The contingent negative variation (CNV): timing isn't everything

Tadeusz W Kononowicz[1] and Trevor B Penney[2]

When participants time intervals ranging from several hundred milliseconds to several seconds a negative polarity waveform, known as the contingent negative variation (CNV), manifests in the ongoing electroencephalogram (EEG). The perceptual and cognitive functions underlying this component are subject to ongoing debate. Moreover, recent evidence suggests that the link between the CNV and behavioral performance is non-linear and changes depending on the cognitive context. We suggest that the CNV reflects a common core preparatory process related to brain system optimization, and other cognitive processes that depend on the specific timing task employed.

Addresses
[1] CEA, DSV/I2BM, NeuroSpin, INSERM, U992, Cognitive Neuroimaging Unit, Univ Paris-Sud, F-91191 Gif/Yvette, France
[2] Department of Psychology and LSI Programme in Neurobiology and Aging, National University of Singapore, Singapore

Corresponding authors: Kononowicz, Tadeusz W (t.w.kononowicz@icloud.com) and Penney, Trevor B (penney@nus.edu.sg)

Contingent negative variation overview

When an action or stimulus is contingent on a preceding stimulus, the initial stimulus elicits a slow negative deflection in the scalp-recorded electroencephalogram (EEG). This voltage change, called the contingent negative variation (CNV), has a fronto-central scalp distribution and normally resolves to baseline when the action or second stimulus occurs. The CNV was first reported by Walter and colleagues ([1], for a brief review in timing contexts, see [2]), who associated it with expectancy and anticipation. Since then, the CNV has been linked to various cognitive and psychophysiological processes ([3]; see Box 1, 'Current status of the field'). Early studies associated the CNV time course to the length of the timed interval [4] and the CNV amplitude to timing accuracy [5]. Subsequently, Macar [6–8], Pouthas

[9,10], and their colleagues interpreted the CNV slope and amplitude as a correlate of the temporal accumulation process proposed in scalar timing theory (STT; [11]). STT posits that an accumulator integrates pulses emitted by a pacemaker, which is a core idea of many models of interval timing [11–13].

Interestingly, certain features of the CNV depend on the specific timing paradigm used. Explicit interval timing tasks can be classified into two broad groups: motor timing and perceptual timing [17]. Motor timing requires the participant to make a motor response demarcating the target interval. For example, the participant may press a response button to terminate a stimulus and indicate that it has been presented for the appropriate amount of time. Perceptual timing requires the participant to make a judgment about the duration of one or more stimuli, but the motor response itself does not affect or represent the target duration. This simple idea is depicted in Figure 1, which also introduces psychological concepts that have been linked to perceptual and motor timing. In the following, we discuss links between these psychological concepts and the CNV in the context of interval timing.

CNV in motor timing

Macar and colleagues [8] proposed that trial-to-trial fluctuations in subjective timing are driven by variations in the current state of the accumulator. To test this idea, Macar *et al.* [8] asked participants to produce a 2.5 s standard duration learned earlier by pressing a response button twice. Trials were *post hoc* categorized into three groups: 'short' productions (2.2–2.4 s), 'correct' productions (2.4–2.6 s), and 'long' productions (2.6–2.8 s). The CNV measured at the FCz electrode, which is typically assumed to measure activity in the SMA when spatial filtering is applied, was largest in the long condition, and smallest in the short condition, with the correct category in between. The positive correlation between produced duration and CNV amplitude was taken as strong evidence that the subjectively experienced interval is directly linked with the amplitude of the CNV. However, more recently other researchers [18] failed to find any covariation between CNV amplitude and duration (also see [19,20]). Instead, they showed a decrease in CNV amplitude over the course of the experiment. This apparent habituation effect contrasts with the assumption that the CNV reflects a stable accumulation process and is inconsistent with the temporal accumulation hypothesis (also see [21]). This and other recent work demonstrates that

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Box 1 Current status of the field.

- The CNV is strongly associated with perceptual and motor timing.
- Multiple brain areas contribute to the global CNV signal.
- The CNV peak in perceptual timing reflects duration of a standard interval stored in working memory.
- Preparation and anticipation are omnipresent cognitive components of the CNV.
- Other components predict subjective time better than the CNV, both in perceptual (N1P2) and motor (beta power) paradigms.

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the interpretation of the CNV from a temporal processing perspective is far from settled [21••,22•,23,24•,25••,26].

