – basal-ganglia–thalamic circuit (ST, subthalamic nucleus; Output, substantia nigra pars reticulata and the external segment of globus pallidus in primates). Green arrows denote excitatory connections; red lines with filled circles denote inhibitory connections (from Bogacz et al., 2010). (b) Human functional imaging data and (c) a more detailed rendering of the corticostriatal circuits implicated in interval timing (from Coull et al., 2010). Blue, green and red lines represent dopaminergic, GABAergic input, and glutamatergic input (FrOp, frontal operculum; GPe, globus pallidus external capsule; GPI, globus pallidus internal capsule; preMotor, premotor cortex; dlPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; Par, inferior parietal cortex; Put, putamen; SMA, Supplementary Motor Area; SNC, substantia nigra pars compacta; VL, ventral lateral nucleus of the dorsal thalamus; VA, ventral anterior nucleus of the dorsal thalamus; IT/MT/ST, inferior/middle/superior temporal cortex).

It has been hypothesized that the BG play a central role in decision processes related to temporal processing and to duration estimation (e.g. Buhusi and Meck, 2005; Coull and Nobre, 2008; Coull et al., 2010; Mauk and Buonomano, 2004). BG appear to be the convergence site of a complex neural network (Fig. 1), wherein they act as ‘coincidence detectors’ of neuronal oscillators for interval timing (Matell and Meck, 2004; Buhusi and Meck, 2005; Lustig et al., 2005; Mauk and Buonomano, 2004).

Given that both action and stimulus motion are strong PeDu modulators (see Section 6.2), it is not surprising that the cerebellum and the motion processing area (MT/V5) are also involved in duration estimation (see Bueti et al., 2008, 2010; Coull and Nobre, 2008; Mauk and Buonomano, 2004; Miall and Reckess, 2002; O’Reilly et al., 2008).

#### 4.2. Pharmacological and patient studies

Psychopharmacological investigations in both animals (e.g. Meck, 1986, 1996; Williamson et al., 2008) and humans (Coull et al., 2010) highlight the key role played by the dopaminergic (DA) system in the timing function. Studies with healthy volunteers reliably show a significant effect of an acute dose of the D2 receptor antagonist (haloperidol) on duration estimation accuracy. Haloperidol reduces temporal sensitivity in both the milliseconds and seconds range (Rammsayer, 1989, 1993, 1997b, 1999), whereas pergolide, a D1/D2 receptor agonist, improves temporal sensitivity in the milliseconds range (Rammsayer, 2006, 2009).

Systematic PeDu distortions in schizophrenic (e.g. Lewis, 1932; Rammsayer, 1990; Scott and Clifford, 1948; Volz et al., 2001) and Parkinson (e.g. Ivry and Keele, 1989; Malapani et al., 2002; Malapani et al., 1998) patients, known to have a poorly functioning DA system and responding well to DA treatments, comfort the modulatory role of the DA system on PeDu. These observations are compatible with the observed loss of dopaminergic neurons in the substantia nigra of Parkinson patients (for a review see Redgrave et al., 2010), so that PeDu has been used as a model of BG dysfunction. However, Parkinson patients show no difficulties in using temporal information to predict the trajectory of a moving object (Bares et al., 2010; Beudel et al., 2008), and present normal reaction time benefits for temporally predictable targets in simple (Jahanshahi et al., 1992, 1993) and choice (Praamstra and Pope, 2007) reaction time tasks. Accordingly, BG appear to be less important in making implicit temporal predictions. Instead, these

patients show deficits on more explicit forms of timing in both motor (where they are particularly affected) and perceptual tasks (see Coull and Nobre, 2008). For example, Parkinson patients temporarily withdrawn from dopaminergic medication show impaired temporal discrimination for tactile, auditory, or visual stimuli (Artieda et al., 1992). Such deficits are observed in both sub-second (Harrington et al., 1998) and supra-second (Smith et al., 2007) time ranges.

To date, neuroimaging and pharmacological investigations have not been drawn together. As noted above, fMRI studies have not yet attempted (or perhaps have not succeeded) to relate BOLD signal and PeDu modulations and the pharmacological literature has not yet shown the extent to which PeDu illusions depend on manipulations of the DA system.

