

Rhythms for cognition: the case of temporal processing

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Time is often thought to consist of units that cycle rhythmically at different scales (seconds, hours, days, seasons).

Accordingly, many models for mechanisms of timing implement rhythmic processes as the neural and cognitive substrate of time. In recent years, neuronal as well as cognitive exploration have revealed rhythmic motifs in the mechanisms governing attention and perception. In this review, we offer a taxonomy for different rhythmic motifs for cognition and explore the utility of this taxonomy in guiding the study of temporal processes.

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Rhythmic properties in behavioral and neural responses

Rhythmic temporal structure is a recurring theme in the field of cognitive neuroscience. Rhythmic temporal structure can be observed in the properties of neural population responses (i.e., neural oscillations) as well as in behavioral manifestations of perceptual and cognitive routines (i.e., perceptual rhythms). The idea that cognition is built on rhythmic properties has gained popularity in recent years [1,2,3^{••}]. Rhythms for cognition are studied in different disciplines (systems neuroscience, psychology, cognitive sciences), covering many different topics (perception, memory, navigation, attention etc.) in vastly different measurement types (e.g., physiology, psychophysics) and species (e.g., human, non-human primate, rodents, amphibian and more).

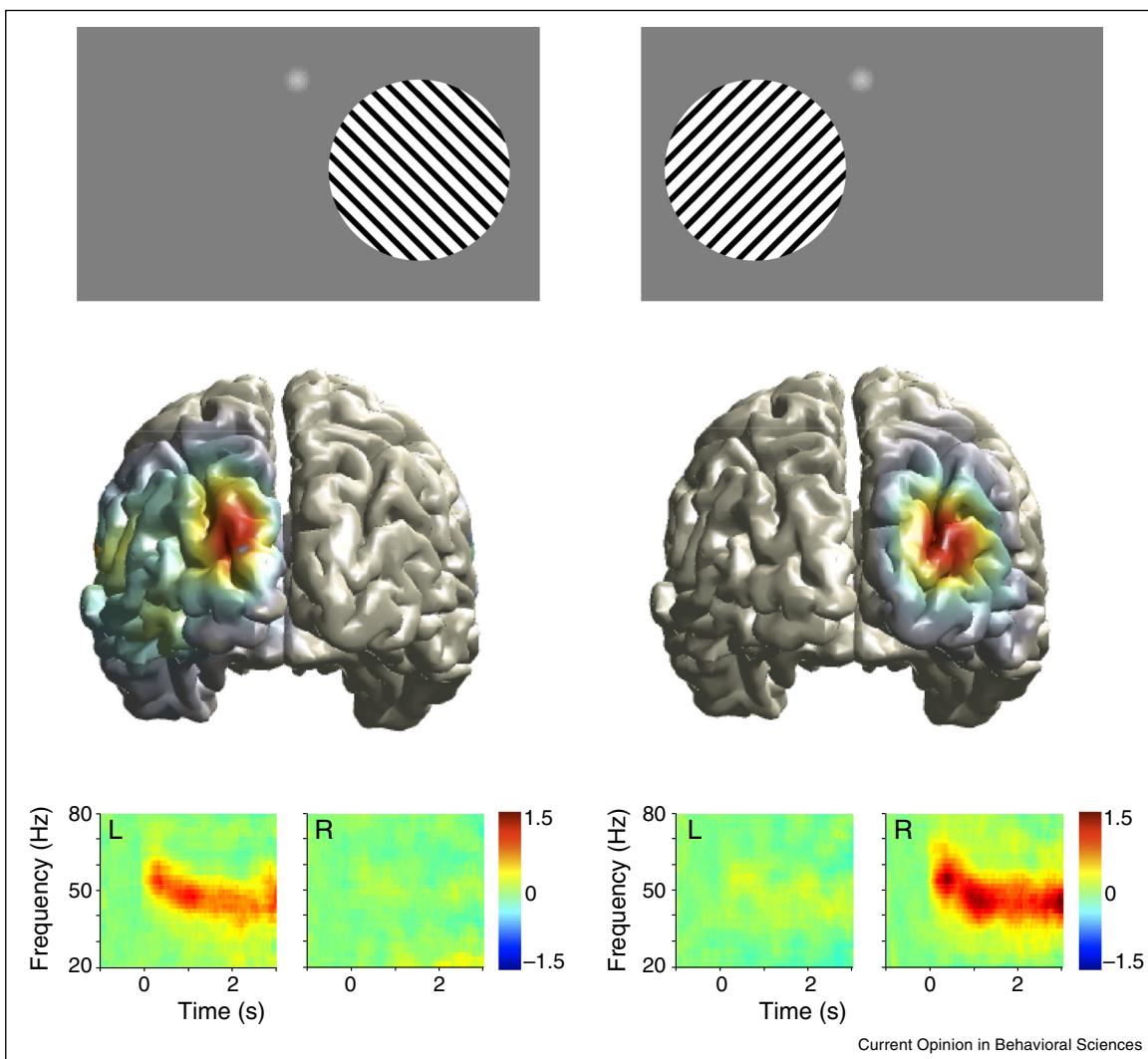
Rhythms in behavioral and neural responses entail by definition a temporal structure, and thus open an interesting possibility for inquiries on timing: could the