SMA activation precedes voluntary movements [28], which suggests that the CNV originating from the SMA in time production tasks may reflect motor preparation [29]. For example, Kononowicz, Sander, and Van Rijn ([30]; also see [31]) asked participants to reproduce durations of 2 s, 3 s and 4 s. The CNV amplitude was larger for the 2 s duration than for the 3 s and 4 s durations. Additionally, larger CNV amplitude was associated with shorter reproduced durations across subjects in all three duration conditions. Although these results are at odds with larger CNV amplitudes reflecting larger temporal accumulations, they are consistent with CNV amplitude reflecting

preparation for action, at least when participants produce or reproduce temporal intervals [26]. Other studies identified another pattern of neural activity as a ramp up that reaches a plateau [19,32] or a decline that is difficult to reconcile with the idea of temporal accumulation [33,34]. Nevertheless, it is noteworthy that the CNV signal results from synchronization of massive neuronal populations that can exhibit different climbing patterns (for review, see [35•]). Specifically, the spiking patterns of single cells were classified into four groups: motor cells, relative timing cells, absolute timing cells, and time accumulator cells, which demonstrates that the CNV can be a gross product of these neural populations [36].

Hence, although a single specific function is often ascribed to the CNV, it may be a composite of several processes [37] that result in the signal reflecting the decision to take an action. Of course, in motor timing a preparatory component related to the activation of motor circuits inevitably will be present in the neuronal activity and may dominate the overall pattern. Hence, perceptual discrimination timing tasks are often employed to limit the contribution of motor related activity to the CNV.

CNV in perceptual timing

A CNV also occurs when participants are asked to judge duration in the absence of a motor response [1], such as a comparison of a current time interval to a remembered standard time interval. Moreover, the CNV amplitude is typically larger for temporal discrimination than for other types of perceptual discrimination task [38] and increases as a function of attention paid to the timing task [39••]. However, the most remarkable finding depicted in Figure 2 is that the CNV deflects approximately when

Figure 1
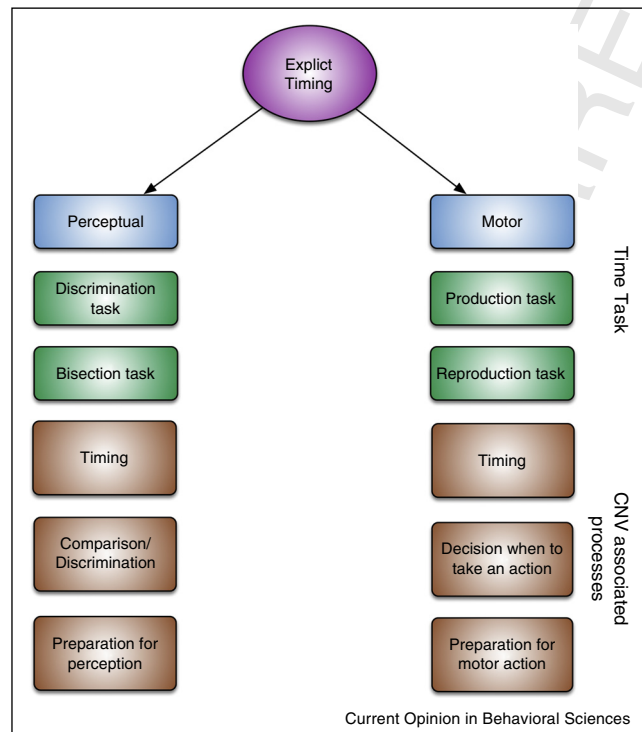
Summary of a common classification of explicit timing including associated tasks (green) and the processes attributed to them (brown).
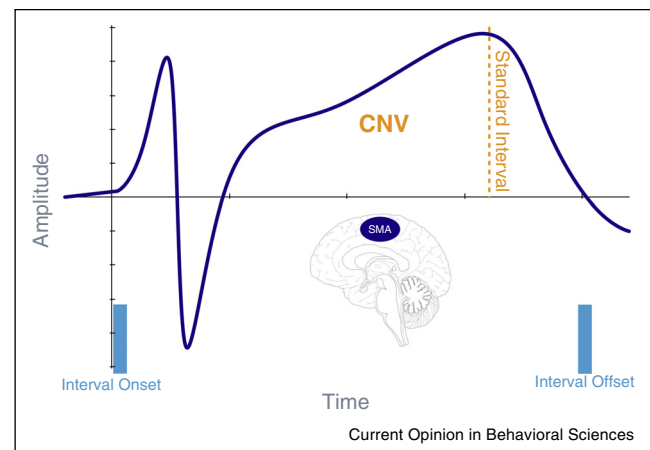
Figure 2

Illustration of the typical development of the CNV when participants are asked to compare a remembered interval to a currently presented interval. Note the CNV resolution at the expected offset time of the standard interval.

the response switches from one category to another (e.g. 'short' to 'long' [40,41]).

The CNV deflection point could reflect a decision variable for when the current interval has exceeded the standard interval (SI) criterion, if one assumes a fixed threshold for this decision [26]. The same CNV effect also can be interpreted as a memory representation of the standard interval [40] Unfortunately, the literature does not adjudicate between these two proposals. Moreover, recent work indicates that other ERP components are related to interval timing processes. For example, Kononowicz and Van Rijn [42] showed that the N1P2 amplitude evoked by the offset of the comparison interval (CI) increases as a function of the temporal distance from the SI. Additionally, the latency of the P2 component follows the hazard rate of the CIs such that the P2 latency decreases as the probability of interval offset increases. In other words, P2 latency was shortest for the longest durations indicating that timing processes continue after the resolution of the CNV (c.f.; [43,44••]). This result suggests that timing information is available after the SI has elapsed, which indirectly implies that the CNV is involved in coding for a general decision variable.

