

Frequency tuning for temporal perception and prediction

Martin Wiener¹ and Ryota Kanai^{2,3,4}



The perception of time and prediction of upcoming events requires coordination between a diverse set of neural regions. Neural oscillations have emerged as a candidate mechanism for neural timing; however, no single frequency has yet emerged as dominant for timing and action. We suggest that different frequency bands may be associated with different neural networks that are context-dependent, such that they are only invoked when a particular task context is encountered. To determine the connection between observed oscillations and these neural networks, causal methods are necessary to disrupt oscillatory activity and measure resultant changes in neural network activity.

Addresses

¹ Department of Psychology, George Mason University, United States

² School of Psychology, University of Sussex, United Kingdom

³ Institute of Cognitive Neuroscience, University College London, United Kingdom

⁴ Department of Neuroinformatics, Araya Brain Imaging, Tokyo, Japan

Corresponding authors: Wiener, Martin (mwiener@gmu.edu) and Kanai, Ryota (kanair@gmail.com)

Current Opinion in Behavioral Sciences 2016, 8:1–6

This review comes from a themed issue on **Time in perception and action**

Edited by **Warren H Meck** and **Richard B Ivry**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 11th January 2016

<http://dx.doi.org/10.1016/j.cobeha.2016.01.001>

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Introduction

The perception of time is one of the hallmarks of consciousness. However, the generation of this ability remains a relatively understudied phenomenon in psychology and neuroscience. Recent trends are now starting to elucidate core elements of neural timing networks, revealing a series of coordinated networks that are flexibly engaged across different timing contexts [1,26]. How these networks communicate with one another and coordinate their activity for perceiving temporal intervals and engaging in temporally precise actions is currently a mystery. In this regard, recent research has turned to the study of oscillatory dynamics as a unifying principle for timing networks in the brain. This trend is not new — oscillations and timing have been linked as far back as

50 years ago and beyond [2] — but previously there was little idea of the constellation of neural regions involved in timing, whereas now researchers can link neural regions supporting timing behavior with the computations potentially being conducted within them.

A neural oscillator or pacemaker is one of the core mechanisms thought to underlie timing and time perception ([3,4]; but see [5]). However, the question remains: what oscillations are important for timing? As yet, there has not been a systematic survey of the different frequency bands involved in temporal processing. The past twenty years of human research into temporal processing mechanisms have focused either on broadband EEG signals (event-related potentials), or on spatial representations via fMRI. The lack of a focus on neural oscillations during this time is somewhat puzzling; if we are to study how time is represented in the brain, then shouldn't we examine those indices of temporal organization? However, the last five years has seen renewed interest in neural oscillations and their role in time perception. This increase has largely been driven by studies investigating predictive mechanisms in the brain [6–8,9**,10,11]. Indeed, recent research suggests that one of the primary functions of the brain is to form predictions, and that the brain is organized along a series of temporal hierarchies of organization, by which incoming sensory signals are parsed and processed [12]. Further research has shown that, when a stimulus fulfills a temporal prediction, the perception of that stimulus is improved [59], an effect that has been related to the phase of delta oscillations [13**]. Additional work has shown that human behavior can adapt itself to the dominant signal duration, such that stimuli occurring at an expected rate are better perceived than those at an unexpected one, regardless of the difference [14**]. Such findings have their roots in Dynamic Attending Theory [15], which posits that attention to events may be allocated ('tuned') in time via the entrainment of endogenous oscillators, such that attention is maximal at the peak of the entrained frequency band.

On the other hand, many models of timing do not employ an oscillatory dynamic for measuring time (see [4,16] for review). Examples of some non-oscillatory mechanisms include state-dependent dynamics, in which the multidimensional trajectory of firing rates in networks of neurons can encode duration [5], memory decay models [17,18], in which the decay rate of a memory representation tracks elapsed time, change detection models, in which timing is accomplished by measuring external changes in the

environment [19,20], as well as delay-line and population coding models, where the tuning properties or connection rates of individual neurons lead to population level estimates of perceived duration [21,22]. However, in all of these cases, it should be noted that, while the computation for measuring elapsed time at the cognitive or neural level is not oscillatory in nature, this does not mean that the *output* of the model, as measured at the macroscale, is necessarily not oscillatory. Indeed, observed oscillations during timing behaviors could reflect either the direct computation or the byproduct of its occurrence, a point we return to below.

