Spontaneous Brain Oscillations and Perceptual Decision Making

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Abstract

Making rapid decisions on the basis of sensory information is essential to everyday behaviors. Why, then, are perceptual decisions so variable despite unchanging inputs? Spontaneous neural oscillations have emerged as a key determinant of trial-to-trial perceptual variability. New work casting these effects in the framework of models of perceptual decision-making has driven novel insight into *how* spontaneous oscillations impact the decision process. Our synthesis reveals that ongoing alpha-band (8–13 Hz) oscillations bias sensory responses in such a way that changes conscious perception but not, surprisingly, the underlying sensitivity of perceptual processing. A key model-based insight is that various decision thresholds do not adapt to alpha-related, moment-to-moment changes in sensory activity, demonstrating a seeming suboptimality of decision mechanisms in tracking internally-generated changes in sensory responses.

Neural oscillations and the decision process

The combination of psychophysical experiment, brain activity measurement, and computational modeling has led to many recent advances in our understanding of the mechanisms that support perceptual decision making [1,2]. Central to current understandings of decision making is the notion that the sensory apparatus provides varying levels of evidence that a particular perceptual feature is present (called **sensory evidence**). For example, the firing rate of neurons in motion-direction-sensitive area MT (middle temporal) in the macaque can be thought of as representing the degree of sensory evidence in favor of the proposition that “motion of direction *X* is present at a particular location”. To trigger the commitment to a decision, sensory evidence must then be evaluated with respect to a threshold (or **criterion**), such that a certain amount of evidence is needed for a decision to be reached [3,4].

An agent’s decision-making ability is limited by a number of factors. Chief among them is moment-to-moment variability in the physiological state of mechanisms that instantiate sensory and decision processes. Recent advances spanning both physiological and computational research have unveiled a systematic relationship between spontaneously occurring brain states prior to sensory input and variability in subsequent perceptual decisions. In particular, **spontaneous oscillations** have emerged as a key predictor of trial-to-trial variability in decision outcomes for identical sensory inputs. Low-frequency neural oscillations, particularly in the **alpha-band** (8–13 Hz), occur spontaneously within many sensory brain areas and have been repeatedly linked to neuronal excitability (see Box 1). Alpha activity is thereby poised to exert a substantial influence on ongoing sensory and decision processing. Conventionally, spontaneous brain activity is operationalized as a neural signal occurring just before stimulus onset. Accordingly, numerous studies have investigated the effect of prestimulus oscillations on stimulus-related behavior. Because much of this work has focused on the relationship between prestimulus alpha activity and behavior, we see an opportunity to synthesize these findings in the framework of decision-making models. Our focus is on recent experiments that use conditions appropriate for the application of decision models, and what this approach tells us about *how* spontaneous alpha changes sensory and/or decision processes to ultimately influence behavior.

Behavioral impact of spontaneous fluctuations in oscillatory power

Many experiments link trial-by-trial variability in the **amplitude** of spontaneous alpha oscillations to behavior without recourse to a formal modeling framework. A commonly used approach is the stimulus **detection task**, where hit rates (see Box 2) and, to a far lesser extent, false alarm rates, are the primary behavioral measure. Several experiments have also used **discrimination tasks,** where objective measures of accuracy (e.g., % correct) are the primary metric, often in tandem with subjective reports of **confidence** or **visibility**. The emerging pattern of behavioral effects related to prestimulus alpha power are described below and summarized in Figure 1. We argue that these relationships constitute the data that a preliminary model of spontaneous oscillations and decision-making needs to explain. We focus here on vision because it is by far the most well-characterized modality, but we consider the generality of these findings to other sensory systems in Box 3.

Hit rate: In typical detection experiments, decision-makers report whether or not they perceived brief, near-threshold stimuli. Typically, behavioral performance is studied by computing the hit rate, i.e., the proportion of “yes, I saw it” responses. A highly-replicated finding is that low prestimulus alpha power leads to increased hit rates for near-threshold visual stimuli [5–15] and magnetically-induced **phosphenes** [16,17].

False alarms: In the context of multisensory illusions, two early experiments found that reduced prestimulus power in the alpha or beta (14–25 Hz) range made participants more likely to report perceiving an illusory visual stimulus [18,19]. This suggests, in concert with an increase in hit rates, a greater propensity towards false alarming (i.e., reporting stimulus presence on stimulus absent trials) when prestimulus power is low.

Discrimination accuracy: Several studies analyzed the relationship between prestimulus brain state and accuracy in visual discrimination tasks. Often, no effects of prestimulus alpha power on the proportion of correct responses is found [20–24], although Wutz and colleagues did find differences between correct and incorrect responses in the beta-band on a task requiring the identification of the number of stimuli in a display [21]. Notably, an experiment employing 50% stimulus present and stimulus absent trials also found no relationship between prestimulus alpha power and the likelihood of a correct response [25], suggesting that any change in hit rate was largely canceled out by a proportional change in false alarms.

Subjective reports: While replicating the finding that prestimulus alpha power does not affect the proportion of correct responses in discrimination tasks, two recent studies additionally demonstrated that lower prestimulus alpha power instead biases observers to report higher confidence in their decisions [26] and higher subjective visibility of the stimulus [27].