#### 5. Multiple clocks?

The foundation of the early clock-models (but ultimately of all psychologically and neurophysiologically based time coding models) is that there is an internal time-base against which the flux of time is gauged. If such a time-base exists, then time perception could be regarded as psychologically ‘absolute’ and equivalent to the local sign-based space perception (Lotze, 1852). Like for the local sign concept, the existence of an immutable time-base is unanimously rejected as both space and time perception are strongly context-dependent (e.g. Fraisse, 1963, 1984; Eagleman, 2008; James, 1890; Schwartz et al., 2007). If so, the existence of multiple clocks to be used for an inter-clock calibration appears to be a reasonable assumption.

That multiple low-level clocks do exist is a direct implication of Johnston’s group (Ayhan et al., 2009; Bruno et al., 2010; Johnston et al., 2006) finding of retinal localized PeDu contractions following a localized adaptation (see also Burr et al., 2007; Morrone et al., 2010). Their data show that adaptation to a flickering Gabor<sup>7</sup> reduces by up to 20% the perceived duration of a 600 ms drifting or flickering Gabor presented at the adapted retinal (or perhaps spatio-temporal) location but not at the symmetrical, non-adapted location. It was therefore concluded that “there is a peripheral, spatially localized, essentially visual component involved in sensing the duration of visual events.” (Johnston et al., 2006, p. 472). It logically follows

<sup>7</sup> A one-dimensional sinusoidally luminance modulated grating whose contrast is modulated by a 2D Gaussian function.

that these time-coding components *exist in parallel* at all retinal locations (see also Ahrens and Sahani, 2011).

Curiously, Johnston's group's data show that the PeDu adaptation effect (PeDu contraction) is about equally strong whether or not the adapting and test stimuli share the same orientation. The implication of such results is that one should be able to measure time simultaneously at different locations *but not for different stimulus features at the same location*. While Johnston et al.'s results are to be expected if the relevant 'visual' clock is subcortical (hence orientation insensitive), they should not hold for features such as spatial frequency (or size) and color for which subcortical structures are selective. This counterintuitive dissociation between location and visual features begs for further testing.

The existence of more than one internal clock is also evidenced by, among others, the fact that auditory durations are judged to be longer than visually defined ones (Goldstone and Lhamon, 1974; Lhamon and Goldstone, 1974), that duration compression around a saccade onset is observed for visual, but not for auditory stimuli (Eagleman, 2005), that duration expansion observed for an unexpected "oddball" event<sup>8</sup> (Tse et al., 2004) does not generalize to other visual or auditory events (Pariyadath and Eagleman, 2007), that there is little temporal learning transfer from the auditory to the visual modality (Grondin et al., 2009), or that, in the presence of a timing 'gap' (e.g. Buhusi and Meck, 2006a,b), rats trained to time three simultaneous durations reset the clock used to time the 'short' duration, stop the 'medium' duration clock, and continue to run the 'long' duration clock (Buhusi and Meck, 2009; see also Matell et al., 2006; Matell et al., 2004; Meck, 1987; Meck and Church, 1984). Electrophysiological studies suggest that the duration of a stimulation can be represented by the local neural activity in the sensorimotor area recruited to process that stimulation without recourse to an homuncular central 'timer' (e.g. Ghose and Maunsell, 2002; Janssen and Shadlen, 2005; Leon and Shadlen, 2003). Transcranial Magnetic stimulation (TMS; e.g. Bueti et al., 2008) and Magnetoencephalography (MEG; e.g. Noguchi and Kakigi, 2006) studies have demonstrated the existence of modality-specific timing mechanisms as well.

It remains that the observed PeDu accuracy drop when subjects monitor more than one duration at a time (e.g. Brown, 2010; Brown and West, 1990; Morgan et al., 2008) is frequently attributed to an attentional sharing with one single clock (e.g. Block and Zakay, 1996; Brown, 2010; Fortin, 2003; Fortin and Massé, 2000; Ornstein, 1969; Thomas and Weaver, 1975; Zakay, 1989), or to the sequential reading out of multiple time intervals by a unique clock (Church, 1978; Gibbon et al., 1984; Morgan et al., 2008; Roberts and Church, 1978). Also, the observed complete transfer of training between the two visual hemispheres in a visual duration discrimination task (Westheimer, 1999) contrasts with Johnston et al.'s (2006) local adaptation results and favors the existence of a central time-measuring device.

