

# Frequency tuning for temporal perception and prediction

Martin Wiener<sup>1</sup> and Ryota Kanai<sup>2,3,4</sup>



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

<sup>1</sup> Department of Psychology, George Mason University, United States

<sup>2</sup> School of Psychology, University of Sussex, United Kingdom

<sup>3</sup> Institute of Cognitive Neuroscience, University College London, United Kingdom

<sup>4</sup> Department of Neuroinformatics, Araya Brain Imaging, Tokyo, Japan

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

2352-1546/© 2016 Elsevier Ltd. All rights reserved.

## 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<sup>\*\*</sup>,27,28<sup>\*</sup>,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 <sup>**</sup> ]	Phase	Visual prediction
	[64 <sup>*</sup> ]	Coupled with beta	Auditory prediction
Theta	[68]	Phase	Sub/supra auditory prediction
	[69]	Power/coupled with beta	Suprasecond visual prediction
	[70 <sup>**</sup> ]	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 <sup>*</sup> ]	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 <sup>*</sup> ]		Power	Sub/supra auditory perceptual timing
[42]		Power	Entrainment with isochronous rhythm
[47]		Power	Subsecond auditory motor timing (continuation)
[64 <sup>*</sup> ]		Coupled with delta	Auditory Prediction
[77]		Power	Subsecond auditory motor timing
[70 <sup>**</sup> ]		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.

## References

1. Merchant H, Harrington DL, Meck WH: **Neural basis of the perception and estimation of time.** *Annu Rev Neurosci* 2013, **36**:313-336.
2. Anliker J: **Variations in alpha voltage of the electroencephalogram and time perception.** *Science* 1963, **140**:1307-1309.
3. Allman MJ, Teki S, Griffiths TD, Meck WH: **Properties of the internal clock: first- and second-order principles of subjective time.** *Annu Rev Psychol* 2014, **65**:743-771.
4. Matell MS, Meck WH: **Neuropsychological mechanisms of interval timing behavior.** *Bioessays* 2000, **22**:94-103.
5. Goel A, Buonomano DV: **Timing as an intrinsic property of neural networks: evidence from in vivo and in vitro experiments.** *Philos Trans R Soc Lond B Biol Sci* 2014, **369**:20120460.
6. Bastos AM, Usrey WM, Adams RA, Mangun GR, Fries P, Friston KJ: **Canonical microcircuits for predictive coding.** *Neuron* 2012, **76**:695-711.
7. Calderone DJ, Lakatos P, Butler PD, Castellanos FX: **Entrainment of neural oscillations as a modifiable substrate of attention.** *Trends Cogn Sci* 2014, **18**:300-309.
8. Kanai R, Komura Y, Shipp S, Friston K: **Cerebral hierarchies: predictive processing, precision and the pulvinar.** *Philos Trans R Soc Lond B Biol Sci* 2015, **370**.
9. Lakatos P, Karmos G, Mehta AD, Ulbert I, Schroeder CE: **Entrainment of neuronal oscillations as a mechanism of attentional selection.** *Science* 2008, **320**:110-113.
- Study demonstrating that delta-band oscillations could entrain to rhythmically presented stimuli and increase attentional gain. Also demonstrates that these low-frequency oscillations can nest higher-frequency waves that are also involved, suggesting that a multitude of frequency bands may act in concert during rhythmic attention.
10. Arnal LH, Giraud AL: **Cortical oscillations and sensory predictions.** *Trends Cogn Sci* 2012, **16**:390-398.
11. Friston K: **The free-energy principle: a unified brain theory?** *Nat Rev Neurosci* 2010, **11**:127-138.
12. Kiebel SJ, Daunizeau J, Friston KJ: **A hierarchy of time-scales and the brain.** *PLoS Comput Biol* 2008, **4**:e1000209.
13. Cravo AM, Rohenkohl G, Wyart V, Nobre AC: **Temporal expectation enhances contrast sensitivity by phase entrainment of low-frequency oscillations in visual cortex.** *J Neurosci* 2013, **33**:4002-4010.
- A follow up to [59], demonstrating that perceptual responses to rhythmically presented stimuli are enhanced, and that this enhancement may be driven by a phase-resetting mechanism in delta oscillations. Further suggests that this phase-entrainment improves the signal-to-noise ratio for perceptual stimuli.
14. Ossmy O, Moran R, Pfeiffer T, Tsetsos K, Usher M, Donner TH: **The timescale of perceptual evidence integration can be adapted to the environment.** *Curr Biol* 2013, **23**:981-986.
- Behavioral study demonstrating that human subjects can adapt to the dominant duration of presented signals. Reveals that, when searching for a temporally variable signal within noise, responses are biased towards those signals clustered around a particular duration.
15. Jones MR, Boltz M: **Dynamic attending and responses to time.** *Psychol Rev* 1989, **96**:459-491.