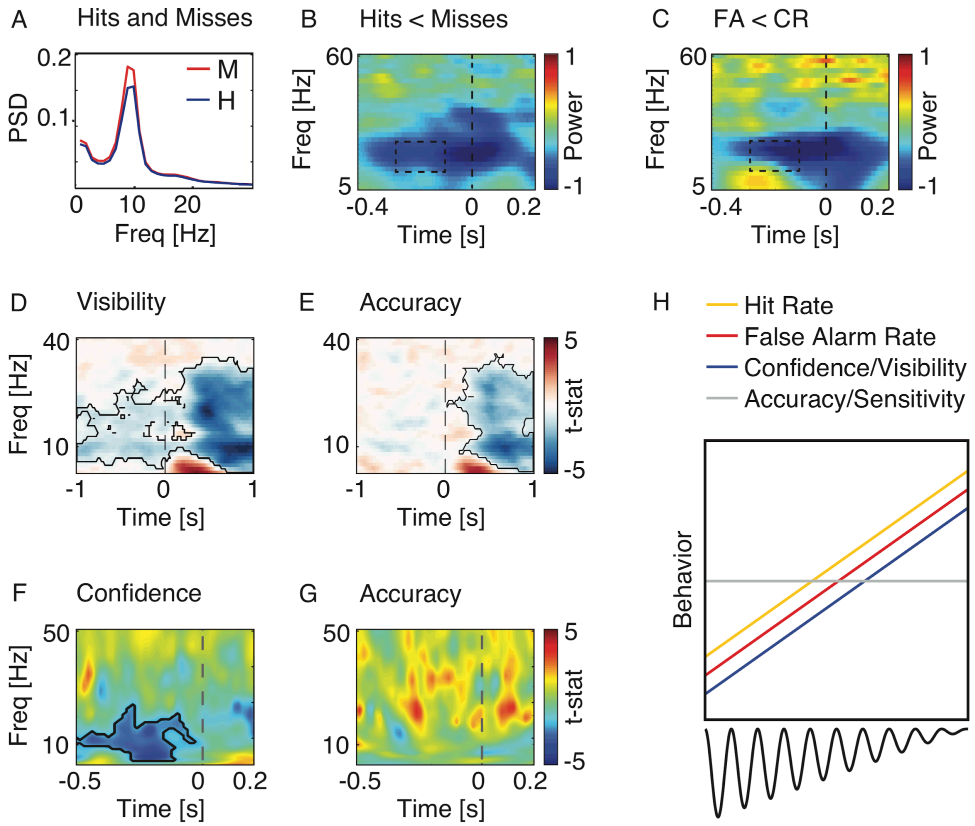

Figure 1. *The relationship between prestimulus power and visual behaviors. A) Power spectrum (PSD) of spontaneous brain activity immediately preceding detected stimuli ("hits"; H) and undetected stimuli ("misses"; M) as measured with MEG over occipital sensors. A highly replicated finding is that alpha amplitude is higher preceding missed stimuli. B) Time-frequency representation of peristimulus EEG power contrasting hits vs. misses and, C) contrasting false alarms vs. correct rejections in a detection task. Recent analyses of stimulus-absent trials reveal that low prestimulus alpha power leads not only to more hits, but more false alarms as well. D) Single-trial multiple regression analysis predicting peristimulus EEG power across time and frequency from subjective visibility ratings and, E) accuracy in a luminance discrimination task. Significant relationships are outlined in black. Note that prestimulus power is negatively related to visibility, but unrelated to accuracy. F) Single-trial multiple regression, predicting EEG power from confidence and, G) accuracy in an orientation discrimination task. Note again that prestimulus alpha power (and adjacent frequencies) has a negative relationship with subsequent decision confidence, but not accuracy. H) Schematic summary of findings. Low prestimulus alpha power leads to higher hit rates, false alarm rates, confidence, and visibility, but does not alter accuracy/sensitivity (d'). This pattern constitutes the behavioral profile that a preliminary decision model will need to explain. Although we schematize these relationships as linear, evidence to date suggests only that they are monotonic. Panel A adapted with permission from [6], B and C from [28], D and E from [27], and F and G from [26].*

Linking oscillations and behavior with models of perceptual decision making

Most studies reviewed in the previous section have relied on ad hoc interpretations of observable data (e.g., oscillatory power and hit rates) to elucidate the latent mechanisms underlying the perceptual effects of prestimulus brain states. However, decision-making mechanisms are not directly observable in the same way that behavior is. We argue that theorizing about the effect of oscillations on behavior can be improved by recourse to a formal model of perceptual decision making that relates observable data to unobservable perceptual and/or neurophysiological mechanisms. A well-established model in perceptual psychophysics [3], which is well-suited to describe perceptual decisions in the kinds of tasks that have been used in this line of research, is signal detection theory (SDT; see Box 2).

We argue that a model-oriented approach offers several advantages over ad hoc interpretations. First, it provides guidance for experimental design: SDT characterizes observers' reports in a detection task as decisions between signal presence and signal absence. Accordingly, estimating SDT parameters in a detection task requires signal-present as well as signal-absent trials. Many previous studies investigating stimulus detection did not include signal-absent trials or did not include them in their analyses, leaving only hit rates on signal-present trials as a measure.

Second, the model-oriented approach allows for more principled interpretation of empirical data. According to SDT, an effect of prestimulus brain state on hit rates can result from a change in sensitivity, criterion, or both. However, the finding of a detrimental effect of strong prestimulus alpha oscillations on hit rates has been predominantly interpreted as a reduction of sensitivity (usually without recourse to SDT). Only recently, two studies investigated the effect of prestimulus power on perceptual decisions using a detection task designed for SDT analysis of sensitivity and criterion [28,29]. Both these studies replicated the finding that weak prestimulus alpha power increases hit rates in stimulus-present trials, but additionally found a similar effect on false alarm rates on stimulus-absent trials, implying that weak prestimulus alpha oscillations induce a more liberal detection criterion. Estimation of SDT parameters confirmed an effect of alpha on criterion, but not d'. That is, observers are more likely to report seeing a stimulus when prestimulus alpha power is low, even when no stimulus is presented. This result is corroborated by work in non-human primates: a composite measure of strong prestimulus neural excitability, which included baseline firing rate and alpha oscillations, predicted a joint increase in false alarm rate and hit rate, i.e., a more liberal detection criterion for prestimulus activity in V1 and V4 but not dorsolateral prefrontal cortex [30]. Furthermore, a novel approach of manipulating observers' detection criterion using stimulus-response reward contingencies [31], showed that experimentally inducing a more liberal criterion causes a reduction of prestimulus alpha amplitude.

