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Neural dynamics of probabilistic perceptual decision making in the human brain

A dissertation submitted in partial satisfaction
of the requirements for the Doctor of Philosophy

in

Neurosciences with a specialization in Computational Neurosciences

by

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2020

The dissertation of Nuttida Rungratsameetaweemana is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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Chair

University of California San Diego

2020

iii

DEDICATION

To Duangta and Somkiat Rungratsameetaweemana

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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The introduction, in full, is a reprint of the material as it appears in: Rungratsameetaweemana, N, Serences, JT. Dissociating the impact of attention and expectation on early sensory processing. *Current Opinion in Psychology, 29,* 181-186, 2019. The dissertation author was the primary author of this paper.

Chapter 1, in full, is a reprint of the material as it appears in: Rungratsameetaweemana, N, Itthipuripat, S, Salazar, A, Serences, JT. Expectations do not alter early sensory processing during perceptual decision-making. *Journal of Neuroscience, 38(24)*, 5632-5648, 2018. The dissertation author was the co-primary author of this paper.

Chapter 2, in part, is currently being prepared for publication of the material. Rungratsameetaweemana, N, Itthipuripat, S, Garci, JO, Serences, JT. The dissertation author was the primary author of this paper.

Chapter 3, in full, is a reprint of the material as it appears in: Rungratsameetaweemana, N, Squire, LR, Serences, JT. Preserved capacity for learning statistical regularities and directing selective attention after hippocampal lesions. *Proceedings of the National Academy of Sciences, 116(39)*, 19705-19710, 2019. The dissertation author was the primary author of this paper.

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PUBLICATIONS

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Nelli, S, Itthipuripat, S, **Rungratsameetaweemana, N**, Serences, JT. The speed-accuracy tradeoff reveals flexible access to accumulating sensory evidence during human decision-making. *Under revision.*

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*Equal contribution

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ABSTRACT OF THE DISSERTATION

Neural dynamics of probabilistic perceptual decision making in the human brain

by

Nuttida Rungratsameetaweemana

Doctor of Philosophy in Neurosciences with a specialization in Computational Neurosciences

University of California San Diego, 2020

Professor John T. Serences, Chair

Our visual world is full of ambiguous sensory signals, from which we have to extract relevant and meaningful information in order to guide optimal actions. To maximize the efficiency of this process, our visual system relies on foreknowledge to prioritize the processing of relevant or expected features. Knowledge of statistical regularities in the environment can lead to faster detection and recognition of objects when they are encountered in an expected context (e.g., a bird in a backyard) than when they are encountered in unlikely context (e.g., a bird in a washing machine). In addition, knowledge about the current task goals can also support faster and more accurate processing of relevant over irrelevant items--a mechanism referred to as selective attention. In what manner do these "top down" modulatory factors individually and jointly affect visual sensory processing, decision making, and behavior? In three studies, we examined how perceptual decision making is modulated by prior expectation about stimulus probabilities alone and in the context where knowledge about the current behavioral goals were available. We examined these effects both neurally via electroencephalography

(EEG) and behaviorally through psychophysics and also in amnesic patients in relation to age-matched controls. To this end, we first devised an experimental paradigm where prior expectation and selective attention could be individually manipulated. The behavioral readouts from this paradigm were continuous which made it possible for the temporal evolution of the effects of expectation and attention on decision process to be probed both behaviorally and in relation to the continuous neural (EEG) measures. We first demonstrated that prior expectation improves decision processes by primarily affecting post-perceptual operations such as initiation and execution of motor responses, instead of directly improving the efficiency of early sensory processing. This finding confirms an idea that has been put forth by traditional theoretical framework that prior expectation affects decision making by preferentially modulating motor responses that correspond to sensory inputs with high probability of occurring. Further, we showed that while both expectation and attention improved behavior, the underlying neural mechanisms that give rise to these effects differed: while attention operates on the early processing of sensory inputs, expectation affects the late stage of decision making by biasing motor responses towards the most likely decision choice. These differential temporal dynamics of expectation and attention were observed bot h behaviorally and neurally. Finally, we demonstrated that an ability to utilize knowledge about current task goals and to form expectation based on statistical regularities of the sensory environment can be independent of a declarative memory system.