The ongoing debate between distributed vs. single-clock timing mechanisms (see reviews by Coull et al., 2010; Coull and Nobre, 2008; Ivry and Schlerf, 2008; van Wassenhove, 2009) may be confused by insufficient consideration of the possibility that different representations of time exist for sub-second (time perception for speech, motor control) and supra-second (conscious time estimation for decision-making) time-ranges (Fraisse, 1963, 1984; Eagleman, 2008; James, 1890; Koch et al., 2009; Lewis and Miall, 2009; Morillon et al., 2009; Penney and Vaitilingam, 2008; van Wassenhove, 2009; Wittmann, 2009). As noted by Ivry and Schlerf (2008) and by Coull and Nobre (2008), most of the evidence for modality-specific multiple clocks has been typically assessed with sub-second durations (Karmarkar and Buonomano, 2007;

Merchant et al., 2008; Morrone et al., 2005; van Wassenhove et al., 2008).

## 6. PeDu modulations

It is well-established that PeDu depends on a large variety of stimulus intrinsic features (such as size, flicker rate, speed) and stimulus extrinsic factors (such as attention, expectation/surprise, emotion, and task demands; see reviews by Eagleman, 2008; Eagleman and Pariyadath, 2009; Fraisse, 1963, 1984; Grondin, 2010; James, 1890; Kaneko and Murakami, 2009; van Wassenhove, 2009). The remainder of this section is limited to a sample of the above with focus on motion (hence space), action, anticipation and attention effects on PeDu.

### 6.1. PeDu and motion

That motion perception instantiates our sense of time has been a perennial notion at least since Aristotle (e.g. Sachs, 1996). The perceptual relationship between perceived space and motion has been extensively documented at least since Hess (1904; see Whitney, 2002) with recent research showing that PeDu of a moving stimulus expands with speed (Brown, 1995; Kaneko and Murakami, 2009). Most of this research focused on the perceived *spatial* distortions entailed either by temporal delays (e.g. Burr, 1979), or by motion (e.g. De Valois and De Valois, 1991). However, with a very few early exceptions (see reviews by Bill and Teft, 1972; Casasanto and Boroditsky, 2008; Jones and Huang, 1982), the effects of space–time interplay on PeDu has been given little psychophysical attention since Helson (1930). The two major phenomena described in this literature were labeled *kappa* (Abbe, 1936; Cohen et al., 1953) and *tau* (Helson, 1930). The kappa effect is the functional dependence of temporal judgments on the spatial context. The tau effect is the corresponding dependence of spatial extent judgments on the temporal context. When two objects drift at different speeds over the same time interval (hence cover different distances), the PeDu of the faster object is longer than the PeDu of the slower object (kappa effect). Conversely, when these same objects cover identical trajectory lengths (hence last for different durations), the trajectory of the faster object is perceived as being longer than that of the slower object (tau effect).

PeDu of a sequence of sensory events was first experimentally shown to depend on their rate (number of events per unit of time) by Vierordt (1868). It was theorized that psychological time is measured in terms of the number of processed events (be they sensory or cognitive), hence as a function of *attentional load* (e.g. Brown, 2008; Fraisse, 1963, 1984; James, 1890). Modern research confirmed that PeDu increases with flicker rate (Kanai et al., 2006) but a preceding (Brown, 1995) and subsequent study (Kaneko and Murakami, 2009) have shown that the critical factor is speed rather than temporal frequency. At the same time it has been known (at least since Duncker, 1929) that perceived speed is *relative*, i.e. it depends on the speed of adjacent objects in motion (e.g. Smagt et al., 2010). It follows that motion and in particular *relative* motion is an ideal tool for testing the relative nature of PeDu. To my knowledge no such study has yet been performed. Testing the interplay between a (visual) 'target' and its 'context' (stimulus features known to modulate PeDu; in this case speed) also raises the question of how the latter is affected by shifting attention from one to the other, yet another unaddressed issue (see below).