Lastly, a model-based approach offers greater explanatory power and makes novel, testable predictions. For instance, if prestimulus alpha oscillations largely bias detection criterion, then only perceptual decisions in tasks requiring the detection of stimulus presence should be affected (so-called "criterion-dependent" tasks), whereas performance on tasks requiring the discrimination of different stimulus features should be unaffected. Indeed, as reviewed above, effects of prestimulus alpha power on performance typically manifest in tasks with a one-dimensional decision space such as detection tasks. In contrast, discrimination tasks, which are based on multi-dimensional decision spaces [3], have usually not yielded similar effects (see [29] for a systematic literature review). Iemi and colleagues [29,32] tested this idea directly by comparing the effects of prestimulus oscillations on performance in several detection and discrimination tasks within participants and with identical stimuli. Indeed, while detection criterion was affected by prestimulus power, the accuracy of location discrimination or orientation discrimination was not. Two recent studies also found null effects of prestimulus power on discrimination accuracy, but, interestingly, found that lower prestimulus alpha increases subjective confidence and visibility ratings [26,27].

How does spontaneous alpha activity change perceptual decisions?

A limitation of SDT is that the criterion parameter can change because of multiple factors [33,34]. For example, because criterion is computed in units of standard deviation relative to the distance from the intersection point between sensory distributions (see Box 2), the criterion that one computes from behavior could change as a result of sensory distribution changes *or* actual evidence-threshold changes (Figure 2). This makes for ambiguity in interpreting criterion effects as being perceptual or decisional in nature. Indeed, criterion effects are often conceptualized as response biases that experimenters should try and control, but criterion changes could also be perceptual in nature [35]. Here we describe four hypothetical scenarios that would lead to the observed relation between prestimulus alpha and criterion, only two of which correspond to a perception-independent response bias.

Decision bias. Criterion changes could come about (as they are often assumed to) by changes in the level of evidence needed to commit to the choice. An observer may choose to require more or less evidence before committing to a decision for reasons that are independent of their perceptual experience of the stimulus. For instance, changing the payoff structure associated with missing a stimulus versus correctly detecting a stimulus could produce an overall bias in an observer's choices that is deliberate. Under this account, spontaneous oscillations might bias the rate that observers report higher/lower confidence or presence/absence of a stimulus for cognitive rather than perceptual reasons. For instance, perhaps participants use a heuristic to estimate their current attentional state, which correlates with ongoing alpha amplitude [25], but which is not actually diagnostic of their perceptual sensitivity.

Motor bias. Criterion estimates could also change if observers more frequently respond "present", not because they are using a different amount of evidence to reach a decision, but because they have a motor bias for the specific effector used to indicate stimulus presence. Such biases have been clearly documented [36]. Under this account, sensory and abstract decision processes would be unaffected by ongoing oscillatory power, which would instead affect, e.g., the excitability of the motor processes involved in issuing a particular response. A motor bias could explain why observers sometimes know that they made the wrong response—as their decision process produced a different outcome than the one they actually selected.

Sensory bias. Rather than a change in the amount of evidence required to report stimulus presence, a change in the measured criterion could also result from a change to the sensory distributions themselves. In this scenario, alpha alters decisions by acting on sensory response distributions in such a way that does not change the separability of signal and noise responses (and thus does not change d’). For example, increasing the means of both signal and noise distributions by an additive factor (with no change in the variances of the distributions) would lead to criterion, but not d’, changes. Such a shift would look like a *relative* criterion change, not because the observer has a deliberate bias to respond with a particular answer, but because their sensory system genuinely represents the world differently. A sensory bias could lead to changes in perceptual appearance (i.e., conscious perception) but need not, as discussed next.

Perceptual bias. If we assume that perceptual experience is not determined by the “first-order” (i.e., primary sensory) representation of a stimulus, but by some higher-order readout or inference based on the sensory state [37], criterion changes can also be accounted for by what we will term a perceptual bias. Take blindsight [38] as an example: putatively, there is some sensory representation suitable for driving above-chance discriminations, but there is no conscious experience. If the contents of conscious experience are reflected in the contents of some higher-order representation, then it is possible that ongoing alpha alters decisions by acting on the higher-order representation directly, bypassing the first-level sensory representation. If low prestimulus alpha made just the higher-order brain area more excitable, this could produce a change in the measured criterion, not because of a strategic bias to respond in a particular way, but because the appearance of the world is genuinely different. The perceptual bias account could explain measured criterion changes *without* changes in the first-order sensory process (contra the sensory bias*)* and without perception-independent response biases (contra the motor and decision biases). In SDT, this could be modelled as a change of the absolute criterion, but not a deliberate one, and where crossing the criterion or not would determine the observers perceptual experience.