temporal structure of cognition be utilized as an internal substrate of time? This idea is quite attractive if one considers that our objective description and measurement of the fourth dimension incorporate cyclic processes at many different scales, as in for example, circadian rhythms. Further, as we will survey, rhythmic processes were proposed as carrying out timing in the brain long before those were associated with cognitive routines.

The goal in the present review is to examine possible links between temporal processing and current notions of rhythms in cognition. Prior to relating rhythms in cognition to temporal processing we discuss a distinction that bears utility for this and other surveys in the field. We propose that rhythms for cognition (encompassing behavioral and neural rhythms) grossly classify into two main types: spontaneous, internally generated rhythms and stimulus driven rhythms. The two types might be separate phenomena coincidentally sharing the property of temporal structure or, alternatively, they might form a single spectrum of rhythmic properties of cognition. We will exemplify each type with findings from the related fields of perception and attention and thus highlight the utility and relevance of this taxonomy.

Spontaneous rhythms

The most basic examples of internally generated or spontaneous rhythms come from studies measuring neural oscillations. For example, in the literature on sensory and perceptual processing a sustained gamma band response (>30 Hz) can be measured from neuronal populations invasively (i.e., in the Local Field Potentials) or noninvasively (using electro- or magnetoencephalography; EEG/MEG; for an example see [Figure 1](#)). A gamma band response increase can be easily elicited by presenting a stimulus to the visual system and is sustained as long as the stimulus remains visible. As a rule, the stronger the stimulus, the stronger the gamma band response. Oscillatory responses in different visual areas in the gamma band have been proposed as a mechanism for inter-areal communication through the engagement of selective synchronization [4,5[•]]. A different example for an internally generated rhythm measured mostly (but not exclusively) with non-invasive physiology (EEG/MEG) is the lateralized alpha response (~10 Hz). In this case, the difference between oscillatory responses in one hemisphere versus the other is associated with the degree of attentional deployment toward one or the other hemifield [6–9]. Functionally, the alpha band response and the lateralization measures are associated with the active suppression of unattended parts of the visual field. That is, the stronger the alpha response, the more suppressed

Figure 1

Contralateral gamma band activity to a grating stimulus measured with magnetoencephalography. Each panel (left and right) shows the stimulus (top), the source reconstruction of the oscillatory source (middle) and the time frequency plot for contra- and ipsilateral sources (bottom). The time frequency plot reveals a typical narrow band increase in activity over baseline that is sustained for the entire stimulus epoch. Additionally, as can be seen, the increase is limited to the contralateral response. The data are from an individual subject. Although different subjects might differ in the precise source location or the particular spectral signature (gamma frequency) this response in strength and in temporal profile is typical when strong stimuli are presented.

the unattended location [7°]. The gamma and alpha band responses are considered internally generated because in both cases there is no temporal structure in the stimulus presented and the rhythmic responses are sustained as long as the functionally relevant epoch lasts and thus, are interpreted as neural signatures of those cognitive functions (e.g., perception or attention).