Recent work by Wiener and Thompson [45••] explicitly investigated how memory and decision factors contribute to the CNV. These authors asked participants to classify durations into short and long categories. Importantly, they used a first-order counterbalanced sequence, which permitted examination of the effect of classification of duration $N-1$ on duration N. In line with the idea that the CNV reflects decisional and memory factors, when the preceding interval was objectively long the CNV deflected later and the current interval was more likely to be judged as short. The second effect demonstrated by Wiener and Thompson [45••] was repetition enhancement, meaning that the CNV was more negative the smaller the temporal distance between adjacent stimuli, with the largest negativity when the same duration was repeated. If the CNV reflected a purely temporal accumulation process, it would not be affected by the preceding trials. To summarize, recent studies mainly suggest that decisional and memory mechanisms influence the CNV.

CNV reflects resource optimization and preparation

Compelling evidence that the interval timing CNV is related to preparation and expectation has been provided by Ng, Tobin, and Penney ([19]; also see [32]). These authors used a duration bisection paradigm in which subjects categorized probe durations as more similar to a short or long anchor. Ng et al. [19] observed a negative deflection that started at the onset of the probe duration. However, the CNV plateaued at the duration value of the short anchor and remained stable until the geometric mean of the anchor durations or stimulus offset, whichever came first, when it resolved. This result can be seen as reflecting maintenance of neuronal assemblies in a state that enables efficient action/perception.

Besides preparation for an upcoming event, the CNV has been linked to other processes such as motor preparation [46], expectation, and anticipation [47–49]. However, the common core concept for these three processes is resource optimization, which is linked to the more physiologically grounded concept of excitability. Initially, work by Elbert ([31], also see [50]) showed that there is a link between detection of visual stimuli and the amplitude of the CNV such that low amplitude corresponds to misses, and high amplitude corresponds to false alarms. This link between detection performance and negativity of the CNV is in line with results showing that the CNV amplitude preceding the start of a trial is higher when participants are cued to respond as fast as possible [51]. Taken together these results suggest that larger CNV amplitude corresponds to larger disinhibition in sensorimotor circuits.

However, the relationship between slow ERP components, like the CNV, and behavioral performance may not be linear. He and Zempel [52•] showed a U-shaped relationship between response speed and electrocorticographic signals such that reaction times were fastest when the amplitude of the slow wave was closest to the average. A U-shaped relationship has also been reported between movement speed and neuronal firing in the premotor cortex [53]. A similar effect may be present in interval timing, where, in at least some tasks, movement speed and timing accuracy are linked. The hypothesis of resource optimization suggests that the efficiency of behavioral performance should be related to decreased neuronal variability across trials. Such a decrease across trials could give rise to enhanced CNV amplitude. Interestingly, Gontier et al. [54•] showed that larger CNV amplitude was related to better behavioral performance when participants were asked to judge durations marked by auditory or visual signals as 'short' or 'long'.

Together these results suggest that there are multiple mechanisms relating slow ERP components and behavior. The first mechanism, which predicts a linear function between neuronal activity and response speed, is based on the idea of accumulation to threshold. For example, release of inhibition in cortico-striatal loops would lead to lower response caution and faster accumulation towards threshold [55] as depicted in Figure 3a. The second mechanism is based on the idea that the brain settles in an optimal state for performance, termed an optimal subspace of firing rates [53] as depicted in Figure 3b. Observations of neuronal population dynamics in monkeys [56] indicated that production of short and long time intervals was associated with approximately the same