16. Hass J, Durstewitz D: **Neurocomputational models of time perception.** *Adv Exp Med Biol* 2014, **829**:49-71.
17. Staddon JE, Higa JJ: **Time and memory: towards a pacemaker-free theory of interval timing.** *J Exp Anal Behav* 1999, **71**: 215-251.
18. French RM, Addyman C, Mareschal D, Thomas E: **Unifying prospective and retrospective interval-time estimation: a fading-gaussian activation-based model of interval-timing.** *Proc Soc Behav Sci* 2014, **126**:141-150.
19. Ahrens MB, Sahani M: **Observers exploit stochastic models of sensory change to help judge the passage of time.** *Curr Biol* 2011, **21**:200-206.
20. Killeen PR, Fetterman JG: **A behavioral theory of timing.** *Psychol Rev* 1988, **95**:274-295.
21. Ivry RB: **The representation of temporal information in perception and motor control.** *Curr Opin Neurobiol* 1996, **6**: 851-857.
22. Mello GB, Soares S, Paton JJ: **A scalable population code for time in the striatum.** *Curr Biol* 2015, **25**:1113-1122.
23. Wiener M, Turkeltaub PE, Coslett HB: **The Image of Time: a voxel-wise meta-analysis.** *Neuroimage* 2010, **49**:1728-1740.
24. Wiener M, Hamilton R, Turkeltaub P, Matell MS, Coslett HB: **Fast forward: supramarginal gyrus stimulation alters time measurement.** *J Cogn Neurosci* 2010, **22**:23-31.
25. Coull J, Nobre A: **Dissociating explicit timing from temporal expectation with fMRI.** *Curr Opin Neurobiol* 2008, **18**:137-144.
26. Wiener M, Matell MS, Coslett HB: **Multiple mechanisms for temporal processing.** *Front Integr Neurosci* 2011, **5**:31.
27. Henry MJ, Oblesser J: **Frequency modulation entrains slow neural oscillations and optimizes human listening behavior.** *Proc Natl Acad Sci U S A* 2012, **109**:20095-20100.
28. Kösem A, Gramfort A, van Wassenhove V: **Encoding of event timing in the phase of neural oscillations.** *Neuroimage* 2014, **92**:274-284.
- MEG study demonstrating that with entrainment to an exogenous rhythm, the shift in timing of stimuli related to that signal can be measured neurally by phase-locked responses. Notably, the presented signal was 1-Hz, suggesting that the brain can exploit a 1-Hz oscillation for temporal prediction.
29. Besle J, Schevon CA, Mehta AD, Lakatos P, Goodman RR, McKhann GM, Emerson RG, Schroeder CE: **Tuning of the human neocortex to the temporal dynamics of attended events.** *J Neurosci* 2011, **31**:3176-3185.
30. Sumbre G, Muto A, Baier H, Poo MM: **Entrained rhythmic activities of neuronal ensembles as perceptual memory of time interval.** *Nature* 2008, **456**:102-106.
31. Nozaradan S, Peretz I, Missal M, Mouraux A: **Tagging the neuronal entrainment to beat and meter.** *J Neurosci* 2011, **31**:10234-10240.
32. Van Kerkoerle T, Self MW, Dagnino B, Gariel-Mathis MA, Poort J, van der Togt C, Roelfsema PR: **Alpha and gamma oscillations characterize feedback and feedforward processing in monkey visual cortex.** *Proc Natl Acad Sci U S A* 2014, **111**:14332-14341.
33. Bosman CA, Schoffelen JM, Brunet N, Oostenveld R, Bastos M, Womelsdorf T, Rubehn B, Stieglitz T, De Weerd P, Fries P: **Attentional stimulus selection through selective synchronization between monkey visual areas.** *Neuron* 2012, **75**:875-888.
34. Sacchet MD, LaPlante RA, Wan Q, Pritchett DL, Lee AK, Hamalainen M, Moore CI, Kerr CE, Jones SR: **Attention drives synchronization of alpha and beta rhythms between right inferior frontal and primary sensory neocortex.** *J Neurosci* 2015, **35**:2074-2082.
35. Rosanova M, Casali A, Bellina V, Resta F, Mariotti M, Massimini M: **Natural frequencies of human corticothalamic circuits.** *J Neurosci* 2009, **29**:7679-7685.