In addition to the investigation of rhythmic neural signatures, we have witnessed a renewed interest in the temporal structure of cognitive functions themselves (i.e., rhythmic perception; rhythmic attention e.g., [10]). Till

date, behavioral rhythms have been measured in at least two ways. First, performance (e.g., detection of a faint target) was found to systematically fluctuate with the phase of a 7.1 Hz oscillation in the ongoing EEG measurement [11]. This means that within the cycles of a 7.1 Hz ongoing response (i.e., occurs before the onset of the defined target) there are worse and better moments. If a faint target, by chance, appeared during a ‘bad’ phase, it was undetected. If it appeared during the ‘good’ phase, it was more often detected. Further evidence was provided by directly measuring the unfolding of behavioral performance following a reset event. For example, Landau and

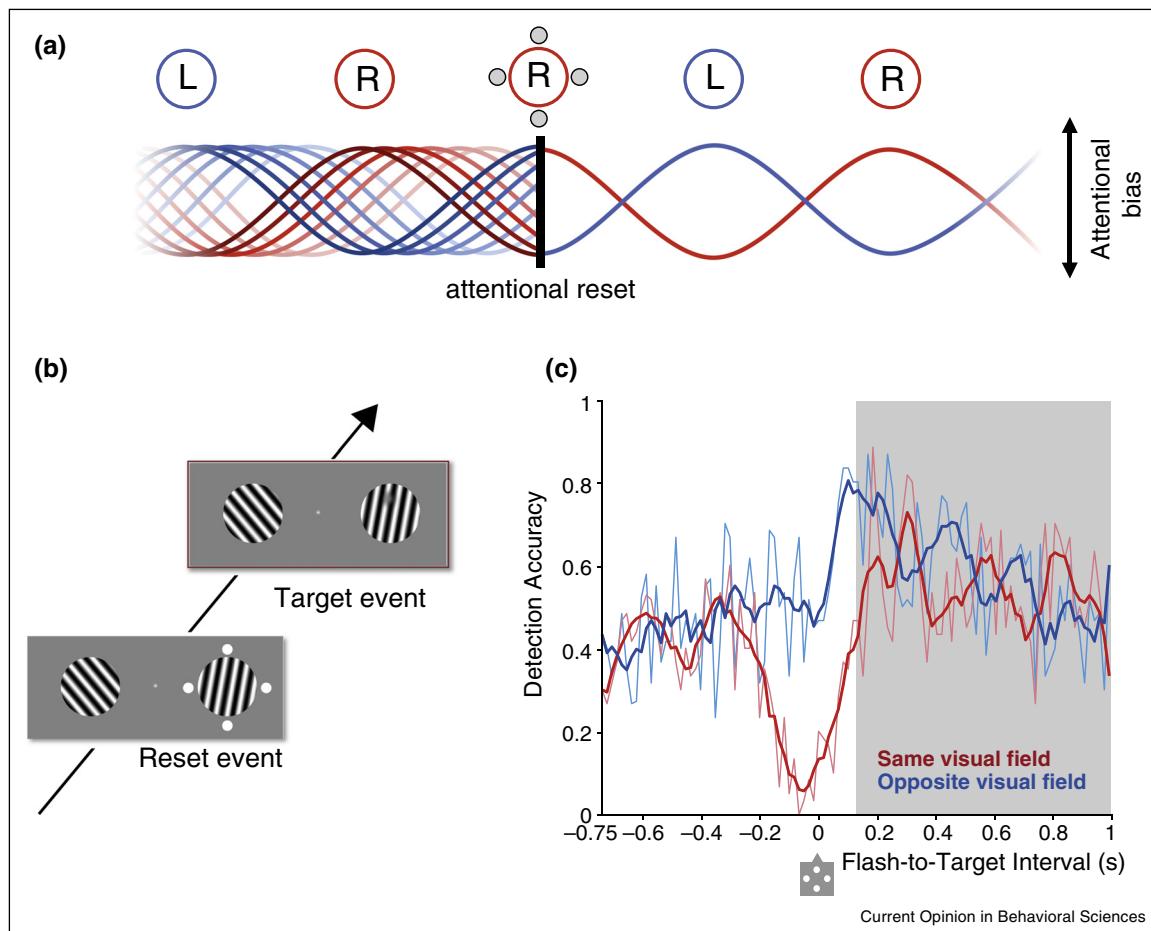
Fries [12] devised a method for measuring behavioral rhythms by the utilization of a reset event that captures attention to one of two locations. Following the reset, performance was assessed finely in time (at a 60 Hz sampling rate). When two locations are behaviorally relevant, each is sampled at 4 Hz in alternation (Figure 2; see also [13–15] for replications and elaborations of these findings). To conclude this section, the cognitive system seems to produce rhythmic temporal structures. Those are present at the neural level but also provide a structure to our perceptions and to the way processing resources (i.e., attention) are deployed.