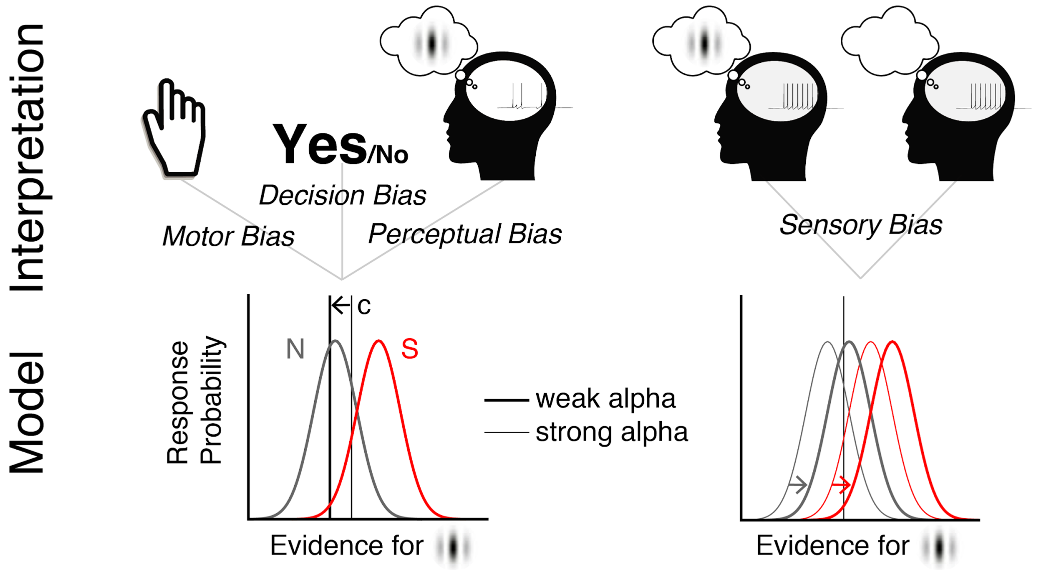

***Figure 2**. Ambiguities in SDT-based criterion changes. Weak prestimulus alpha could lead to the measurement of a more liberal criterion for several reasons. The left panel depicts a model where sensory distributions (signal; S and noise; N) remain the same but the amount of evidence needed to report stimulus presence changes (indicated here by the leftward shift of the vertical line*

representing criterion). This could be caused by a motor bias (the effector used to report stimulus presence is more excitable when alpha is weak), a decision bias (weak alpha produces a deliberate strategy to respond "stimulus present" more often), or a perceptual bias (weak alpha directly changes perceptual experience, without changing the sensory distributions). Alternatively (right panel), the same measured criterion shift could manifest if the sensory distributions change while the absolute criterion remains the same (indicated here by the rightward shift of the sensory distributions). Under the sensory bias account, weak alpha increases sensory responses, resulting either in a change in perceptual experience or a non-conscious sensory bias (empty thought bubble). Current evidence suggests a sensory bias with concurrent change in perceptual experience.

Teasing apart different forms of bias in perceptual decision making is a challenging task because often the same behavioral pattern can manifest through multiple sensory or decision-related processes. However, careful task design and simultaneous recordings of sensory- and decision-related brain processes suggest that ongoing alpha oscillations bias perceptual experience by acting directly on sensory processes. In the following, we describe a new model that qualitatively captures known effects.

Spontaneous alpha activity biases subjective perception and early sensory processing

Recently, Iemi et al [39] examined how prestimulus oscillatory power modulates early visual event-related potentials (ERP) in response to a high-contrast stimulus that produces a C1 ERP component (Figure 3). The C1 peaks around 80 ms post-stimulus and is thought to reflect the initial afferent volley of activity in the primary visual cortex [40,41]. Thus, any modulation of the C1 component by prestimulus alpha power would be strong evidence for a sensory effect. Indeed, it was found that states of high prestimulus alpha/beta power led to a suppression of the C1 amplitude, indicating an inhibitory effect on early visual sensory processing [39]. This result is consistent with prior experiments linking ongoing alpha power to visuocortical multiunit activity [30,42–44] and fMRI BOLD responses [45].

Although the effect of alpha on SDT criterion seems to be caused by an effect of alpha on afferent visual responses, do alpha-related changes in sensory responses impact conscious perception, or just non-conscious sensory processing? Several lines of evidence suggest that prestimulus alpha power alters perceptual experience, *per se*. As mentioned, experiments using subjective report scales have shown increased reports of visual awareness and confidence in response to stimuli presented during states of low alpha power [26,27,46]. Similarly, studies applying transcranial magnetic stimulation to the visual cortex to produce illusory percepts (i.e., phosphenes), have shown that reports of phosphene visibility are dependent on prestimulus alpha levels [16,17]. These findings demonstrate that subjects seem to have reportable, conscious access to their alpha-related changes in sensory processing, suggestive of a change in perceptual appearance.

Strong evidence for a perceptual locus (as opposed to a decision or motor bias) comes from a recent experiment in which the authors compared stimulus detection probabilities in a two-interval forced-choice *detection* experiment (2IFC detection) to stimulus discrimination accuracy in a 2IFC *discrimination* experiment [32]. In 2IFC detection, a stimulus is presented in one of two intervals but not the other, whereas in 2IFC discrimination, a stimulus is presented in both intervals, but one stimulus is designated a target based on some feature (e.g., its orientation). If alpha power leads to a decision or motor bias such that one is more likely to respond during the interval with the lowest alpha power, then accuracy on trials when alpha happened to be lowest during the target interval would be higher for both 2IFC detection and discrimination. However, if alpha has the perceptual effect of making an observer more likely to see *any* stimulus (regardless of its actual presence), then sorting trials according to relative alpha levels during the target interval would only impact detection accuracy, not discrimination. Indeed, the authors found an effect only in 2IFC detection, but not discrimination. In other words, low alpha power seems to make stimuli *appear* more visible, rather than bias observers' deliberate decision process or output effectors.