### 6.2. PeDu, action, and anticipation

Motion is not only a perceptual event. On many occasions it is integrated into and inseparable from action. Catching a ball, releas-

<sup>8</sup> It should be noted that the PeDu *expansion* of unexpected events may in fact result from the PeDu *contraction* of the repeated (non-oddball) stimuli, possibly as a consequence of adaptation (Eagleman, 2008; Eagleman and Pariyadath, 2009).

ing one's fingers when launching it, crossing (or not crossing) a street in the presence of an approaching car, synchronizing one's walking pace with that of a companion, etc., are all time-gauged actions that can be looked upon as *implicit* time estimators (in the context of other motions) involving a *predictive* behavior (e.g. Coull, 2009; Coull and Nobre, 2008). Moreover, anticipating/expecting *when* an action will take place is often associated with the preparation of that specific action (e.g. O'Reilly et al., 2008) so that even without a motor output, implicit timing may nonetheless entail a latent motor behavior. No surprise then that time prediction and action have been jointly studied both behaviorally (for reviews, see Ivry and Richardson, 2002; Requin, 1980) and by neuroimaging techniques (e.g. Bortoletto and Cunnington, 2010; Cotti et al., 2011; Sakai et al., 2000) and have been shown to share neuroanatomical substrates (particularly in the left parietal/pre-motor cortex areas; Assmus et al., 2005; Coull and Nobre, 1998; Rushworth and Taylor, 2006; but see Buetti et al., 2008). Perturbation of the dopaminergic D2 receptor system, commonly associated with motor function, has also been associated with timing (Meck, 1996; Rammesayer, 1997b, 2009) suggesting a neurochemical overlap between the two processes.

Anticipation is thought of as an implicit timing operation coupled with a motor response (Coull, 2009; Coull and Nobre, 2008) and has been frequently studied with a synchronization task (Coull and Nobre, 2008; Mamassian, 2008; Gorea et al., 2010; Gorea and Rider, 2011) and modeled as a process computing the hazard function (Buetti et al., 2010; Coull, 2009; Cui et al., 2009; Ghose and Maunsell, 2002; Janssen and Shadlen, 2005; Nobre et al., 2007). As such, it has been shown that anticipation responses can be modulated by manipulations of the time interval between a target and a 'go' signal (e.g. Buetti et al., 2010; Janssen and Shadlen, 2005) but also by the cost-function associated with subject's timing accuracy (e.g. Mamassian, 2008; Maloney and Mamassian, 2009).

In contrast to implicit timing, explicit timing requires deliberate assessment of PeDu via either time interval discrimination – a purely perceptual task –, or interval reproduction – which involves a motor behavior. Gorea et al.'s (2010) data show a close to significant time estimation accuracy advantage of active (manual time interval reproduction) over passive (comparison with a probe interval) tasks. Chronostasis (the apparent longer time taken by the second hand of a clock to move to its next position when one first looks at it) has been originally explained in terms of an action induced phenomenon (Brown and Rothwell, 1997; Yarrow et al., 2001) particularly so when the onset of the clock hand's motion is voluntarily triggered by subject's saccade or hand movement (Haggard, 1999; Yarrow et al., 2001; Yarrow and Rothwell, 2003; Park et al., 2003; but see Alexander et al., 2005; Hunt et al., 2008). Instead, PeDu appears to be compressed during saccade preparation (Morrone et al., 2005). These studies suggest that action or action preparation (whether or not relevant to the duration estimation task per se) modulates both the bias and the accuracy of PeDu judgments. With the exception of these rather scarce studies, little is known on the relation between PeDu and action. Assessing the putative differences between passive (perceptually based) and active (perception plus motor action) duration estimations, with the latter involving or not an anticipatory motor task, remains a largely unexplored field.

### 6.3. PeDu and attention

Attention is probably the most frequently used PeDu modulating factor (see Brown, 2008, 2010; Coull, 2004). By definition, the distinction between a 'target' and its 'context' refers to what a subject attends/does not attend to, respectively. It is well known (at least since Posner, 1980) that attending to a location or to a specific object enhances one's sensitivity at that location or for that specific