Stimulus driven rhythms

Behavioral changes as well as neural signatures have been investigated in response to stimuli that contain a rhythmic temporal structure by design. The theoretical relevance of

behavioral and neural dynamics in response to rhythmic stimuli is motivated by the fact that the natural input to our senses is often regular. For example, language contains temporal regularity. Music and other environmental sounds often take on a rhythmic temporal structure (e.g., [16–19]). In the lab, presenting regular rhythmic stimuli produces both a brain response and behavior that follow the stimulation rhythm. That means that in the neural response one can single out a rhythmic response modulation that is at the same frequency of the presented rhythmic stimulus. This phenomenon is called neural entrainment and has been documented in different modalities [20–23]. Most recently, investigators have found an interesting link between neural entrainment and perceptual performance. Notably, both in vision and in audition, it has been found that neural entrainment is accompanied by rhythmic modulations of behavioral performance (e.g., [10,24–26]). In

Figure 2



The logic and practice of measuring behavioral fluctuations using a reset event. (a) The approach assumed that ongoing rhythms are spontaneously at different phases and therefore are difficult to measure directly in behavior. However, if the ongoing rhythms could be reset, than their phases are no longer random, that is, they are locked to the reset. In the case of distributed attention left (L) and right (R) locations a reset that captures attention to one of the locations determines where spatial attention is. From that point detection performance can be assessed in order to assess the unfolding of spatial attention. (b) Example stimuli used in [12] where this logic was applied to study distributed spatial attention. (c) Results from [12] demonstrating that a reset to one of two locations reveals rhythmic fluctuations at each location. Performance at the two locations was fluctuating in alternation.

addition, behaviorally measured enhancements due to entrainment may provide a mechanism relevant to temporal expectation (see below). Entrainment has also been found to play an interesting role in attentional selection. Besle *et al.* [27] compared entrainment to attended and unattended rhythmic stimuli. They found different delays in the tracking of attended and unattended stimuli; that is, the phase of the entrainment for attended versus unattended stimuli were significantly different. Attention to a rhythmic stimulus is therefore accompanied by selective temporal tuning of the entrained response [28,29]. At this point, it is unclear whether driving the cognitive system at an external rhythmicity harnesses the same mechanisms that are at play when the cognitive system generates its own rhythms. However, the idea of selective temporal tuning to rhythmic stimuli guided by attention provides an interesting connection between the system's sensitivity to regularity in the environment (i.e., stimulus driven) and the system's own ability to generate rhythmic temporal structure spontaneously.

Rhythmic properties of cognition and timing

Above we introduced the significance of rhythmic motives in cognition, discussing spontaneous neural oscillations and rhythmic fluctuations of behavioral performance. In the following, we will discuss whether the temporal structure inherent to these processes can be utilized as an internal substrate of time. Since this issue is dedicated to interval timing, our considerations are targeted at situations in which explicit time perception occurs. However, important new hypotheses about the involvement of rhythmic processes in explicit timing can be drawn from implicit timing situations, also termed temporal expectations.

Spontaneous rhythms as the substrate of interval timing

More than a century ago, James [30] wondered whether ‘we have a sort of special sense for pure time?’. ‘Pure time’, a pure sense of time that is divorced from the perceptual content being timed. The minimal requirement for this theoretical possibility, however, is the existence of an internal metric of time that governs mental temporal processing. Utilizing internal rhythms as a measurement for the passage of time would seem like a parsimonious account for a substrate of time. Many timing models assume an internal clock that relies on a pacemaker producing ‘tics’ that inform the subjective sense of time [31–33]. Acceleration or deceleration of the pacemaker’s rate (spontaneous or induced) should coincide with over- or underestimation of time, respectively. The pacemaker’s tics are often assumed to be temporally regular, making the pacemaker an internal oscillator. Neural oscillations may provide an implementation of these kinds of models. Evidence for the biological plausibility for an internally oscillating pacemaker comes from circadian timing, which, on a much slower rhythmic scale, is governed by oscillations emitted by the

suprachiasmatic nucleus [34]. However, to date a unique neural substrate for such a pacemaker has not been identified for timing in the range of milliseconds to seconds. Several candidate processes and structures have been proposed as manifestations of the pacemaker, including the heart rate [35], as well as neural computations carried out by the cerebellum, basal ganglia, the supplementary motor area and frontal cortical regions [36,37]. Other studies attempted to characterize the dominant frequency of an internal pacemaker reaching results ranging from approximately 5 Hz [38], over 13 Hz [39] to 50 Hz [40].