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Figure 3
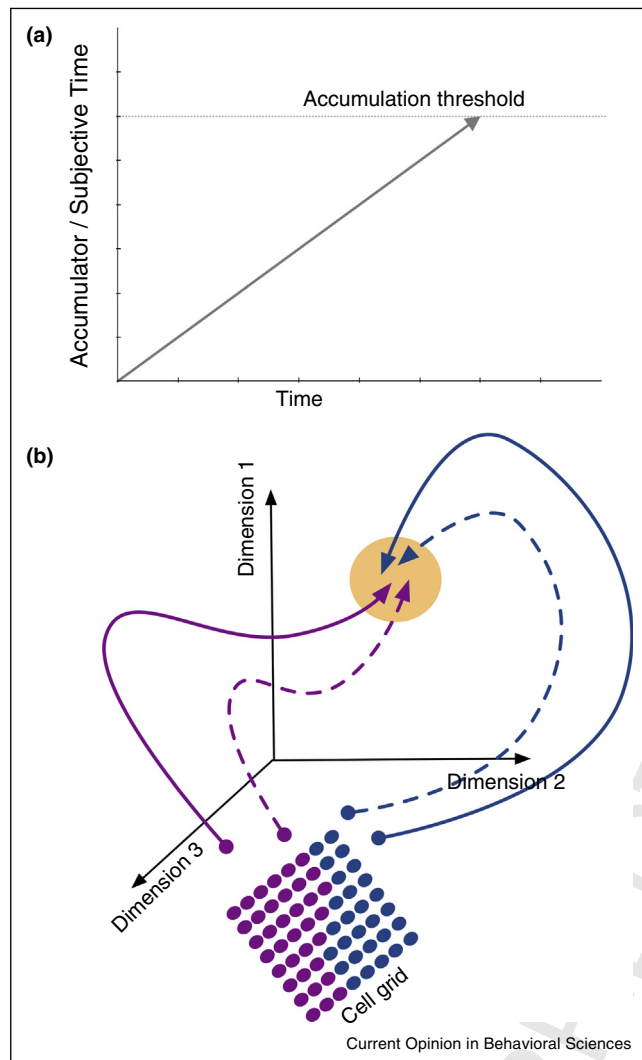
Two theoretical approaches to preparation and duration coding. **(a)** The first approach proposes that activity has to reach a certain level for a movement to be triggered. **(b)** The second approach is based on the idea of optimization and proposes that preparation relies on a search through the state space for an optimal configuration of neuronal firing. We have labeled the three axes as dimensions because they could refer to specific components of neuronal firing, but they could also refer to more global signals measured with EEG/MEG. The solid and dashed traces depict the short and long produced intervals because the production of short and long time intervals is associated with similar paths in multidimensional space [56]. However, short and long categories deviate from each other before arriving at the same destination point. Different grid colors illustrate the idea that spatially segregated neuronal populations express different directories through multidimensional space. Note that spatially segregated populations could also code for different durations.

direction and the same converging point in multidimensional space. However, short and long categories deviated from each other on the way to the convergence point (see dashed and solid lines in Figure 3b, which depict short

and long trials, respectively). Note that in Figure 3b (also see [56]) the overall population state is driven towards higher firing rates, which explains a global potential increase as measured by the CNV. Additionally, the idea of spatial coding of time [57] is represented by the color coded grid in Figure 3b. Within this framework, spatially segregated neuronal populations [58] can differentially express temporal durations, presumably giving rise to non-linear patterns covarying with subjective time. In other words, the CNV could result from a mixture of these two processes, where climbing activity reflects a search for the optimal configuration of neuronal firing. Moreover, the state dependent networks model, which is based on the idea that time can be encoded as a trajectory in the multidimensional space of a recurrent neural network, can be trained in a way that it will exhibit a linear ramp [59,60], suggesting that climbing activity can be reconciled with the idea of coding time in an optimal neuronal subspace.

In sum, the CNV could reflect the process of controlling the brain's excitability in preparation for an upcoming internal or external stimulus [31]. In other words, the CNV can be interpreted as a marker of resource optimization through alternating levels of excitability. However, more complex processes could contribute to the CNV. Therefore, dependencies between timing, anticipation and preparation processes and CNV features have to be established.

CNV and oscillations

An old idea in the timing literature is that alpha oscillations provide clock pulses [61] or reflect fluctuations of attention giving rise to the subjective estimate of time. However, neither of these ideas has received much support ([62]; c.f. [19]). Moreover, in spite of newer results showing EEG power modulation in timing tasks the importance of EEG oscillations in interval timing and their link to the CNV remains elusive. In the following, we briefly review some of the relevant findings.

Gamma power increased over fronto-central and parietal regions when participants attended to duration as compared to stimulus intensity [63], suggesting a functional role of gamma in attention to time. It is important to note that this effect is distinct from the typical optimization of attention in time involving alpha and theta oscillations [64,65]. Gamma originating from the left inferior frontal cortex has also been implicated in auditory temporal perception learning [66] because gamma band power in the auditory cortex and in the left inferior frontal gyrus increases after temporal modulation rate training. Moreover, the gamma peak is correlated with auditory duration magnitude [67]. Interestingly, gamma and beta power modulations covary with beat processing [68,69]. For example, Fujioka *et al.* [69] showed that beta oscillations predict the occurrence of subsequent stimuli in a rhythmic sequence. However, another possibility is that these beta effects reflect involvement of the motor system in timing,

as has been shown in a synchronization-continuation task [68]. Importantly, any oscillatory effect should be carefully interpreted in light of the specific paradigm employed. Whereas previous studies used cortical entrainment to drive modulations of beta amplitude [68,69], a recent suprasecond interval-timing study, in which participants initiated to-be-timed intervals spontaneously, showed that motor related post-movement beta synchronization predicted the length of the current temporal interval [62]. Hence, the nature of this beta effect could be different than in the studies using entrainment paradigms. Interestingly, analysis of the same data at the same electrode location (FCz) failed to reveal a relationship between CNV amplitude and produced duration [18]. Although CNV and beta oscillations correlate in a continuous performance task [70] showing preparedness of the motor system to react quickly, other results [18,62] suggest that these two measures reflect functionally and neurophysiologically distinct mechanisms. Indeed, earlier work claimed that the CNV reflects synchronization of post-synaptic potentials in pyramidal cells [71] and beta oscillations primarily reflect action of populations of interneurons [72].