We argue that most if not all findings in the visual domain regarding modulation of perceptual decisions by spontaneous fluctuations in alpha power can be qualitatively accounted for by a **baseline sensory excitability model** (BSEM; Figure 3C). This model has three key features: 1) We suggest that spontaneous alpha amplitude exerts a *global* change in the baseline firing rates of sensory neurons, regardless of their particular feature preferences. In detection tasks, this baseline change affects both the stimulus-absent and stimulus-present responses equally, such that no change in d' is evident (consistent with the empirical findings discussed in the previous sections). In discrimination tasks, sensory responses in the detectors tuned to *both stimulus alternatives* are increased by the same amount, leaving their discriminability, and hence the accuracy of discrimination responses, unchanged. 2) In concert with changes to baseline firing levels in sensory brain areas, BSEM also proposes that the criterion used to report stimulus presence (or confidence/visibility level) is not appropriately updated to compensate for the new state of the sensory representations. Thus, lower prestimulus power leads to more frequent reports of stimulus presence, more false alarms, and higher levels of reported confidence and visibility, all without affecting detection or discrimination sensitivity. 3) Lastly, in order to explain changes in confidence ratings in discrimination tasks, we propose that confidence criteria are set perpendicular to the *detection* axis for each stimulus, rather than parallel to the *discrimination* axis. This amounts to the claim that confidence is computed, not as the balance of evidence between two alternatives (e.g., distance from the discrimination axis), but as the overall amount of evidence for the selected response—a notion gaining independent support from a number of recent psychophysical and neural studies on perceptual confidence [47–57]. In point 1 above, we assume for simplicity that baseline excitability has an additive (linear) effect on firing rates in sensory areas. This assumption can be relaxed, however, and a model where alpha has a multiplicative effect on firing can also explain the results if we further assume that the trial-to-trial variability of neural responses scales with alpha such that the signal-to-noise ratio is unchanged (for example, see [47]).

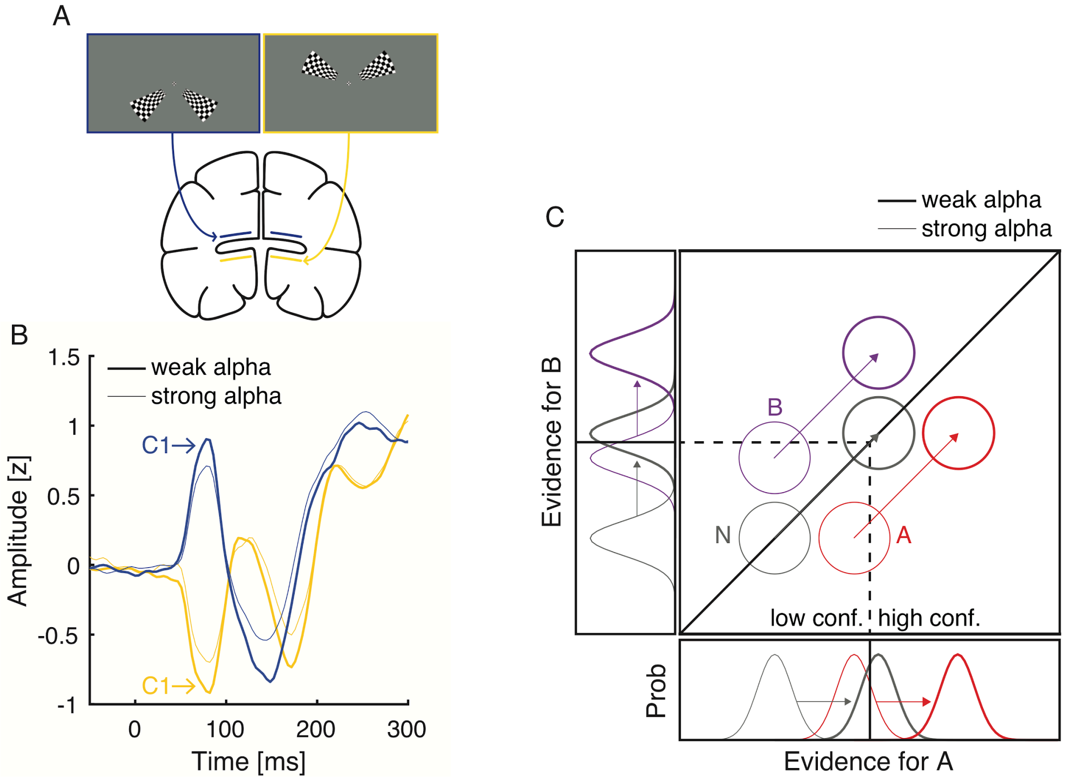

Figure 3. *Sensory modulation by alpha and a SDT model. A) In this EEG study, large C1 responses were elicited by bilateral stimulation in the upper (yellow lines) and lower (blue lines) visual field, corresponding to the lower and upper banks of the calcarine sulcus (V1; coronal plane). Due to the similarity in orientation of the cortical sheet, bilateral responses would, in theory, sum to produce a large C1 component whose polarity inverts for lower versus upper visual field stimuli. B) C1 ERP over occipital electrodes as a function of upper or lower visual field and high or low prestimulus alpha power. Strong prestimulus alpha power had a suppressive effect on the C1, indicating, presumably, an inhibition of stimulus-related firing in primary visual cortex when alpha is strong [39]. C) The Baseline Sensory Excitability Model (BSEM). Center panel shows a SDT representation of a discrimination task where circles represent bivariate probability distributions of sensory evidence as viewed “from above” for two stimulus alternatives (A and B) as well as no stimulus (or “noise”; N). The solid diagonal line represents the optimal discrimination boundary separating class A from B. Reduced spontaneous alpha power causes larger sensory responses in all feature detectors, modelled as a diagonal translation (arrows) of the evidence distributions without increasing the separability (d’) of the distributions. BSEM explains increased confidence without accuracy changes by assuming that confidence criteria (dashed line separating evidence values associated with low and high confidence) are placed according to the absolute level of evidence associated with each choice, rather than as distance from the discrimination boundary. Thus, lower alpha leads to increased probability of surpassing the criterion for high confidence. Subpanels below and to the left of the center panel show the projection of the sensory evidence distributions onto the one-dimensional detection space. When detecting stimulus A, for example, low alpha increases both the noise and evidence-for-A distribution, explaining increased hits and false alarm observed in detection experiments. The*

alignment of confidence and detection criterion highlight the proposed similarity in judgment type according to BSEM. Panels A and B adapted with permission from [39].