Of course, neural oscillations need not implement timing through a single pacemaker with a dominant rhythm (as already suggested by Treisman *et al.* [39]). The striatal beat frequency model (SBF) assumes multiple oscillators at different frequencies ([41–43]; see also [44]) and postulates an interplay between distributed oscillators from the (mostly frontal) cortex and thalamus. The oscillators can reset their rhythms to the onset of a relevant stimulus to achieve timing of an interval. In this model, spiny neurons located in the striatum serve as coincidence detectors for oscillatory patterns and can tune to specific patterns through adjustment of synaptic connections (see [45] for a description of the relevant biological properties of these neurons). Concerning the oscillators and their biological implementation, few studies have actually provided evidence for truly rhythmic metric of time. Matell *et al.* [46] found that neurons in rats’ striatum and anterior cingulate encode durations in their firing rate, which peaked at the expected duration. However, this signal is not strictly oscillatory, since a linear readout of firing rate at a given time point could account for the elapsed duration. Accordingly, ramping neural activity, a ubiquitous property of neurons in many brain regions, could provide the substrate of time [47], which would be better described by the metaphor of an hourglass filling with elapsed time rather than a rhythmic clock. Parker *et al.* [48••] recently provided evidence for a rhythmic metric of time, showing that dopamine-driven theta oscillations in rodents’ medial frontal cortex reset to the onset of a to be judged time interval, as proposed by the SBF (see also [49]), and that this reset is related to behavioral outcome. However, more research is needed to uncover the nature and specificity of the neural oscillators proposed by the SBF.

Other studies have provided evidence for the involvement of spontaneous neural oscillations in interval timing, without making specific assumptions about the underlying timing model. In principle, fluctuations in power of spontaneous oscillations at different frequencies could be recruited by an internal timer, to compute the organism’s own time, as proposed by the timing models above. Already in the sixties, Anliker [50] suggested that variations of the peak of alpha oscillations (7–12 Hz) relate to

interval timing, which is in line with the suggestion of Treisman *et al.* [40] of a dominant pacemaker rhythm at 12.8 Hz. More recently, Rohenkohl and Nobre [51] found that the amplitude of alpha oscillations reflected temporal expectations, but this study did not involve explicit temporal judgments. A recent study by Kononowicz *et al.* [49] suggests that the power of beta oscillations (15–30 Hz) at the onset of a to be timed interval, signals thought to originate in brain areas associated with motor processing, predicts whether the interval will be over or underestimated. The oscillating neuronal populations described in these studies do not necessarily belong to a dedicated timing system. Similar fluctuations in oscillatory power occur in the absence of a timing task and might reflect attentional or motor preparation evoked by the task at hand. How exactly the amplitude of these oscillations would be translated into a neural metric for time that codes for the accumulation of temporal information during an interval is an important open question.

Internal rhythms associated more specifically with the accumulation of temporal information might consist in slow oscillations in the delta and low theta bands (0.1–7 Hz), which could align with the relevant time intervals. As described above, Parker *et al.* [48^{**}] recently provided compelling evidence for a role of 4 Hz oscillations in interval timing, which reset their phase at the onset of a time interval. Further evidence could indirectly be drawn from the suggestion that delta and theta oscillations contribute to slow ramping brain potentials (the contingent negative variation), which in turn have been found to vary with time judgments ([52^{*},53,54], see also Kononowicz and Penney, this issue). Finally, the involvement of slow rhythms in timing functions has been described for implicit timing situations [52^{*},55,56]. Importantly, the range of durations that could be timed by slow oscillators would not have to be limited to the period of the relevant oscillations. By combining multiple slow oscillators, a temporal resolution below a single oscillator's period can be achieved such that timing results from the properties of a neuronal network [57]. Furthermore, it is conceivable that slow oscillations related to timing trigger the preparatory effects in higher frequency bands, for example, in the alpha or beta bands which have been observed in explicit and implicit timing situations [51,52^{*},58–60]. Evidence for this suggestion comes from studies examining coupling between slow and fast oscillations in relation to timing [48^{**},52^{*},55]. An important question is to what extent the slow oscillations observed in these paradigms are spontaneous, or whether they are actually induced by stimulus rhythms, even in paradigms that are not described as rhythmic per se (see also the discussion of stimulus driven rhythms below). In order to examine this question, future studies should include measurements of spontaneous neural oscillations, for example, at rest and their interaction with stimulus-induced oscillations at different frequencies.

