Journal Club

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The Temporal Dynamics of Evidence Accumulation in the Brain

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Review of Werkle-Bergner et al.

People organize the world in perceptual categorizations, which helps them to navigate through and interact with their environment. Often, this requires a perceptual decision: e.g., is this a snake or a water hose? How the brain processes sensory information into a perceptual choice is a central issue in the neurosciences. Nowadays, the field of perceptual decision-making is dominated by the concept of an accumulation-to-bound process that describes the decision process as an accumulation of sensory evidence toward a decision threshold. The decision is made when evidence in favor of one alternative over the other exceeds the decision threshold (Fig. 1; for review, see Gold and Shadlen, 2007). These accumulation-to-bound models are able to describe and predict response time distributions and error rates simultaneously across a large variety of perceptual decision making tasks. These models are not only behaviorally intuitive, but have proven to be neurobiologically plausible as well (Gold and Shadlen, 2007; Forstmann et al., 2011). Therefore, neuroscientists aim to identify and understand the neuronal processes that drive the accumulation process.

Recently, this aim was addressed in a study by Werkle-Bergner and colleagues (2014) published in *The Journal of Neuroscience*. In their study, the authors provide evidence for cooperative spatiotemporal dynamics of slow and fast EEG signals that enhance the information processing in perceptual decision-making. Participants took part in an experiment in which they performed three different perceptual decision-making tasks, in which they were required to choose whether a number was odd or even, whether a letter was a vowel or a consonant, or whether a simple figure was symmetric or asymmetric. Stimuli were shown only for a brief period of time (50 ms), and were masked afterward. In addition to decision-trials, null-trials were added, in which no stimulus was presented. This was done to quantify the differences in brain activity between trials where sensory information was available with trials where no sensory evidence was available. During all three tasks, brain activation was measured using EEG. The high temporal resolution of EEG allows assessment of the dynamics of within-trial processes related to the perceptual choice.

Most EEG studies focus primarily on measurements of frequency and amplitude of the EEG signal. The slow-wave theta frequency band is involved in perceptual decision-making processes (Cavanagh et al., 2011; van Vugt et al., 2012). However, during the decision process, changes in neural firing rates are likely to occur at different timescales and across

different brain regions, reflecting a sequence of neural processes such as encoding, integration, and the control of sensory information until the required motor response has been made. Therefore, the decision process is likely a broadband phenomenon, rather than an isolated change in oscillatory power (van Vugt et al., 2012).

Indeed, the study by Werkle-Bergner et al. (2014) shows that oscillations in both the theta and alpha band play a role in the temporal development of a perceptual choice. First, the authors show that in all three tasks, the dynamics of theta oscillations in the frontocentral brain regions mapped onto the time course of the accumulation process: after stimulus encoding, theta band activity increased until the initial response was made, after which it decreased back to baseline. Second, in all three tasks, a decrease in the alpha band signal (desynchronization) was measured at regions localized toward the more posterior regions of the brain. This alpha desynchronization occurred simultaneously with the increase in theta band and resynchronized again after a choice was made. Both theta and alpha effects were highly related to the trial-by-trial differences in response times, leading the authors to suggest that both frequency bands serve a role in the accumulation process: the frontocentral theta oscillations reflect sensory accumulation, while the desynchronized posterior alpha oscillations facilitate this process by the release of neural inhibition of the sensory signal.

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Figure 1. Schematic representation of an accumulation-to-bound model. The model assumes that sensory information starts to accumulate over time at a certain starting point, and with a certain accumulation rate, until a decision threshold is reached. The non-decision time is the time needed to encode sensory information and/or execution of a motor response.

Interestingly, Werkle-Bergner et al. (2014) not only investigated changes in oscillations within the specific bands of interest (alpha and theta), but measured the temporal development of the signal-entropy as well. The entropy of the EEG signal is assumed to reflect the degree of information that is encoded by neural spiking, with more information for the desynchronized signal (for review, see Hanslmayr et al., 2012). Therefore, when desynchronized posterior alpha oscillations facilitate the accumulation process, one would expect larger entropy (i.e., a “richer” neural code) during the accumulation process in the posterior regions. Indeed, the study by Werkle-Bergner et al. (2014) showed that the alpha desynchronization was accompanied by an increase in the entropy during the accumulation process, supporting the idea that the alpha oscillations reflect the active processing of sensory information during the accumulation process.

The data from Werkle-Bergner et al. (2014) show that multiple brain regions work in concert at different timescales to make the perceptual decision at hand. Although the strong relationship between response times and brain activity suggest that both alpha and theta frequency bands are involved in the accumulation process, alternative explanations are also possible. From the perspective of an accumulation-to-bound model, different latent processes could potentially drive the variance in response-time distributions. For example, the height of the decision threshold, which reflects response caution, also affects the speed with which decisions are made. It has been shown that individuals differ in their threshold settings, and that the decision threshold fluctuates from trial to trial (van Maanen et al., 2011). Furthermore, theta band activity has been associated with adaptations of the deci-

sion threshold (Cavanagh et al., 2011). The increase in frontocentral theta activity described by Werkle-Bergner et al. (2014) appears to start before the initial response with an equal duration (Werkle-Bergner et al., 2014, their Fig. 4), which could reflect ramping activity toward a motor response, represented by the decision threshold. Such an interpretation would be in line with theta-related threshold settings reported earlier (Cavanagh et al., 2011).