Despite this recently emerging evidence of beta oscillations in timing, a long standing conjecture proposes that variations in speed and power of alpha oscillations should be involved in coding of temporal intervals (see [73] for a review). Indeed, there is a substantial body of evidence that alpha rhythm strongly contributes to implicit timing by facilitation of sensory processing (e.g. [65]). However, the role of alpha oscillations in explicit timing is far from clear [19,58]. Therefore, it remains to be established whether alpha oscillations serve as a substrate of internal clock [73] or contribute to working memory processes in interval timing [15].

Recent work suggests that alpha oscillations may contribute to the evolution of slow evoked components. Although oscillatory activity is viewed as being symmetric around zero, the peaks of alpha oscillation can be modulated more strongly than the troughs [74] and if averaged over multiple trials alpha may cause a shift in slow components such as the CNV. Therefore, contributions of this less conventional neuronal mechanism to the CNV should be considered together with conventional explorations of oscillatory power.

In sum, there is emerging evidence that beta oscillations carry temporal information in motor timing or at least that beta interacts with timing mechanisms. However, the specific contribution of alpha, beta, and other frequency bands to perceptual timing remains an open question.

Dopaminergic modulations of the CNV

Interestingly, both CNV [75] and beta oscillations [76] are modulated by impairments of L-Dopa and studies in animals have shown that alterations of dopamine modulate the

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> **Box 2 Future directions and outstanding questions.**
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> - How can we account for inconsistent results relating CNV amplitude to the subjective perception of time?
> - Can we differentiate climbing neural activity and persistent/ sustained patterns of slow activity and their contribution to working memory, preparation, and anticipation?
> - What is the functional difference between slow signals originating from different brain areas (e.g. SMA and rIFG)?
> - How do patterns of spiking within a given neuronal population relate to slow local field potentials within the same area?
> - What are the neurophysiological mechanisms that give rise to the CNV and climbing neural activity?
> - Can we identify the brain structures which provide the temporal information contributing to the CNV, for example by means of dynamic causal modeling?

strength of ramping activity [77,78]. Interestingly, brain structures that are affected by dopaminergic modulations correspond to the key anatomical components implicated in the SBF model ([79], also see [80•]), which proposes that a set of pre-frontal cortex neurons oscillate at various frequencies in the prefrontal cortex. At the onset of an interval, these oscillators are phase-reset and at the offset of the interval the unique pattern of the cortical oscillators is decoded by medium spiny neurons in the striatum that work as coincidence detectors [81]. Given the crucial role of dopamine in the SBF model the links between the SBF, CNV and beta oscillations warrant further investigation.

Conclusion

The contradictory CNV results in motor timing ([8]; c.f. [18,30]) and perceptual timing [22•,25••,42] may stem from the fact that various processes contribute to the CNV at the scalp level. Thus, the future challenge lies in an appropriate unmixing of these signals and attribution to specific perceptual and cognitive processes (see Box 2, 'Future directions and outstanding questions').

Uncited references

[14,16,27].

Conflict of interest statement

Nothing declared.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Walter WG, Cooper R, Aldridge VJ, McCallum WC, Winter AL: **Contingent negative variation: an electric sign of sensorimotor association and expectancy in the human brain**. *Nature* 1964, **203**:380-384.

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2. Ng KK, Penney TB: **Probing interval timing with scalp-recorded electroencephalography (EEG)**. *Adv Exp Med Biol* 2014, **829**: 187-207.

3. Tecce JJ: **Contingent negative variation (CNV) and psychological processes in man**. *Psychol Bull* 1972, **77**:73-108.

4. Ruchkin DS, McCalley MG, Glaser EM: **Event related potentials and time estimation**. *Psychophysiology* 1977, **14**:451-455.

5. McAdam DW: **Slow potential changes recorded from human brain during learning of a temporal interval**. *Psychon Sci* 1966, **6**:435-436.

6. Macar F, Vitton N: **An early resolution of contingent negative variation (CNV) in time discrimination**. *Electroencephalogr Clin Neurophysiol* 1982, **54**:426-435.

7. Macar F, Besson M: **Contingent negative variation in processes of expectancy, motor preparation and time estimation**. *Biol Psychol* 1985, **21**:293-307.

8. Macar F, Vidal F, Casini L: **The supplementary motor area in motor and sensory timing: evidence from slow brain potential changes**. *Exp Brain Res* 1999, **125**:271-280.

9. Pfeuty M, Ragot R, Pouthas V: **Relationship between CNV and timing of an upcoming event**. *Neurosci Lett* 2005, **382**:106-111.