Temporal context and frequency tuning

Despite the increase in research focusing on oscillatory mechanisms in timing and prediction, no frequency band has yet emerged as dominant for temporal processing and time perception (see Table 1). Instead, nearly every frequency band has been associated with temporal processing at some level. While the diversity of oscillation frequencies implicated in time perception may appear surprising, it mirrors emerging findings over the past ten years demonstrating that temporal processing networks are context specific. That is, different neural networks are likely to be invoked, depending on the temporal features of the task being completed [23–25]. In this case, such

features may relate to the explicit or implicit nature of the timing task, whether the intervals tested are sub or supra-second, require a timed output of the motor system — so-called ‘motor’ timing, or are based in a psychophysics paradigm — so-called ‘perceptual’ timing. This evidence has suggested that timing in the brain is an adaptive process, by which networks are flexibly engaged by means of their appropriateness to the task at hand [26]. In this regard, one would not expect a single frequency band to dominate all of temporal processing, just as one might not expect a single brain region to mediate all forms of time in the brain. Indeed, a particular frequency band might be invoked during a particular timing task context, but not others, as that oscillation is the optimal one in that context for measuring and predicting intervals of time [27]. In concordance with this, numerous studies of attention and timing have shown neural entrainment effects in response to exogenous rhythms [9^{**},27,28^{*},29–31]. This work has demonstrated that, when a rhythmic stimulus is presented, neural oscillations will become entrained to that rhythm, such that the alignment of phase enhances perceptual responses to rhythmically embedded stimuli. Many of these studies have presented stimuli at relatively low frequencies, which have led to entrained oscillations in the delta band. This finding does not mean that delta oscillations are

Table 1

Studies investigating neural oscillations and timing mechanisms, divided into commonly studied frequency bands. The parameter column indicates which particular feature of the oscillation was related to the task or function column. We here dissociate prediction tasks from timing tasks, in accordance with the distinction of Coull and Nobre [25], where prediction does not require subjects to pay direct attention to the passage of time per se. This list is meant to be merely representative, but not exhaustive, and does not include the many recent studies on rhythmic entrainment.

Frequency	Authors	Parameter	Task/function
Delta	[13 ^{**}]	Phase	Visual prediction
	[64 [*]]	Coupled with beta	Auditory prediction
Theta	[68]	Phase	Sub/supra auditory prediction
	[69]	Power/coupled with beta	Suprasecond visual prediction
	[70 ^{**}]	Power	Suprasecond visual motor timing
Alpha	[79]	Power	Suprasecond visual prediction
	[71]	Power	Sub/supra visual prediction
	[72]	Power	Suprasecond visual prediction
	[65]	Power	Subsecond visual perceptual timing
	[73]	Power	Sub/supra visual prediction
	[64 [*]]	Power	Auditory timing update
	[74]	Power	Suprasecond intermodal prediction
	[66]	Phase	Subsecond intermodal perceptual timing
	[75]	Phase	Sub/supra visual prediction
	Beta	[72]	Power
[49]		Power	Entrainment with isochronous rhythm
[76 [*]]		Power	Sub/supra auditory perceptual timing
[42]		Power	Entrainment with isochronous rhythm
[47]		Power	Subsecond auditory motor timing (continuation)
[64 [*]]		Coupled with delta	Auditory Prediction
[77]		Power	Subsecond auditory motor timing
[70 ^{**}]		Power	Suprasecond visual motor timing
Gamma	[78]	Power	Subsecond auditory perceptual timing
	[49]	Power	Prediction and violation of beat
	[67]	Power	Preparation for subsecond visual perceptual timing
	[47]	Power	Subsecond auditory motor timing (synchronization)

crucial for temporal predictions per se, but that they are the most appropriate or optimal for forming predictions about the timing in that context.

One of the primary functions of neural oscillations, it is presumed, is to coordinate activity within and between neural circuits [6,32–34]. Here, the connection with context-specific timing networks suggests that different frequency bands should correspond with different timing networks. Experimental evidence has suggested that different neural regions naturally resonate at particular frequency bands [35,36]. This organization has been suggested to lie along a rostral–caudal gradient, with frontal areas naturally oscillating at higher, gamma band frequencies, and progressively slower oscillations toward the occipital lobe. Yet, this likely belies the complexity of neural circuitry, as both high and low frequency oscillations have been found within neural circuits across all levels of the brain, including occipital cortex [32,33]. Regardless, at the macroscale level, one might expect a particular network of regions invoked during a timing task to oscillate at a particular frequency, depending on the direction of influence (top-down vs. bottom-up) and the nature of the task. Furthermore, high frequency oscillations, which may not be appropriate for longer-range communication between neural regions, may be ‘nested’ within slower frequency ranges [9**].

Notably, the concept of a broad array of oscillations in time perception has been suggested previously, as a core tenet of the Striatal Beat Frequency model of timing (SBF; [37,38]). According to this model, the basal ganglia act as a coincidence detector of oscillating cortical input, such that intervals are learned by marking the phase relation among oscillators at the start and stop points of particular intervals of time. Crucially, SBF does not presume dominance of one particular frequency band, but rather broadband coincidence detection can be achieved with a sufficiently large and diverse number of oscillators, operating at different frequencies and phases. Yet, while the SBF model presumes frequency independence, the appropriateness of a particular set of oscillators may still be a factor. In this regard, beta oscillations are of particular interest. Beta oscillations have traditionally been associated with motor functions [39], although they may be less well understood than oscillations in other frequency bands [40]. Recent research has implicated beta oscillations in numerous non-motor functions, such as perceptual decision-making [41,42] and local visual feature processing [43*]. Yet, this does not preclude the involvement of the motor system in non-motor functions. Indeed, beta oscillations are thought to coordinate activity between the supplementary motor area (SMA), basal ganglia, and thalamus during timing behavior. Notably, the SMA and parts of the basal ganglia are the most commonly activated areas across neuroimaging studies of time perception, suggesting that they form part of a core, supramodal network for timing in