Implications for perceptual decision making and models thereof

If BSEM is accurate, it would imply a violation of the so-called "optimal" or "Bayesian" confidence hypothesis, which states that confidence is an optimal read-out of the probability that a decision is correct. The optimal view is explicit in numerous computational models of perceptual decision making [58–63]. Because BSEM proposes that confidence criteria do not (perfectly) adjust to trial-to-trial fluctuations in alpha-driven changes in sensory responses, it can explain empirical cases where alpha has been shown to selectively impact confidence/visibility ratings without changing discrimination accuracy [26,27,31]. The inability to appropriately update these subjective criteria would thus violate optimal confidence.

A corollary of imperfect criteria adjustment is that the decision process does not, on individual trials, follow that of an ideal observer. The internal mechanisms for setting detection and confidence criteria seemingly does not have access to alpha-related changes in sensory excitability and cannot, therefore, update criteria based on the expected distribution of sensory responses at different levels of cortical excitability. This is perhaps unsurprising in an SDT framework, because only a single sample of evidence is postulated to underlie decisions on each trial, making it difficult to know whether that sample is coming from a distribution of high or low sensory excitability. However, it is perhaps more surprising that spontaneous fluctuations in sensory excitability are not taken into account under some other decision models that posit, for example, that a full distribution over possible stimulus values is represented on each trial and forms the basis for confidence [61,64].

Attention-induced fluctuations in oscillatory power

The studies reviewed above have focused on fluctuations in oscillatory power that are spontaneous in the sense that they were not induced by experimental manipulations of attention or motivation. Of course, this does not rule out that "spontaneous" fluctuations simply reflect fluctuations in participants' self-controlled attention or other states. When attention is experimentally manipulated, for example by cueing task-relevant locations or stimulus features, alpha power typically decreases in cortical areas representing the relevant location [65,66] or feature [67]. The topographical distribution of alpha power can even be used to track the focus of spatial attention with high precision [68–70]. This cue-induced shift of alpha power has been interpreted as a gating mechanism, amplifying relevant information through greater excitability in task-relevant areas and suppressing distraction through greater inhibition in task-irrelevant areas [71,72]. This notion is supported by studies showing that cue-induced lateralization of alpha power suppresses processing of distracting stimuli in cortical areas corresponding to the unattended visual, tactile, or auditory location [73–75], but see [76].

Is the finding that spontaneous fluctuations of alpha power affect SDT criterion rather than sensitivity at odds with the finding that cue-induced topographical shifts of alpha power affect accuracy? Not necessarily. First, spontaneous fluctuations of excitability in experiments where the location or feature of the upcoming stimulus is unknown to the subject will affect, on average, relevant and irrelevant information to the same extent with no net effect on accuracy. By contrast, cue-induced fluctuations of alpha power can selectively enhance relevant or suppress irrelevant information, possibly resulting in a net increase in accuracy. Second, psychophysical studies have shown that spatial cueing indeed induces a more liberal detection bias at attended compared to unattended locations [77,78]. It remains to be shown whether the effect of selective attention on criterion can be accounted for by BSEM.

Concluding remarks and future directions

Here we have focused on the relationship between spontaneous oscillatory activity, principally in the alpha-band, and subsequent perceptual decisions. Prior to the application of SDT models, the predominant understanding was that reductions in prestimulus alpha amplitude led to more accurate perceptual decisions (though see [18] for a non-model-based approach that reaches a similar conclusion as our synthesis). Instead, reduced prestimulus alpha biases observers to report stimuli more often, regardless of their presence, to feel that stimuli are more visible, and to feel more confident in their discrimination choices. Rather than being a bias due to cognitive or motor factors, the evidence we review suggests that this bias is sensory in origin and changes the observer's perceptual experience without improving the sensitivity of their decisions.

We suggest a SDT-based model, BSEM, that qualitatively captures these effects by assuming that high amplitude spontaneous alpha activity inhibits sensory responses quite globally — for all representations of sensory evidence involved in the decision process — and that detection and confidence criterion do not fully adapt to dynamic, alpha-related change in sensory representations. We advocate for more work applying decision models to link spontaneous oscillations to perceptual decision making through neurally plausible computations. In particular, the popular drift diffusion model has rarely been applied in this domain and could leverage RT data to gain additional mechanistic insight (see Box 4). Population coding models [64,79,80], which have almost never been applied to this question, may also be a fruitful avenue to explore along with tasks that these models capture well, such as perceptual estimation. However, even within a relatively simpler SDT framework, questions remain. For instance, are alpha effects on neural responses additive, multiplicative, or non-monotonic? Does prestimulus alpha influence the magnitude of sensory responses or the trial-to-trial variability of sensory responses as well? These questions are well characterized within a SDT framework and could be addressed empirically by further physiological characterization of the effects of alpha on single neuron and population responses and across a range of stimulus values (e.g., across the neural contrast response function). Simultaneous recordings of multiple neurons could also address questions about the effect of alpha on noise correlations and population-level information content, if any. Lastly, there is clearly much to learn about the functional generality of alpha oscillations across sensory modalities (Box 3). One advantage of the modelling approach advocated for here is that it permits the effects of spontaneous brain activity in different sensory modalities to be compared within a common framework.

BOX 1. Alpha genesis and neural excitability

Critical to understanding the functional/mechanistic role of the alpha rhythm, will be an understanding of its generation. Despite decade of research, conclusive empirical and modelling work on this question is still limited.