10. Pouthas V, George N, Poline JB, Pfeuty M, Van de Moorteele PF, Hugueville L, Ferrandez AM, Lehéricy S, Le Bihan D, Renault B: **Neural network involved in time perception: an fMRI study comparing long and short interval estimation**. *Hum Brain Mapp* 2005, **25**:433-441.

11. Gibbon J, Church RM, Meck WH: **Scalar timing in memory**. *Ann N Y Acad Sci* 1984, **423**:52-77.

12. Taatgen NA, Van Rijn H, Anderson J: **An integrated theory of prospective time interval estimation: the role of cognition, attention, and learning**. *Psychol Rev* 2007, **114**:577-598.

13. Shi Z, Church RM, Meck WH: **Bayesian optimization of time perception**. *Trends Cogn Sci* 2013, **17**:556-564.

14. Allman MJ, Meck WH: **Pathophysiological distortions in time perception and timed performance**. *Brain* 2012, **135**:656-677.

15. Gu BM, Van Rijn H, Meck WH: **Oscillatory multiplexing of neural population codes for interval timing and working memory**. *Neurosci Behav Rev* 2015, **48**:160-185.

16. Van Rijn H, Gu B-M, Meck WH: **Dedicated clock/timing-circuit theories of interval timing and timed behavior**. *Adv Exp Med Biol* 2014, **829**:75-99.

17. Coull J, Nobre AC: **Dissociating explicit timing from temporal expectation with fMRI**. *Curr Opin Neurobiol* 2008, **18**:137-144.

18. Kononowicz TW, Van Rijn H: **Slow potentials in time estimation: the role of temporal accumulation and habituation**. *Front Integr Neurosci* 2011, **5**:48.

19. 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.

20. Tamm M, Uusberg A, Allik J, Kreegipuu K: **Emotional modulation of attention affects time perception: evidence from event-related potentials**. *Acta Psychol* 2014, **149**:148-156.

21. Mento G, Tarantino V, Sarlo M, Bisiacchi PS: **Automatic temporal**
•• **expectancy: a high-density event-related potential study**. *PLOS ONE* 2013, **8**:e62896.
This study demonstrates development of the CNV in participants that were awake, yet not actively engaged in a temporal task. The CNV deflected at the standard interval duration.

22. Herbst SK, Chaumon M, Penney TB, Busch NA: **Flicker-induced**
• **time dilation does not modulate EEG correlates of temporal encoding**. *Brain Topogr* 2014, **28**:559-569.
Study showing that modulation of flicker frequency does not affect CNV amplitude.

23. Kononowicz TW, Van Rijn H: **Tonic and phasic dopamine fluctuations as reflected in beta power predict interval timing behavior**. *Procedia Soc Behav Sci* 2014, **126**:47.

24. Wittmann M: **The inner sense of time: how the brain creates a**
• **representation of duration**. *Nat Rev Neurosci* 2014, **14**:217-223.

25. Wiener M, Kliot D, Turkeltaub PE, Hamilton RH, Wolk DA,
•• Coslett HB: **Parietal influence on temporal encoding indexed by simultaneous transcranial magnetic stimulation and electroencephalography**. *J Neurosci* 2012, **32**:12258-12267.
This study shows how parietal TMS stimulation affects subjective perception of time intervals and CNV amplitude.

26. Van Rijn H, Kononowicz TW, Meck WH, Ng KK, Penney TB: **Contingent negative variation and its relation to time estimation: a theoretical evaluation**. *Front Integr Neurosci* 2011, **5**:91.

27. Van Rijn H, Kononowicz T, Vidal F, Casini L, Wiener M, Penney TB, Ng KK: **The role of the SMA and the contingent negative variation in interval timing**. *Procedia Soc Behav Sci* 2014, **126**:27-28.

28. Deecke L, Scheid P, Kornhuber HH: **Distribution of readiness potential, pre-motion positivity, and motor potential of the human cerebral cortex preceding voluntary finger movements**. *Exp Brain Res* 1969, **7**:158-168.

29. Coull J, Vidal F, Burle B: **When to act, or not to act: that's the SMA's question**. *Curr Opin Behav Sci* 2016, **8**:14-21.

30. Kononowicz TW, Sander T, Van Rijn H: **Neuroelectromagnetic signatures of the reproduction of supra-second durations**. *Neuropsychologia* 2015, **75**:201-213.

31. Elbert T, Ulrich R, Rockstroh B, Lutzenberger W: **The processing of temporal intervals reflected by CNV-like brain potentials**. *Psychophysiology* 1991, **28**:648-655.

32. Tanaka M: **Cognitive signals in the primate motor thalamus predict saccade timing**. *J Neurosci* 2007, **27**:12109-12118.

33. Goel A, Buonomano DV: **Timing as an intrinsic property of neural networks: evidence from in vivo and in vitro experiments**. *Philos Trans R Soc B* 2014, **369**:20120460.