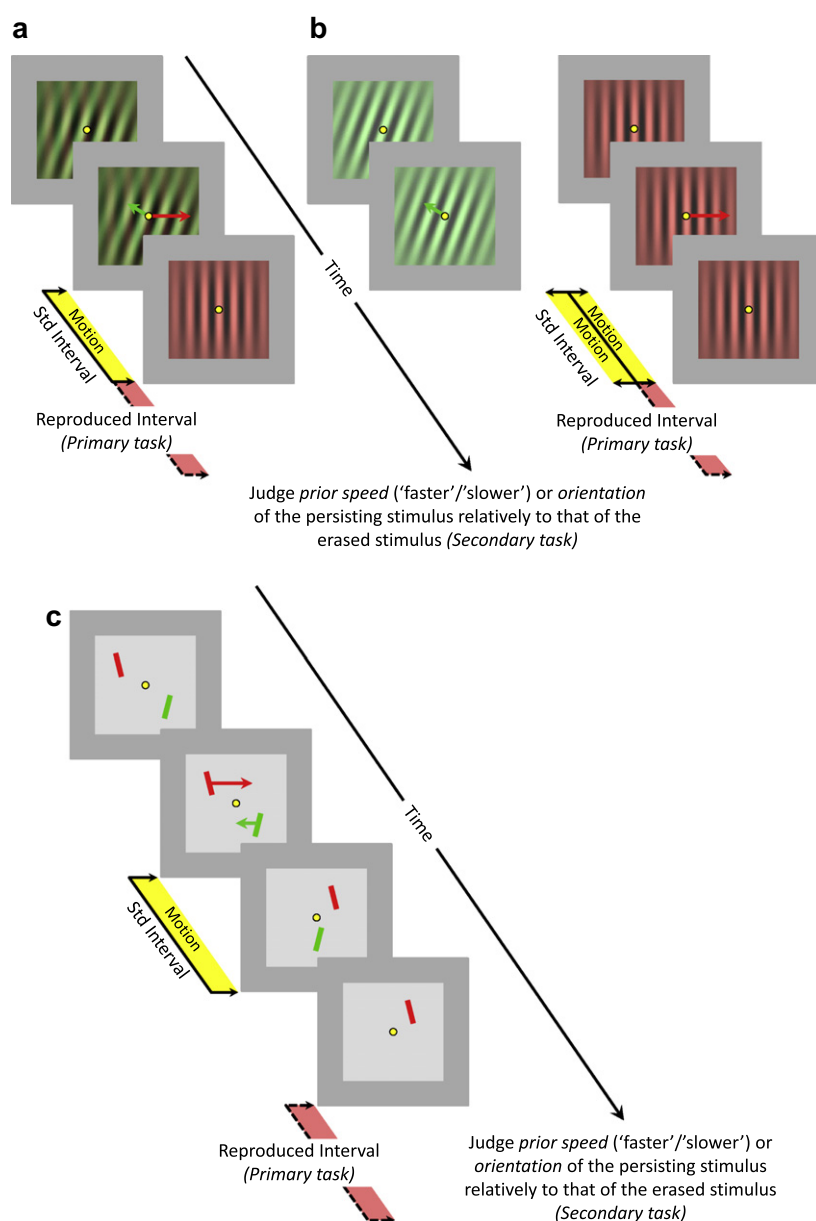
object (Carrasco, 2011). It is also established that the absence of attention does not necessarily reduce performance to chance level. In other words events can be processed, albeit less accurately, even in the absence of attention. Attended events appear to last longer than non-attended ones<sup>9</sup> and decrease the PeDu of a concurrent event (Brown, 2008, 2010; Fraisse, 1963, 1984; James, 1890; Tse et al., 2004; Vierordt, 1868; Yeshurun and Marom, 2008). The general notion accounting for such effects is that there is a counter that keeps track of the number of units of temporal information processed for a given perceived event (e.g. Thomas and Weaver, 1975; Brown, 2008, 2010) and that the number of units of temporal information that are counted decreases/increases when attention is drawn from/to processing the duration of an interval (e.g. Tse et al., 2004). Attention to time also decreases PeDu variability (e.g. Brown, 2008, 2010; Ruthruff and Pashler, 2010). Improvements in behavioral performance when selectively attending to temporal rather than non-temporal stimulus features are accompanied by specific increases in the activity of functionally specialized, and anatomically discrete brain regions such as pre-SMA and the frontal operculum (Coull et al., 2004; Coull, 2009; Coull and Nobre, 1998; Coull et al., 2004; Livesey et al., 2007; Morillon et al., 2009).