Alpha pacemaker cells (termed high-threshold bursting cells; HTC) have been discovered in the lateral geniculate nucleus (LGN) of the cat thalamus. In vivo and in vitro study of HTC has uncovered that they account for 20-30% of cat LGN neurons, burst at alpha frequencies, synchronize locally via gap-junctions, inhibit (via interneurons) thalamic relay neurons that project to visual cortex, and are strongly coherent with alpha rhythms simultaneously recorded from the animal's scalp [86–88]. These findings suggest a feed-forward alpha-based mechanism for controlling excitatory input to visual cortex. In addition to thalamic generators, the distribution of alpha activity across cortical layers has been interpreted to suggest possible cortical contributions, either from within layers of early visual cortex, via interactions with the thalamus, or via feedback from generators in higher-order cortical areas [42,89–96].

Whatever the generator(s), there is clear evidence that alpha amplitude in many cortical areas is inversely related with measures of cortical excitability, such as spontaneous and task-related single-unit firing rates in humans [97], rodents [98] and monkeys [99], as well as population-level activity measures of excitation (multi-unit activity [42,92,95]; gamma-band oscillations [44]; and hemodynamic BOLD fMRI signal [45,100], but see [101]). Spontaneous alpha amplitude also predicts within- and between-subject variation in the likelihood of phosphene perception following magnetic stimulation of early visual cortex [16,17,102]. Importantly, prestimulus alpha amplitude is inversely related to early visual responses even when controlling for possible confounding mechanisms, such as a baseline shift of non-zero mean oscillations, non-oscillatory rotations or offsets in the neural power spectrum, or moment-to-moment variability in fatigue [39], suggesting a true oscillatory effect.

BOX 2: Signal Detection Theory

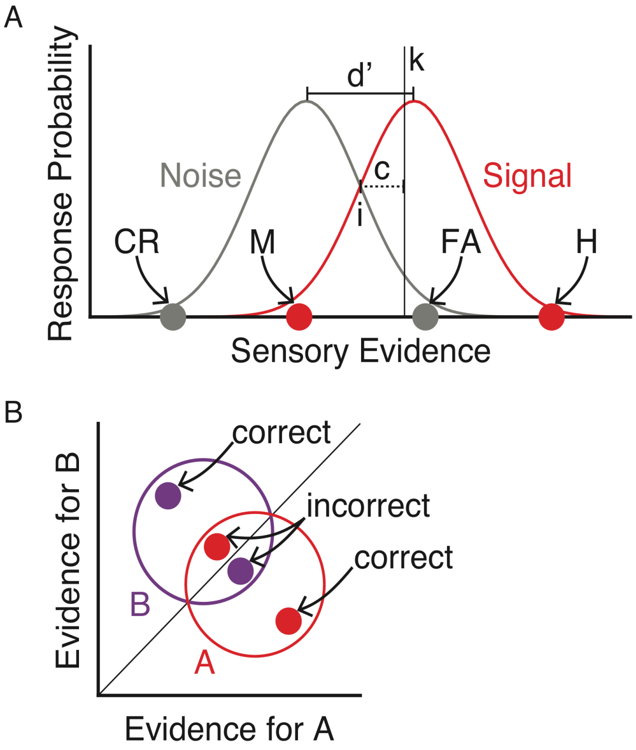

Figure I A) Detection task. According to SDT [3], observers decide on stimulus presence vs. absence by evaluating the strength of internal responses (i.e., sensory evidence) along a single response dimension, resulting in a one-dimensional decision space. An internal response can be due to noise (stimulus-absent trials) or a signal (stimulus-present trials). These responses can be represented by probability distributions, indicating response mean and variability across trials. Filled circles represent sensory evidence values on four hypothetical trials, with color representing the distribution that generated the evidence. Observers report “stimulus present” if the response exceeds the detection criterion (vertical line) and “stimulus absent” otherwise. Accordingly, observers’ reports can be categorized as hits (H;“present” report; stimulus present trials), misses (M;“absent” report; stimulus present trials), false alarms (FA;“present” report; stimulus absent trials) and correct rejections (CR;“absent” report; stimulus absent trials). The placement of the criterion determines how much evidence is required for “stimulus-present” responses. The criterion *c* can be estimated from the empirical z-transformed hit rates (*HR*) and false alarm rates (FAR) as:

$$c = -\frac{1}{2}(z(HR) + z(FAR))$$

Note that *c* is computed from behavior and is in standard deviation units *relative* to the intersection (*i*) of the sensory evidence distribution. In contrast, the value *k*, here, denotes the *absolute* level of sensory evidence needed to commit to a choice, which is unknown from behavior but presumably is represented in the brain.

Detection sensitivity, or d' (d-prime), describes how separable signal and noise are and is given by the distance between the means of the probability distributions relative to their standard deviations. This can be estimated from behavior as:

$$d' = z(HR) - z(FAR)$$

B) Discrimination task. Stimulus features are processed by feature-selective channels with overlapping tuning functions, such that stimulus category A (e.g., left tilt) strongly activates channel A, but also, to a lesser extent, channel B (e.g., right tilt), resulting in a two-dimensional decision space. Observers decide on the stimulus category by comparing the "location" of the responses in both channels to a decision criterion (diagonal line). Discrimination accuracy is limited by the overlap (i.e., mean and spread) of the response distributions across trials. In this figure, assuming an unbiased decision criterion, a sample of evidence from the A distribution that produces larger sensory evidence in the A channel will produce the correct response, "A". If, because of variability, the response was larger in channel B, then the incorrect response "B" would be issued instead.