Introduction:

Dissociating the impact of attention and expectation

on early sensory processing

Dissociating the impact of attention and expectation on early sensory processing

Nuttida Rungratsameetaweemana[1] and John T Serences[1,2,3]

Most studies that focus on understanding how top-down knowledge influences behavior attempt to manipulate either 'attention' or 'expectation' and often use the terms interchangeably. However, having expectations about statistical regularities in the environment and the act of willfully allocating attention to a subset of relevant sensory inputs are logically distinct processes that could, in principle, rely on similar neural mechanisms and influence information processing at the same stages. In support of this framework, several recent studies attempted to isolate expectation from attention, and advanced the idea that expectation and attention both modulate early sensory processing. Here, we argue that there is currently insufficient empirical evidence to support this conclusion, because previous studies have not fully isolated the effects of expectation and attention. Instead, most prior studies manipulated the relevance of different sensory features, and as a result, few existing findings speak directly to the potentially separable influences of expectation and attention on early sensory processing. Indeed, recent studies that attempt to more strictly isolate expectation and attention suggest that expectation has little influence on early sensory responses and primarily influences later 'decisional' stages of information processing.

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Attention, expectation, and perceptual inference

Over the past 40–50 years, a tremendous amount of effort has been spent trying to understand how prior knowledge shapes human information processing from the earliest stages of sensory analysis to decision-making to the execution of motor responses. Prior knowledge is a 'top-down' modulatory factor to the extent that priors reflect internal states and neural representations that could influence perception and behavior [1]. One important 'top-down' factor relates to knowledge about the probability that certain stimuli will occur in a specific context: a traffic light is likely to turn red after it turns yellow, a toaster is likely to be on top of a counter instead of under the kitchen sink, and so forth [2,3]. These top-down priors also code for more complex statistical regularities about stimulus identity and component features: a building is likely to have structures that are composed of straight lines rather than curvatures. Thus, expectations based on fore-knowledge can exert a powerful influence on object identification and scene understanding [2,3], and a growing body of research focuses specifically on the impact of expectations on early sensory processing [4,5**,6].

Another type of top-down knowledge pertains to the relevance of specific stimuli in the context of current behavioral goals: when looking for your car in the parking lot, knowledge of its color, shape, and size can be exploited to improve search efficiency by reducing the set of stimuli that must be interrogated. Critically, expectations about statistical regularities and knowledge about relevant features could have dissociable influences on information processing, as the probability that a stimulus will be encountered in a given context is not necessarily linked to its behavioral relevance [4,5**]. Thus, following Summerfield and de Lange, we define expectation as the mechanism that operates based on the probability of stimulus occurrence, and we define attention as the mechanism that operates based on the behavioral relevance of different stimuli [4,5**].

The classic Posner cueing paradigm highlights the difficulties associated with dissociating the effects of expectation from the effects of attention. The task manipulates the probability that a target stimulus will appear on the left or the right of fixation, and participants have to press a button when they detect the onset of the peripheral light [7]. This manipulation alters the probability that the target stimulus will appear in one spatial location, which in turn leads to faster response times and more accurate responses. This seminal result, which has given rise to thousands of subsequent studies using variants of this basic paradigm, was originally interpreted as evidence for more efficient early sensory processing related to the selective deployment of spatial attention. However, later work demonstrated that these results, as well as results from more complex visual search tasks, can often be explained via an increase in the willingness of participants to indicate that they saw a target at the cued location, irrespective of how much sensory evidence was present to support a 'yes' response (i.e. the cue led to a change in decisional factors) [8–11].

This debate about how to interpret what is perhaps the most widely used paradigm in the field of 'selective attention' illustrates two important points. First, this simple variant of a cueing paradigm conflates the theoretically distinct notions of expectation (where a stimulus is likely to appear) and attention to relevant features in the environment (which spatial position is likely to contain the task-relevant information). As a result, any influence of the cue on information processing is difficult to attribute to either factor or to some combination of the two. Second, the behavioral results can be explained either by a change in the sensitivity of early sensory processing or by a change in decisional factors. Importantly, similar issues arise in many other studies within the literature, as experimenters typically manipulate either the probability that a known target stimulus will appear or they manipulate information about which stimulus is most task-relevant. As a result, the field lacks a coherent framework that respects the potentially distinct influence of different types of top-down knowledge on sensory processing. In turn, the lack of a clear framework has important implications for canonical models of

2

information processing such as the notion of perception as inference [12,13] [see Box 1], as well as for long-standing debates about the cognitive penetrability of perception [14–16].

The effects of attention and expectation on cortical information processing

Very few studies have independently manipulated expectation and attention to assess the impact of each factor on sensory processing. However, studies that attempt to focus on either expectation or attention have claimed that both factors modulate pre-stimulus neural responses [17,18], stimulus-evoked responses [19•,20–22,23•,24–27], and the efficiency of sensory read-out by putative decision mechanisms in parietal and frontal cortex [28–31]. For the sake of brevity, we focus here on response modulations in early sensory cortices, both before and after a stimulus has been presented. We first briefly review studies about the effects of selective attention on these responses, and then review recent studies that attempt to experimentally dissociate attention and expectation to assess the separability of their effects on early sensory processing.