The behavioral and neuroimaging literature is agnostic as to if and how contextual and attentional effects on PeDu interact. All other things being equal, is the PeDu of a target/attended stimulus equally affected by the specifics of a contextual/non-attended stimulus as the PeDu of the contextual/non-attended stimulus is by the specifics of the target/attended one? Assessments of such attentional effects on time estimation, both behaviorally and neurally are still to be accomplished.

## 7. PeDu distortions and relative clock readings

In their review paper, Eagleman and Pariyadath (2009) enumerate ten stimulus properties shown to modulate PeDu. They are: brightness, size, numerosity, motion, novelty/predictability, temporal frequency, looming, filled (vs. empty) intervals, pattern complexity and number of events (see their Table 1). Of these, motion, temporal frequency, looming and number of events can be reduced to just one factor, namely observable changes per time unit. It can be argued that the filled/empty interval feature is also part of this category. If so, the stimulus properties affecting PeDu reduce to only five. To these, one should add attention (see Section 6.3), action (see Section 6.2), causality (e.g. Haggard et al., 2002; Eagleman and Holcombe, 2002), adaptation/recalibration (Cunningham et al., 2001; Haggard et al., 2002; Fujisaki et al., 2004; Stetson et al., 2006), task difficulty (e.g. Fortin et al., 1993; Petrusic and Baranski, 2009), emotion (e.g. Angrilli et al., 1997; Stetson et al., 2007) and drugs (e.g. Rammesayer, 2009). Clearly, many of these effects occur at different time scales and can be interpreted in many ways. Eagleman and Pariyadath's (2009) choice was meant to support their claim that duration is coded in units of internal response energy (see Section 3.3). It is difficult to see how this hypothesis can account for PeDu modulating factors such as causality, task difficulty or emotion. Be it as it may, the 'energy model' like all the models mentioned in Section 3 are *one clock-reading* models that can be, in principle, accommodated one way or another to account for all the time modulating factors above. If so, resorting to a simultaneous reading of multiple clocks is superfluous. Hence, demonstrating that the same physical time interval can be judged within the very same context shorter or longer than a reference becomes a critical test of the 'relative clock reading' hypothesis. The next section suggests a number of such possible tests.

<sup>9</sup> "Awareness of *change* is thus the condition on which our perception of time's flow depends" (James, 1890, p. 620).



**Fig. 2.** Three experimental designs meant to test the relativity of PeDu of a given interval under the same stimulating conditions. The temporal interval to be estimated always consists in two distinct stimuli (different speeds, orientations and colors) whose different speeds (colored arrows) are such as to induce different PeDu modulations. The two stimuli may (a) or may not overlap spatially (b, c). The last frame in each plot denotes the end of the temporal interval to be reproduced. Subjects have to decide how one of the attributes of this persisting stimulus differs from the erased stimulus (faster or slower speed, clockwise or counter-clockwise oriented) by pressing one of two key after a time interval reproducing the standard interval (see text for more details).

## 8. Testing paradoxical estimates of PeDu

As noted in the previous section, basically all the observed PeDu distortions can be reinterpreted within the frame of the relative readings of two (or more) simultaneous clocks. The experimental paradigms used to assess such distortions do not lend themselves, however, to testing paradoxical PeDu effects. Several of these paradigms are presented below, as they apply to spatio-temporal manipulations of the stimuli to be timed, to the involvement of action and anticipation in the PeDu assessment, and to the manipulation of subjects' attention in such assessments.

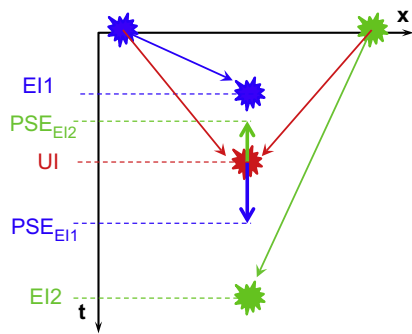
### 8.1. Spatio-temporal perceptual modulation effects

Higher temporal frequencies and/or speeds lead to PeDu dilation. By necessity such effects are relative to stimuli of lower temporal frequency and/or speed. All studies having assessed them

used sequential low–high frequency/speed stimulations. What if these parameters are presented simultaneously? To isolate their effects from attentional ones, the timing task should be such that subjects pay equal attention to the two sets of parameters at the same time. Instead, the PeDu report should be manipulated so as to induce primary post hoc consideration of only one set of parameters but in relation to the other set.