34. Schneider BA, Ghose GM: **Temporal production signals in parietal cortex**. *PLoS Biol* 2012, **10**:e1001413.

35. Merchant H, Harrington DL, Meck WH: **Neural basis of the**
• **perception and estimation of time**. *Annu Rev Neurosci* 2013, **36**:313-336.
Excellent review of the neural substrates of interval timing.

36. Merchant H, Zarco W, Pérez O, Prado L, Bartolo R: **Measuring time with different neural chronometers during a synchronization-continuation task**. *Proc Natl Acad Sci U S A* 2011, **108**:19784-19789.

37. Mento G: **The passive CNV: carving out the contribution of task-related processes to expectancy**. *Front Hum Neurosci* 2013, **7**:827.

38. Mitsudo T, Nakajima Y, Takeichi H, Tobimatsu S: **Perceptual inequality between two neighboring time intervals defined by sound markers: correspondence between neurophysiological and psychological data**. *Front Psychol* 2014, **5**:937.

39. Liu Y, Zhang D, Ma J, Li D, Yin H, Luo Y: **The attention modulation**
•• **on timing: an event-related potential study**. *PLOS ONE* 2013, **8**:e66190.
Important study demonstrating that the CNV amplitude increases as a function of attention devoted to time.

40. Macar F, Vidal F: **The CNV peak: an index of decision making and temporal memory**. *Psychophysiology* 2003, **40**:950-954.

41. Pouthas V, Garnero L, Ferrandez AM, Renault B: **ERPs and PET analysis of time perception: spatial and temporal brain mapping during visual discrimination tasks**. *Hum Brain Mapp* 2000, **10**:49-60.

42. Kononowicz TW, Van Rijn H: **Decoupling interval timing and climbing neural activity: a dissociation between CNV and N1P2 amplitudes**. *J Neurosci* 2014, **34**:2931-2939.

43. Tarantino V, Ehlis AC, Baehne C, Boreatti-Huemmer A, Jacob C, Bisiacchi P, Fallgatter AJ: **The time course of temporal discrimination: an ERP study**. *Clin Neurophysiol* 2010, **121**:43-52.

44. Van Wassenhove V, Lecoutre L: **Duration estimation entails predicting when**. *Neuroimage* 2015, **106**:272-283.
•• One of the few magnetoencephalographic studies of time perception. It demonstrates how duration estimation is affected by context and surprise.

45. Wiener M, Thompson JC: **Repetition enhancement and memory effects for duration**. *Neuroimage* 2015, **113**:268-278.
•• Intriguing study showing how the length of previously presented intervals modulates CNV amplitude in the current trial.

46. Gaillard AWK: **The late CNV wave: preparation versus expectancy**. *Psychophysiology* 1977, **14**:563-568.

47. Brunia CHM, Damen EJP: **Distribution of slow brain potentials related to motor preparation and stimulus anticipation in a time estimation task**. *Electroencephalogr Clin Neurophysiol* 1988, **69**:234-243.

48. Mnatsakanian EV, Tarkka IM: **Task-specific expectation is revealed in scalp-recorded slow potentials**. *Brain Topogr* 2002, **15**:87-94.

49. Tarkka IM, Basile LF: **Electric source localization adds evidence for task-specific CNVs**. *Behav Neurol* 1998, **11**:21-28.

50. Li Q, Hill Z, He BJ: **Spatiotemporal dissociation of brain activity underlying subjective awareness, objective performance and confidence**. *J Neurosci* 2014, **34**:4382-4395.

51. Boehm U, Van Maanen L, Forstmann B, Van Rijn H: **Trial-by-trial fluctuations in CNV amplitude reflect anticipatory adjustment of response caution**. *Neuroimage* 2014, **96**:95-105.

52. He BJ, Zempel JM: **Average is optimal: an inverted-U relationship between trial-to-trial brain activity and behavioral performance**. *PLOS Comput Biol* 2013, **9**:e1003348.
• This study shows that the relationship between slow components, such as the CNV, and behavioral performance can be non-linear.

53. Churchland MM, Byron MY, Ryu SI, Santhanam G, Shenoy KV: **Neural variability in premotor cortex provides a signature of motor preparation**. *J Neurosci* 2006, **26**:3697-3712.

54. Gontier E, Hasuo E, Mitsudo T, Grondin S: **EEG investigations of duration discrimination: the intermodal effect is induced by an attentional bias**. *PLOS ONE* 2013, **8**:e74073.
• This study demonstrated the importance of stimulus modality on the CNV amplitude in a timing task.

55. Van Maanen L, Brown SD, Eichele T, Wagenmakers EJ, Ho T, Serences J, Forstmann BU: **Neural correlates of trial-to-trial fluctuations in response caution**. *J Neurosci* 2014, **31**: 17488-17495.

56. Merchant H, Bartolo R, Pérez O, Méndez JC, Mendoza G, Gámez J, Yc K, Prado L: **Neurophysiology of timing in the hundreds of milliseconds: multiple layers of neuronal clock in the medial premotor areas**. *Adv Exp Med Biol* 2014, **829**: 143-154.