To summarize, the idea of neural oscillations serving as a metric of time seems plausible in light of existing timing models, but as of yet, no unique substrate of a pacemaker nor a dominant frequency has been identified. It seems plausible that multiple oscillators, especially at lower frequencies, contribute to a neural metric of time. The exact properties of this metric, however, are far from being clear. For example, information may be coded in particular frequencies of oscillatory activity or in particular phases of a certain oscillation. Furthermore, as complex as the code may be, decades of psychophysics and phenomenology illustrate that a timing model has to integrate the neural metric(s) of time toward a binary time judgment ('this interval was long/short'). The striatal beat frequency theory provides one plausible suggestion for how that integration might be achieved.

Stimulus driven rhythms – do they drive or distort temporal processing?

As described earlier, rhythmic properties of external stimulation are encoded automatically by the human cognitive system, for example, by adjustment of frequency and phase of neural oscillations to follow the stimulus rhythm [54]. In addition, the frequency of the entrained neural oscillations modulates behavioral performance, although evidence diverges as to whether events that occur in phase or in anti-phase with the stimulus rhythm are processed more efficiently [24,61–64]. For instance, Mathewson *et al.* [63,64] demonstrated that visual awareness for a masked stimulus is improved if the stimulus is in phase with a preceding rhythmic sequence. Here, stimuli were presented at approximately 12 Hz and the phase of an entrained oscillation at the same frequency at the moment of stimulus presentation predicted whether it would be perceived or not. Modulation of performance by the temporal structure of preceding input can be explained within the framework of temporal expectations [65]. Knowing *when* relevant input will occur allows the cognitive system to prepare and thus process the input more efficiently. As shown by the above example, temporal structures in the environment are automatically extracted and used to create temporal expectations about future stimuli.

Neural oscillations seem to provide the substrate for stimulus driven temporal expectations, especially in rhythmic paradigms and can occur, in principle, at any frequency. Several studies have reported temporal expectations to be reflected in stimulus driven oscillations in the delta (0.1–4 Hz) and theta (4–7 Hz) bands [56,66–68], particularly in their phase. For example, Wilsch *et al.* [56] demonstrated that enhanced delta phase coherence reflects enhanced temporal expectations with elapsed time. If the phase of entrained stimulus oscillations provides a metric of time used to encode temporal expectations this metric could also be used by the models described above (e.g., the SBF model) to produce explicit

judgments of time. To date, very few studies have addressed whether temporal expectations and interval timing rely on the same mechanisms, but the representations of time might overlap at least partially [69]. The idea that the phase of stimulus driven neural oscillations also provides a code for more explicit forms of timing seems promising in light of a recent study by Kösem *et al.* [70], who showed that shifts in subjective time (leading to perceived simultaneity of auditory and visual stimuli) directly relate to shifts in the phase of entrained delta oscillations from auditory cortex. However, future research should examine the dependence on stimulus modality and frequency specificity at which these effects occur, because in principle, entrainment effects can be created at higher frequencies, for example, in the alpha band [63].

Effects of stimulus rhythms on interval timing have been studied extensively from a somewhat different angle. As we know from experience, our perception of time is tightly coupled to the perceptual content of the respective time interval and can diverge considerably from objectively elapsed time. Numerous studies have provided empirical confirmation for this phenomenon [71–74]. Many of these studies were motivated by the idea that the perception of change during a time interval provides the basis for perceived duration [75]. These seminal notions have even led to the suggestion that perceived duration could be computed from processing of sensory stimulus change [76–78]. Change in this respect can imply any dynamic aspect of the content of a time interval, including changes in intensity, number, or displacement across space. Although James, Fraisse, and others who describe change as a dominant factor in the encoding of time have not necessarily realized change as *rhythmic* change – studies investigating the impact of externally presented rhythmic stimuli inevitably form a continuation of these ideas.