To achieve that, subjects could be asked to perform in parallel with the timing task a comparison task bearing either on the stimuli parameters known to modulate PeDu (e.g. speed), or on one of their PeDu-unrelated parameters (e.g. orientation). For example, subjects can be presented for a standard time interval with two drifting stimuli (e.g. Gabor patches spatially overlapping<sup>10</sup> –

<sup>10</sup> In this case their spatio-temporal characteristics should be such as to preserve their identity, i.e. preventing the two patches from binding into a unitary pattern (see Kim and Wilson, 1993).



**Fig. 3.** Space-time plot of two expected time intervals (EI; in-between the two 'blue' and the two 'green' 'flashes') whose durations are such that their unexpected ending (unexpected interval, UI; middle 'red' 'flash') occurs at half the duration of the longer one and at twice the duration of the shorter one. It is expected that when each of these EI-s is run separately and subjects are asked to judge the interval between the first and the unexpected flash, their points of subjective equality (PSE) will be shifted forward and backward in time for the short and long EI (blue and green arrows), respectively. What would happen when the two EI-s are run concurrently? (See text).

Fig. 2a – or not – Fig. 2b) differing in both, speed and orientation (and/or spatial frequency, color, etc.). The end of the time interval to be judged would be marked by the disappearance of one of the two stimuli with the persisting one, the probe, now motionless. The probe would indicate that subjects should report (secondary task) its previous speed (or its orientation) *relative* to the speed (or orientation) of the erased stimulus (faster/slower or rotated clockwise/counter-clock-wise). This report should be made by pressing one of two keys *after a period of time reproducing the standard interval* (primary task). The secondary task ensures that subjects pay equal attention to the two stimuli. Its bearing on the PeDu of the standard interval depends on which of the stimuli features are to be compared. The logic is that the duration of the very same compound stimulus will be judged differently depending on which of its components is considered *a posteriori* and the more so when the feature to be reported on in the secondary task is a PeDu modulator (i.e. speed but not orientation). This design can be declined in many different ways. For example, the drifting patches could be replaced with two objects drifting at different speeds over the same time interval (hence covering different spatial intervals). The faster object should be perceived as lasting longer than the slower one (kappa effect; see Section 6.1). At the end of their motion, only one of the two objects would remain visible and subjects could be asked to specify either its prior speed or, say, its orientation relative to that of the erased object after a time interval reproducing their PeDu of the joint event (Fig. 2c).

### 8.2. Action modulated PeDu

As noted above, the relation between PeDu and action remains to be clarified. Reproduction of standard time intervals (one of the most frequently used time estimation procedures; e.g. Doehring, 1961; Grondin, 2010) has always been implemented by means of subjects either sustaining a key-press for a duration equivalent to their PeDu of the standard interval, or performing two key-presses delimiting their PeDu of the standard. How PeDu may vary depending on the action(s) subjects are required to perform during the reproduced interval has not been considered. Suppose subjects are required to reproduce their PeDu of a standard interval by means of writing down a short or a long word (or perhaps draw a simple – e.g. circle –, or complex – e.g. octagon – geometrical figure). The short word (or simple geometrical figure) would require a relatively slow hand motion and the long word (or complex geometrical figure) a relatively fast one. Would subjects' reproduction of the standard depend on these hand motions?

Let's now complicate the design by having subjects perform a slow or fast action *during* the standard interval specified by the presentation of a fast or slowly moving patch. The end of the standard and the beginning of the reproduction interval would be indicated by the offset of the patch and the onset of a static symbol of one of two colors indicating that subjects have to estimate the duration of the moving stimulus or the duration of their own action. As in the design described in Section 8.1, the 'two-clock' hypothesis predicts that PeDu should depend on subjects' retrospective consideration of the 'focal' process (indicated by the color of the symbol) relative to the non-focal process.