57. Hass J, Herrmann JM: **The neural representation of time: an information-theoretic perspective**. *Neural Comput* 2012, **24**:1519-1552.

58. Kiani R, Cueva CJ, Reppas JB, Peixoto D, Ryu SI, Newsome WT: **Natural grouping of neural responses reveals spatially segregated clusters in prearcuate cortex**. *Neuron* 2015, **85**:1359-1373.

59. Buonomano DV, Maass W: **State-dependent computations: spatiotemporal processing in cortical networks**. *Nat Rev Neurosci* 2009, **10**:113-125.

60. Buonomano DV, Laje R: **Population clocks: motor timing with neural dynamics**. *Trends Cogn Sci* 2010, **14**:520-527.

61. Treisman M: **Temporal discrimination and the indifference interval: implications for a model of the "internal clock"**. *Psychol Monogr Gen Appl* 1963, **77**:1-31.

62. Kononowicz TW, Van Rijn H: **Single trial beta oscillations index time estimation**. *Neuropsychologia* 2015, **75**:381-389.

63. 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.

64. Cravo AM, Rohenkohl G, Wyart V, Nobre AC: **Endogenous modulation of low frequency oscillations by temporal expectations**. *J Neurophysiol* 2011, **106**:2964-2972.

65. Wilsch A, Henry MJ, Herrmann B, Maess B, Obleser J: **Alpha oscillatory dynamics index temporal expectation benefits in working memory**. *Cereb Cortex* 2014, **25**:1938-1946.

66. Van Wassenhove V, Nagarajan SS: **Auditory cortical plasticity in learning to discriminate modulation rate**. *J Neurosci* 2007, **27**:2663-2672.

67. Busch NA, Debener S, Kranczioch C, Engel AK, Herrmann CS: **Size matters: effects of stimulus size, duration and eccentricity on the visual gamma-band response**. *Clin Neurophysiol* 2004, **115**:1810-1820.

68. 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.

69. 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.

70. Bickel S, Dias EC, Epstein ML, Javitt DC: **Expectancy-related modulations of neural oscillations in continuous performance tasks**. *Neuroimage* 2012, **62**:1867-1876.

71. Birbaumer N, Elbert T, Canavan AG, Rockstroh B: **Slow potentials of the cerebral cortex and behavior**. *Physiol Rev* 1990, **70**:1-41.

72. Porjesz B, Almasy L, Edenberg HJ, Wang K, Chorlian DB, Foroud T, Goate A, Rice JP, O'Connor SJ, Rohrbaugh J: **Linkage disequilibrium between the beta frequency of the human EEG and a GABAA receptor gene locus**. *Proc Natl Acad Sci U S A* 2002, **99**:3729-3733.

73. Kononowicz TW, Van Wassenhove V: **In search of oscillatory traces of the internal clock**. *Front Psychol* 2016, **7**:224.

74. Mazaheri A, Jensen O: **Asymmetric amplitude modulations of brain oscillations generate slow evoked responses**. *J Neurosci* 2008, **28**:7781-7787.

75. Mallet N, Pogosyan A, Sharott A, Csicsvari J, Bolam JP, Brown P, Magill PJ: **Disrupted dopamine transmission and the emergence of exaggerated beta oscillations in subthalamic nucleus and cerebral cortex**. *J Neurosci* 2008, **28**:4795-4806.

76. Linssen AMW, Vuurman EFPM, Sambeth A, Nave S, Spooren W, Vargas G, Santarelli L, Riedel WJ: **Contingent negative variation as a dopaminergic biomarker: evidence from dose-related effects of methylphenidate**. *Psychopharmacology (Berl)* 2011, **218**:533-542.

77. Parker KL, Chen KH, Kingyon JR, Cavanagh JF, Narayanan NS: **D$_1$-dependent 4 Hz oscillations and ramping activity in rodent medial frontal cortex during interval timing**. *J Neurosci* 2015, **34**:16774-16783.

78. Kononowicz TW: **Dopamine-dependent oscillations in frontal cortex index "start-gun" signal in interval timing**. *Front Hum Neurosci* 2015, **9**:331.

79. Mattel MS, Meck WH: **Cortico-striatal circuits and interval timing: coincidence detection of oscillatory processes**. *Cogn Brain Res* 2004, **21**:139-170.

80. Plichta MM, Wolf I, Hohmann S, Baumeister S, Boecker R *et al.*: **Simultaneous EEG and fMRI reveals a causally connected subcortical–cortical network during reward anticipation**. *J Neurosci* 2013, **33**:14526-14533.
• EEG-fMRI study revealing how connectivity between the thalamus, striatum, and SMA modulate the CNV.

81. Buhusi CV, Meck WH: **What makes us tick? Functional and neural mechanisms of interval timing**. *Nat Rev Neurosci* 2005, **6**:755-765.