In addition to the decision threshold and the accumulation process, other latent processes add to the variance in response times. These processes are not directly related to the decision process itself, and include the encoding of sensory information and the execution of a motor response. Interestingly, in the study by Werkle-Bergner et al. (2014), both patterns of alpha and theta oscillations show a change in activity in the posterior regions after stimulus onset. The authors interpret these data as related to stimulus encoding, since changes were unrelated to the variance in response time. Since the change in frontocentral theta activity appear strongest for a rather fixed duration around the time of the response, non-decision (motor) effects could explain these data as well.

The proposed alternative explanations illustrate that it is difficult to establish which process is reflected by the relationship between brain activity and response times. To further clarify the exact role of spatio-temporal dynamics of slow and fast EEG signals in perceptual decision-making, accumulation-to-bound models can be applied to the behavioral data. Such a model-based approach decomposes the behavioral data into latent processes, allowing brain activity to be associated with a particular cognitive process more precisely and more confidently (Forstmann et al., 2011). For instance, the model can help to identify components of the EEG signal that are specifically related to the rate of the accumulation and the individual differences herein (Philiastides et al., 2006; van Vugt et al., 2012).

Using such a model-based approach, van Vugt et al. (2012) identified theta band oscillations that were associated with the rate of accumulation, giving credence to the interpretation of the frontocentral theta results by Werkle-Bergner et al. (2014). However, in the study by van Vugt et al. (2012), the accumulation process was related to decrease of the theta band activity (van Vugt et al., 2012), rather than an increase, as was found in the study by Werkle-Bergner et al. (2014). When one considers that a decrease (desynchronization) in oscillatory power reflects a richer neural signal, reflected by

larger entropy (Hanslmayr et al., 2012; Werkle-Bergner et al., 2014), one could argue that the accumulation process would be related to a decrease, rather than an increase, of the EEG signal. Along these lines, the decrease (desynchronization) of the posterior alpha activity reported by Werkle-Bergner et al. (2014) might be a better proxy for the evidence accumulation than the increase in frontocentral theta activity. Note that the alpha desynchronization is clearly aligned with the time between stimulus onset and the initial response (Werkle-Bergner et al., 2014, their Fig. 4), which supports such an interpretation.

In short, the study by Werkle-Bergner et al. (2014) emphasizes the importance of temporal high-resolution imaging to understand the underlying dynamics that drive the decision process. The findings indicate that there is no such thing as an accumulation area in the brain. Rather, the study by Werkle-Bergner et al. (2014) underscores that the process of sensory integration is distributed across different regions and different timescales. Finally, the combination of power and entropy analysis offers a promising approach to investigate the temporal dynamics of the latent processes underlying perceptual decision-making.

References

- Cavanagh JF, Wiecki TV, Cohen MX, Figueroa CM, Samanta J, Sherman SJ, Frank MJ (2011) Subthalamic nucleus stimulation reverses medio-frontal influence over decision threshold. *Nat Neurosci* 14:1462–1467. [CrossRef Medline](#)
- Forstmann BU, Wagenmakers EJ, Eichele T, Brown S, Serences JT (2011) Reciprocal relations between cognitive neuroscience and formal cognitive models: opposites attract? *Trends Cogn Sci* 15:272–279. [CrossRef Medline](#)
- Gold JJ, Shadlen MN (2007) The neural basis of decision making. *Annu Rev Neurosci* 30:535–574. [CrossRef Medline](#)
- Hanslmayr S, Staudigl T, Fellner MC (2012) Oscillatory power decreases and long-term memory: the information via desynchronization hypothesis. *Front Hum Neurosci* 6:74. [CrossRef Medline](#)
- Philiastides MG, Ratcliff R, Sajda P (2006) Neural representation of task difficulty and decision making during perceptual categorization: a timing diagram. *J Neurosci* 26:8965–8975. [CrossRef Medline](#)
- van Maanen L, Brown SD, Eichele T, Wagenmakers EJ, Ho T, Serences J, Forstmann BU (2011) Neural correlates of trial-to-trial fluctuations in response caution. *J Neurosci* 31:17488–17495. [CrossRef Medline](#)
- van Vugt MK, Simen P, Nystrom LE, Holmes P, Cohen JD (2012) EEG oscillations reveal neural correlates of evidence accumulation. *Front Neurosci* 6:106. [CrossRef Medline](#)
- Werkle-Bergner M, Grandy TH, Chicherio C, Schmiedek F, Lövdén M, Lindenberger U (2014) Coordinated within-trial dynamics of low-frequency neural rhythms controls evidence accumulation. *J Neurosci* 34:8519–8528. [CrossRef Medline](#)