- TMS-EEG study demonstrating that distinct cortical areas produce natural oscillations at different, dominant frequencies. By perturbing resting activity with TMS, global oscillatory activity that reacted could be determined as the brain returned to rest. Demonstrates a rostro-caudal gradient with frequency, such that higher frequency oscillations are located in progressively 'higher' cortical regions.
36. Groppe DM, Bickel S, Keller CJ, Jain SK, Hwang ST, Harden C, Mehta AD: **Dominant frequencies of resting human brain activity as measured by the electrocorticogram.** *Neuroimage* 2013, **79**:223-233.
37. Matell MS, Meck WH: **Cortico-striatal circuits and interval timing: coincidence detection of oscillatory processes.** *Cogn Brain Res* 2004, **21**:139-170 <http://dx.doi.org/10.1016/j.cogbrainres.2004.06.012>.
38. Gu BM, van Rijn H, Meck WH: **Oscillatory multiplexing of neural population codes for interval timing and working memory.** *Neurosci Biobehav Rev* 2015, **48**:160-185.
39. Baker SN: **Oscillatory interactions between sensorimotor cortex and the periphery.** *Curr Opin Neurobiol* 2007, **17**:649-655.
40. Engel AK, Fries P: **Beta-band oscillations – signaling the status quo?** *Curr Opin Neurobiol* 2010, **20**:156-165.
41. Haegens S, Nacher V, Hernandez A, Luna R, Jensen O *et al.*: **Beta oscillations in the monkey sensorimotor network reflect somatosensory decision making.** *Proc Natl Acad Sci U S A* 2011, **108**:10707-10713.
42. Fujioka T, Trainor LJ, Large EW, Ross B: **Internalized timing of isochronous sounds is represented in neuromagnetic beta oscillations.** *J Neurosci* 2012, **32**:1791-1802.
43. Romei V, Driver J, Schyns PG, Thut G: **Rhythmic TMS over parietal cortex links distinct brain frequencies to global versus local visual processing.** *Curr Biol* 2011, **21**:334-337.
- Demonstration of Rhythmic TMS, showing that bursts administered at different frequency bands (theta or beta) to the right parietal cortex can induce different behavioral changes.
44. Aparicio P, Diedrichsen J, Ivry RB: **Effects of focal basal ganglia lesions on timing and force control.** *Brain Cogn* 2005, **58**:62-74.
45. Shin JC, Aparicio P, Ivry RB: **Multidimensional sequence learning in patients with focal basal ganglia lesions.** *Brain Cogn* 2005, **58**:75-83.
46. Fujioka T, Trainor LJ, Large EW, Ross B: **Beta and gamma rhythms in human auditory cortex during musical beat processing.** *Ann NY Acad Sci* 2009, **1169**:1189-1192.
47. Bartolo R, Prado L, Merchant H: **Information processing in the primate basal ganglia during sensory-guided and internally driven rhythmic tapping.** *J Neurosci* 2014, **34**:3910-3923.
48. Schroeder CE, Lakatos P: **Low frequency neuronal oscillations as instruments of sensory selection.** *Trends Neurosci* 2009, **32**:9-18.
49. Thut G, Miniussi C: **New insights into rhythmic brain activity from TMS-EEG studies.** *Trends Cogn Sci* 2009, **13**:182-189.
50. Chanes L, Quentin R, Tallon-Baudry C, Valero-Cabre A: **Causal frequency-specific contributions of frontal spatiotemporal patterns induced by non-invasive neurostimulation to human visual performance.** *J Neurosci* 2013, **33**:4401-4412.
51. Thut G, Veniero D, Romei V, Miniussi C, Schyns P, Gross J: **Rhythmic TMS causes local entrainment of natural oscillatory signatures.** *Curr Biol* 2011, **21**:1176-1185.
52. Wiener M: **Transcranial magnetic stimulation studies of human time perception: a primer.** *Timing Time Percept* 2014, **2**:233-260.
53. Jones CRG, Rosenkranz K, Rothwell JC, Jahanshahi M: **The right dorsolateral prefrontal cortex is essential in time reproduction: an investigation with repetitive transcranial magnetic stimulation.** *Exp Brain Res* 2004, **158**:366-372.
54. Kanai R, Chaieb L, Antal A, Walsh V, Paulus W: **Frequency-dependent electrical stimulation of the visual cortex.** *Curr Biol* 2008, **18**:1839-1843.
55. Antal A, Paulus W: **Transcranial alternating current stimulation (tACS).** *Front Hum Neurosci* 2013, **7**:317.