### 8.3. Anticipation modulated PeDu

Anticipation can be regarded as a PeDu estimate and has been studied as such with behavioral, physiological and imagery methods (e.g. Luce, 1986; Janssen and Shadlen, 2005; Coull, 2009). To the current state of knowledge, no study has asked the question of how subjects estimate the duration of an unexpected interval (UI). Suppose that the UI is set so as to be twice longer than an expected short interval EI1 and twice shorter than an expected long interval EI2 = 4 × EI1 so that there is only one single UI that subjects are required to estimate (Fig. 3). This procedure allows the appraisal of two points of subjective equality, i.e. in the context of EI1 (PSE<sub>E1</sub>, blue arrow) and of EI2 (PSE<sub>E2</sub>, green arrow). Intuition suggests that PSE<sub>E1</sub> > UI and PSE<sub>E2</sub> < UI (see also Estel, 1885; Miyauchi and Nakajima, 2005). Now let's combine the two EIs in the same trial at two retinal locations. Subjects can now be asked a neutral or 'biased' question. The neutral question would just be to judge the UI. The expectation is that the hypothetical opposite sign PSE shifts to be observed in the single interval case will cancel out so that the PSE will be unbiased. The biased question would specify that the UI interval should be judged with respect to one of the two first flashes (the flash on the left side associated with EI1 in Fig. 3 or the flash on the right side associated with EI2). As in the previous paradigms (Sections 8.1 and 8.2), the two-clock hypothesis would predict in this case forward or backward PSE shifts depending on whether the question involves EI1 or EI2, respectively (as in the single interval experiment).

### 8.4. Attention modulated PeDu

All the dual-task and/or dual-stimuli paradigms above required that attention be equally distributed over the concurrent stimulations (the duration-coding phase) with the hypothesized context-induced PeDu change meant to occur during the retrospective PeDu report (or reproduction) phase. This paradigm easily translates into a Posner-like, attention modulation paradigm if one of the two concurrent stimuli (possibly coupled with an action) whose duration is to be judged is cued. As above, the standard interval bracketed by the onset of the two stimuli and the offset of one of them is to be reproduced by turning off the persistent stimulus (post-cue) that is or is not the one that has been cued (valid or invalid cue, respectively). The idea here is that the PeDu of the same global physical stimulus would differ depending on the congruence/incongruence between the attended stimulus and the post-cue.

## 9. Conclusions

Any sensory process can be regarded as a *generalized contrast* or *figure-ground* extraction operation. Be it a dot, a shape, a color, a face or a landscape, the 'figure' exists (and hence can be detected, discriminated from other figures or identified) by virtue of it standing out against a background (i.e. anything different from the



figure). The first critical point made in this review was that duration perception involves an equivalent contrast extraction process not only between the readings of the same clock over two (or more) time intervals but also between the simultaneous readings of two (or more) clocks for the same time interval, the 'figure' and the 'ground' clocks. This notion goes along with the view that the figure- and ground-clocks need not be predetermined so that any given physical interval may yield as many figure/ground contrasts as available clocks. It follows that, depending on subject's choice of the figure-clock, the same physical time interval can be experienced within the same stimulation conditions as either contracted or dilated with respect to some reference.

Comparing a figure-clock reading with the readings of the ground-clock(s) is equivalent to a normalization operation. Divisive normalization (or 'gain control'; e.g. Levitt and Lund, 1997) is a well-established notion in sensory physiology (e.g. Ohshiro et al., 2011) and in visual psychophysics (e.g. Watson and Solomon, 1997). In all such studies, the 'figure' is pre-specified and mandatory so that for the same stimulation conditions the measured 'contrast' is always the same. This has also been the case in time perception studies where subjects were presented with a one-dimensional event and asked to judge or reproduce its duration. A physical time interval can however be filled with many simultaneous external (and internal, e.g. thoughts) event streams activating as many clocks. It should then be possible to induce subjects to using one specific 'figure-clock' both during and/or after the test interval.

The last section of this article introduced a few experimental designs meant to test the proposition that, when the many clocks are materialized by different properties of a given stimulus configuration or by subjects' actions, the same time interval can be experienced differently within the same stimulation context. The proposed experimental designs were such as to induce subjects to give priority to one of these putative clocks while using the remaining clock as a reference. While such cues are likely to also operate in everyday life, the issue of how such priority comes about in the absence of any obvious cue remains to be elucidated. It is also possible that our measure of duration is based on the reading of more than one 'figure-clock'. The rules that govern their putative combination are a matter of future exploration.

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