BOX 3: Function of spontaneous oscillations in other sensory modalities

Several experiments using auditory detection tasks observed lower alpha power prior to hits compared with misses [103,104] (though see [105] for a negative finding). During an auditory lexical decision task, no effect of prestimulus alpha on discrimination accuracy was found [106]. In a 2AFC pitch discrimination task, lower prestimulus alpha power predicted higher confidence ratings despite the two pitches being identical [46]. Using a frequency discrimination task, no relationship between prestimulus low-frequency power and perceptual choices was found [107]. Thus, there is growing evidence that ongoing alpha impacts auditory detection and discrimination in a similar manner to vision, yet model-based approaches in this domain are rare.

In the somatosensory domain, several experiments using detection tasks have found lower alpha power preceding hits [108–111]. In one of few SDT analyses of spontaneous alpha and tactile detection, Craddock et al. [112] found that higher prestimulus alpha activity correlates with a conservative criterion, just as in vision. In one of the few causal experiments, 10-Hz alternating current stimulation was found to specifically modulate tactile detection criterion, but not sensitivity [113]. A recent study using a simultaneous detection and localization task found that high prestimulus alpha activity was related to a more conservative criterion in the detection task, but also lower accuracy in the localization task [114]. However, the relationship between power and somatosensory perceptual decisions may be nonlinear: several studies found that prestimulus alpha and hit rates are related by an inverted U-shape function [115–118].

Complicating the picture, Haegens et al. [119] demonstrated that reduced prestimulus alpha power in the macaque somatosensory cortex correlates with a conservative detection criterion, contrary to reports in the visual modality and to [112]. This inconsistent finding may be explained by several reasons: (1) reward scheduling may have influenced the monkey’s perceptual decision making; (2) the suggested inverted U-shape relationship makes it possible that discrepant results arise from sampling power from a limited range of the inverted U-curve.

BOX 4: Expanding to other models of perceptual decision making

Though useful as a starting point, a limitation of SDT is that it does not encompass salient aspects of behavior like response time (RT). To better understand how spontaneous oscillations influence perceptual decisions, future work will need to incorporate oscillatory effects into other modelling frameworks such as the drift diffusion model (DDM). The DDM casts perceptual decision making as the accumulation of a decision variable over time towards a boundary representing a choice [4]. A recent experiment [31] using a detection task found that strategic shifts in criterion led to changes in alpha power. The corresponding changes in RT and choice behavior were best accounted for by a diffusion model with a bias in the drift rate for stimulus-present choices. That is, deliberately shifting towards a more liberal criterion reduces ongoing alpha power, which leads to faster evidence accumulation towards a “stimulus present” decision, but slower accumulation towards the “stimulus absent” boundary.

In a task combining elements of detection and discrimination, lower spontaneous alpha predicted faster RT and more rapid evidence accumulation (as inferred from a neurophysiological index of the decision variable, the centroparietal positivity potential) [120]. This too implies that prestimulus alpha can impact evidence accumulation dynamics and should have systematic effects on RT distributions. In general, though, the effects of spontaneous alpha on RT are heterogenous and sometimes null [6,22,43,121]. Moreover, in discrimination tasks, it is unclear how the DDM could capture the finding that discrimination accuracy is unaffected by prestimulus alpha as, all things being equal, changes to evidence accumulation rates typically translate to changes in accuracy. Lastly, the impact of alpha on confidence reports has not been systematically explored in DDM, yet the DDM can naturally account for confidence [59], suggesting a promising avenue of future research whereby a systematic modeling framework could help integrate and explain many disparate findings.

GLOSSARY

Alpha-band: Oscillations between 8–13 Hz, ubiquitous in sensory systems, cortical and subcortical structures, and closely linked with neural excitability (see Box 1). Many experiments have focused on alpha and perceptual decisions.

Amplitude: The magnitude of an oscillation, often measured in volts for EEG and tesla for MEG. (Power is amplitude squared.)

Baseline sensory excitability model: A SDT-based model proposed here that describes the relationship between spontaneous alpha amplitude and sensitivity, criterion, confidence, and sensory responses and which qualitatively captures known effects in the visual modality. See Figure 3.

Confidence/Visibility: Both are subjective reports about perceptual processing. Confidence is a subjective estimate of the likelihood that a decision was correct, whereas visibility is a subjective report about the clarity or intensity of a perceptual experience. Several different types of reporting scales are commonly employed in the literature [122].

Criterion: The amount of sensory evidence needed to commit to a decision. See Box 2 for an important distinction between absolute and relative understandings of criterion.

Detection task: A task that requires an observer to detect the presence of a particular stimulus or feature. Responses are typically coded as “present” or “absent” and hit rates and false alarm rates can be computed. Detection tasks are sometimes classified as *criterion-dependent* because observers are prone to adopting, for various reasons, different criteria for responding “present”. This fact renders the use of accuracy (% correct) or hit rate problematic as measures of performance.

Discrimination task: Discrimination differs from detection in that that the stimulus is typically always visible but requires the discrimination of one of its features. Discrimination tasks are sometimes classified as *criterion-free* because observers are thought to seldom have a bias for one stimulus alternative over another (e.g., left or right tilt), rendering accuracy (% correct) a viable measure of performance that often mirrors d’.

Excitability: A state of higher or lower probability of firing in a neural population (either spontaneously or in response to a stimulus).

Phosphene: In this context, phosphenes are visual experiences induced via brain stimulation. Under constant stimulation intensity, the probability of perceiving a phosphene is often used as an indirect measure of the excitability of the stimulated area.

Sensory evidence: The evidence that a sensory mechanism (e.g., a neuron) has for a particular feature (e.g., a vertical line) being present in the environment.

Spontaneous Oscillations: Spontaneous oscillations refer to rhythmic fluctuations in neuronal membrane potentials not caused by any experimental or task variables (such as attention, stimulus presentation, etc.). Spontaneous activity is often operationalized as activity during a *prestimulus* time window, since variability in brain activity at this moment is not caused by any experimental event. Care must be taken to reduce potential influences from unmeasured experimental variables such as expectations or fatigue.

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