## 6 Time in perception and action

56. Herrmann CS, Rach S, Neuling T, Struber D: **Transcranial alternating current stimulation: a review of the underlying mechanisms and modulation of cognitive processes.** *Front Hum Neurosci* 2013, **7**.
57. Helfrich RF, Schneider TR, Rach S, Trautmann-Lengsfeld SA, Engel AK, Herrmann CS: **Entrainment of brain oscillations by transcranial alternating current stimulation.** *Curr Biol* 2014, **24**:333-339.
- tACS-EEG paper demonstrating simultaneous application of both techniques. Further demonstrates that tACS, precisely aligned in phase to ongoing alpha oscillations, can alter those oscillations in individuals and with behavioral effects.
58. Kanai R, Paffen CL, Hogendoorn H, Verstraten FA: **Time dilation in dynamic visual display.** *J Vis* 2006, **6**:1421-1430.
59. Rohenkohl G, Cravo AM, Wyart V, Nobre AC: **Temporal expectation improves the quality of sensory information.** *J Neurosci* 2012, **32**:8424-8428.
60. Coslett HB, Wiener M, Chatterjee A: **Dissociable neural systems for timing: evidence from subjects with basal ganglia lesions.** *PLoS ONE* 2010, **5**:e10324.
61. Quentin R, Elkin Frankston S, Vernet M, Toba MN, Bartolomeo P, Chanes L, Valero-Cabre A: **Visual contrast sensitivity improvement by right frontal high-beta activity is mediated by contrast gain mechanisms and influenced by fronto-parietal white matter microstructure.** *Cereb Cortex* 2015. (in press).
62. Treisman M, Brogan D: **Time perception and the internal clock: effects of visual flicker on the temporal oscillator.** *Eur J Cogn Psychol* 1992, **4**:41-70.
63. Herbst SK, Chaumon M, Penney TB, Busch NA: **Flicker-induced time dilation does not modulate EEG correlates of temporal encoding.** *Brain Topogr* 2015, **28**:559-569.
64. Arnal LH, Doelling KB, Poeppel D: **Delta-beta coupled oscillations underlie temporal prediction accuracy.** *Cereb Cortex* 2015, **25**:3077-3085.
- MEG study demonstrating that two different frequency bands can be functionally coupled when making temporal predictions about the occurrence of an event. Further demonstrates that alpha oscillations following a response can be linked to updated representations in memory.
65. Ng KK, Tobin S, Penney TB: **Temporal accumulation and decision processes in the duration bisection task revealed by contingent negative variation.** *Front Integr Neurosci* 2011, **5**:77.
66. Van Driel J, Knäpen T, van Es DM, Cohen MX: **Interregional alpha-band synchrony supports temporal cross-modal integration.** *Neuroimage* 2014, **101**:404-415.
67. Sperduti M, Tallon-Baudry C, Hugueville L, Pouthas V: **Time is more than a sensory feature: Attending to duration triggers specific anticipatory activity.** *Cogn Neurosci* 2011, **2**:11-18.
68. Wilsch A, Henry MJ, Herrmann B, Maess B, Obleser J: **Slow-delta phase concentration marks improved temporal expectations based on the passage of time.** *Psychophysiology* 2015, **52**: 910-918.