An influential study in this respect by Kanai *et al.* [72] quantified ‘change’ emitted by the environment by using visual flicker and showed that time judgments, measured in a reproduction task, increase with flicker frequency (see [78,79] for related approaches). In order to study this phenomenon and examine the neural dynamics accompanying it, Herbst *et al.* [80] measured the entrained response to the sensory temporal structure using EEG. Perceived duration in a temporal comparison task was not accounted for by the amplitude of the entrained neural oscillations (i.e., the degree to which the visual system tracked the stimulus) but rather correlated with the subjective rating of the stimuli as flickering versus steady. These findings suggest that higher level processes leading to the subjective perception of the flicker, rather than low level sensory properties, at least as they were measured in this study, inform temporal judgments. The assumption that the amount of change (operationalized

as flicker frequency) informs temporal judgments is further challenged by the results of a follow up study by Herbst *et al.* [81], in which the influence of flicker on temporal judgments was investigated in a temporal bisection task.

To conclude, the mechanism by which stimulus rhythms provide the substrate of time may not be direct or simple. Different factors might contribute to flicker-induced time dilation, such as frequency range used, timing task type (e.g., reproduction, comparison, or bisection) and display parameters. The cascade of processes that are involved in forming temporal judgments make it difficult to disentangle the exact influences of external rhythms on temporal processing. Nevertheless, the influence of stimulus flicker on temporal processing offers an excellent test case for timing models.

Rather than assuming that the sensory processing of changes provides a substrate for timing, one could assume that an internal rhythm could be speeded up or slowed down by adjusting its frequency and/or phase to an externally presented rhythm (see [82] for a detailed explanation of entrainment mechanisms in timing models). Penton-Voak *et al.* [83] showed that click trains presented prior to a time interval increase perceived duration, and explained their findings as the result of an entrained (or sped up) pacemaker. Wiener *et al.* [84] demonstrated that repetitive TMS stimulation over the right supramarginal gyrus increased perceived duration of visual stimuli. Importantly, in these studies the click trains or rTMS were presented before the relevant time interval. Thus the duration dilation cannot be explained as an influence of the interval’s content. As outlined in the previous section, however, the biological implementation of a pacemaker is unclear and thus the ‘speeding up of the clock’ assumption remains on the theoretical level.

If one assumes multiple oscillators, there are of course plenty of possibilities for entrainment effects that might result in rather complex patterns. In a recent paper, Hashimoto *et al.* [85] showed that flicker-induced time dilation in a temporal discrimination task depends on the peak *and* the distribution of frequency, and can be integrated by the striatal beat frequency model (described above), assuming multiple oscillators entrained differentially by the frequencies of the flicker.

Combining the research on influences of stimulus driven rhythms on timing with sensitive neural measurements of neural rhythms might form an avenue toward illuminating the relevance and potential of rhythms of cognition for temporal processing.

Discussion and future directions

At the outset of this review we offered a distinction between internally generated rhythms and externally

driving rhythms. This distinction provided an opportunity to shortly survey the type of physiological models that inspire the cognitive neuroscience of perception and attention, cognitive functions that are tightly linked to temporal processing. As we survey the literature on timing, a slightly less cohesive picture emerges. Presently, theoretical attempts that postulate a single rhythmic pacemaker lack sufficient supporting evidence. On the other hand, rhythmic signatures that play a role in temporal processing are subject to critique for potentially being evidence for cognitive functions that are not purely temporal processing. It seems likely that there is no unique substrate of time, like a clock ticking at a defined rate. Instead, timing may be achieved by a flexible system that can recruit rhythmic input from both internal and external sources and combines these to an overt estimate of time if needed. Looking into the future, there seems to be room for more comprehensive models exploring rhythmic properties of cognition. Although these attempts are as old as the field of psychology, current notions of such rhythmic properties may inspire new ways to probe the promise of unraveling a neural code which in itself presents a temporal structure. Finally, the degree to which spontaneous internally generated rhythms and externally driven rhythms tap into the same processes or even better engage in a mechanistic interplay may also inform questions of how rhythmic properties might be utilized in temporal processing.

Conflict of interest statement

Nothing declared.

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