the brain [1,23,24]. This connection may indicate that beta oscillations are particularly important for temporal processing. Yet, the case remains that beta oscillations are not observed during all timing tasks; furthermore, lesions of the basal ganglia in humans do not produce gross timing deficits, with the exception of timed tapping tasks in some cases [44,45,60], during which beta oscillations have mostly been associated [46,47]. This finding suggests that redundancies exist amongst oscillations and time perception, as they likely do with different networks [26]. If a particular frequency band or network is lost, a second one may become available to overcome the loss and prevent a behavioral deficit. One hypothetical way to test this would be to disrupt a particular neural region or set of regions during a timing task, and see if a different frequency band is now invoked.

Causal inferences from neural oscillations

But how can we know if any of these oscillations are causally linked to temporal perception? That is, as stated above, do the oscillations observed in any of these tasks reflect an actual computation, or an epiphenomenal feature? For example, the entrainment of slow oscillation (e.g. delta or alpha) to predicted events could simply reflect consequences of fine temporal adjustments of sensitivity to upcoming sensory events [48]. As such, they may not be directly involved in computation of durations, whereas other frequencies may play a more direct role in the computation and/or experience of time. In order to test this relationship, stimulation techniques are necessary. In animals, microstimulation via implanted electrodes may be an option, but in humans current methods are indirect. Two tools are readily available. Transcranial Magnetic Stimulation (TMS) is a disruptive technique whereby magnetic fields generated close to the scalp induce an orthogonal electrical field within superficial layers of the cortex. Recent work has demonstrated that high-frequency TMS, whereby TMS is rhythmically administered in a ‘burst’ of pulses, can induce frequency-specific oscillations in a particular neural region [49]. Moreover, the effects of TMS can be frequency-dependent, depending on the region stimulated and the task being engaged, and when compared to TMS administered at a control frequency or with random timing [50,51]. Moreover, the effect of rhythmic stimulation can be thought of as affecting a particular network of regions connected to the stimulated ‘hub’, that will depend on both the frequency that network oscillates at and the connective strength of that network [61]. Under this framework, Rhythmic-TMS studies provide a precise tool for testing if a particular region and frequency band are involved in a particular function. The use of TMS in studies of time perception has been reviewed elsewhere [52], but it is noteworthy that no studies have yet used this technique to test the involvement of a particular frequency band in time perception. There are, however, some interesting hints. High-frequency TMS has been used previously in studies of time perception, most notably to

stimulate regions of the cerebellum, parietal, and prefrontal cortex (reviewed in [52]). To date, these studies have all used stimulation in the alpha or beta frequency range (10 or 20 Hz). For example, stimulation of the right supramarginal gyrus at 10 Hz leads to increases in perceived duration [23,24], whereas stimulation of the right dorsolateral prefrontal cortex at 20 Hz leads to decreases in duration reproduction [53]. The question thus remains whether the effects found in these studies are specific to the frequency ranges that were stimulated, or if stimulation at higher or lower frequency ranges would induce similar findings.

A second tool for altering neural oscillations is transcranial alternating-current stimulation (tACS) [54,55]. Although employed less often than direct current stimulation, tACS is gaining prominence as a means for causally testing neural oscillations [56]. Although tACS does not have the fine spatial or temporal resolution as rhythmic TMS, it is an easier and potentially safer technique to administer to humans, and can cover a wider area of tissue. Furthermore, both tACS and Rhythmic-TMS may be administered simultaneously with EEG, allowing a powerful measure of oscillatory function in response to induced changes. Additional applications can link tACS and TMS together with ongoing EEG fluctuations, such that stimulation can occur at a precise point in the phase of an oscillation, or in anti-phase to an ongoing oscillation [57*].

Finally, independent of these tools for manipulating function, it must of course be recognized that exogenous entrainment to a flickering visual or rhythmic auditory stimulus is sufficient to induce oscillations, as mentioned previously. Indeed, early studies of temporal perception and oscillatory activity suggested that entrainment to rhythmic stimuli at frequency bands could be used to probe the internal timekeeping system, by measuring the rebound from entrainment. However, this work concluded that no single frequency band dominated the spectrum for timing behavior [62]. Still, a long-standing observation in studies of time perception is that the presentation of click-trains or flickering stimuli can dilate the perception of temporal intervals [58]. As yet, no study has employed this method during EEG to examine oscillatory activity during temporal dilation (but see [63]).

Summary

There has been renewed interest in the past ten years in temporal perception and prediction mechanisms. Part of this interest comes from recent trends for a better understanding of dynamic mechanisms in the brain, which necessarily entails a better understanding of temporal processes, while another part comes from an increase in interest in predictive mechanisms [8,11]. Researchers are now afforded with a great prospect for examining how neural circuits and regions coordinate their activity during temporal perception and action. We here suggest that

oscillations are a key to understanding these computations, which may be context specific, and will require causal manipulations to better understand their function.

Conflict of interest

Nothing declared.

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