69. Cravo AM, Rohenkohl G, Wyart V, Nobre AC: **Endogenous modulation of low frequency oscillations by temporal expectations.** *J Neurophysiol* 2011, **106**:2964-2972.
70. Kononowicz TW, van Rijn H: **Single trial beta oscillations index time estimation.** *Neuropsychologia* 2015, **75**:381-389.
- A re-analysis of an earlier broadband EEG study investigating the Contingent Negative Variation and time estimation. Notably, the previous study found no association between the broadband response and time estimates. However, after decomposing the data into distinct frequency bands, an association with beta and theta oscillations was found. Nicely demonstrates that oscillations may provide 'hidden' information in broadband EEG that can be temporally informative.
71. Babiloni C, Miniussi C, Babiloni F, Carducci F, Cincotti F, Del Percio C, Sirello G, Fracassi C, Nobre AC, Rossini PM: **Sub-second "temporal attention" modulates alpha rhythms. A high-resolution EEG study.** *Brain Res Cogn Brain Res* 2004, **19**:259-268.
72. Praamstra P, Kourtis D, Kwok HF, Oostenveld R: **Neurophysiology of implicit timing in serial choice reaction-time performance.** *J Neurosci* 2006, **26**:5448-5455.
73. Rohenkohl G, Nobre AC: **Alpha oscillations related to anticipatory attention follow temporal expectations.** *J Neurosci* 2011, **31**:14076-14084.
74. Van Diepen RM, Cohen MX, Denys D, Mazaheri A: **Attention and temporal expectations modulate power, not phase, of ongoing alpha oscillations.** *J Cogn Neurosci* 2015, **27**:1573-1586.
75. Samaha J, Bauer P, Cimaroli S, Postle BR: **Top-down control of the phase of alpha-band oscillations as a mechanism for temporal prediction.** *Proc Natl Acad Sci U S A* 2015, **112**: 8439-8444.
76. Carver FW, Elvevag B, Altamura M, Weinberger DR, Coppola R: **The neuromagnetic dynamics of time perception.** *PLoS ONE* 2012, **8**:e42618.
- MEG study demonstrating that beta oscillations are associated with the detection of a target interval. Further links the timing of these oscillations to the right inferior frontal gyrus, a region highly implicated in time perception studies (see [23]). Important for demonstrating an association with beta and time perception that is not explicitly motor related; however, it should be noted that the button responses were speeded, which may explain beta recruitment via motor processes.
77. Bartolo R, Merchant H: **Beta oscillations are linked to the initiation of sensory-cued, movement sequences and the internal guidance of regular tapping in the monkey.** *J Neurosci* 2015, **35**:4635-4640.
78. Kaiser J, Leiberg S, Rust H, Lutzenberger W: **Prefrontal gamma-band activity distinguishes between sound durations.** *Brain Res* 2007, **1139**:153-162.
79. Zold CL, Shuler H: **Theta oscillations in visual cortex emerge with experience to convey expected reward time and experienced reward rate.** *J Neurosci* 2015, **35**:9603-9614.