The impact of attention to relevant features on early sensory processing

Many single-unit physiology [32] and fMRI [17] studies demonstrate that attending to relevant locations modulates neural responses in early visual cortex, even before a stimulus is presented [33–35]. Manipulating the relevance of spatial positions or low-level visual features also modulates the SNR and feature-selectivity of sensory-evoked responses that are associated with attended stimuli [24,27,33,36–41]. For example, work by Treue *et al.* demonstrated that attention increases the precision of motion-selective population response profiles in MT, and more recent fMRI work shows that these increases in feature-selectivity can occur even in the absence of an overall increase in the BOLD response [19•,20] (Figure 1a,b). Critically, at least some of these studies cued a behaviorally relevant feature, such as a location or a direction of motion, without inducing any expectation about the probability of the likely target feature [19•,36,39]. Thus, according to the operational definitions of attention and expectation outlined above, both pre-stimulus and post-stimulus modulations appear to occur due to manipulations of behavioral relevance, independent of changes in event probabilities.

The impact of expectation on early sensory processing

Initial reports regarding the impact of expectation on sensory-evoked responses demonstrated that large-scale cortical responses measured with fMRI were smaller than responses associated with unexpected stimuli [21,22,25]. This finding is consistent with generative models that frame perceptual inference as the iterative combination of priors with sensory evidence, because sensory evidence that is consistent with priors can support a rapid perceptual inference without the need for extensive processing. In turn, total cortical activity, as measured using methods such as fMRI, should be lower compared to situations where disparate priors and sensory evidence must be reconciled. In addition to attenuated BOLD responses, studies also suggest that expected stimuli evoke a more precise feature-selective pattern of responses in early visual cortex compared to response patterns associated with unexpected stimuli, similar to the modulations observed with feature-based attention [19•,36,42]. Again, this observation is in line with the idea that consistent priors and sensory evidence should lead to a precise inference, even though overall cortical activity is reduced.

In one study, Kok *et al.* [23•] used fMRI and a task that cued participants on a trial-by-trial basis that an impending target was either going to be a 45° or a 135° oriented grating. The authors analyzed the pattern of responses across voxels in primary visual cortex (V1) using multivariate pattern classification analysis (MVPA) and demonstrated that expectation increased the separability between response patterns associated with each grating, even before stimulus onset (Figure 1c,d). MRI studies have also shown that expectation for a particular object category can bias pre-stimulus activation in face-selective regions of IT cortex [43,44]. Finally, spontaneous fluctuations in pre-stimulus fMRI signals in sub-regions of visual cortex predict the probability that a particular feature or object will be reported when viewing an ambiguous or weak sensory stimulus [42,45]. These spontaneous fluctuations may reflect endogenously mediated shifts in expectation, and they highlight the Bayesian notion that small shifts in expectation can have a large impact on perceptual inference when sensory evidence is weak or ambiguous [5••].

Reconciling the effects of attention and expectation on early neural modulations in sensory cortices

Despite the apparent similarity of the early neural modulations attributed to selective attention and to changing expectations, studies that manipulate expectation typically have done so by explicitly providing prior information about the identity of an upcoming stimulus (e.g. a 45° or 135° grating, as in Refs. [18,23•]). As a result, participants not only knew what target feature to expect, but they also knew what target feature was relevant to performing the behavioral task on each trial. A similar argument can be made about several other studies [18, 46–50,51•,52•,53] and based on the operational definitions of attention and expectation articulated in Summerfield and de Lange, the expectation cue can be expected to induce a shift of attention to the cued (expected) stimulus feature [5••]. Given this consideration, any changes in behavior or associated modulations in early visual cortex were likely influenced to an unknown degree by both expectation and selective attention as opposed to expectation alone.

Recently, several studies have tried to more directly compare the effects of expectation and attention on behavior and on neural responses in visual cortex. One behavioral study used cues to manipulate the probability that a faint stimulus would be presented. These expectation cues increased both hits and false-alarm rates, whereas manipulating stimulus relevance (attention) improved the precision of sensory processing by selectively lowering false-alarm rates [53]. Using the reverse-correlation method and modelling, this study further suggested that the differential effects of attention and expectation could be accounted for by the fact that attention suppressed internal noise and thus increased precision while expectation biased the baseline activity of sensory processing in favor of the cued stimulus. In addition, a fMRI study found that attention increased the separability of response patterns associated with

Figure 1
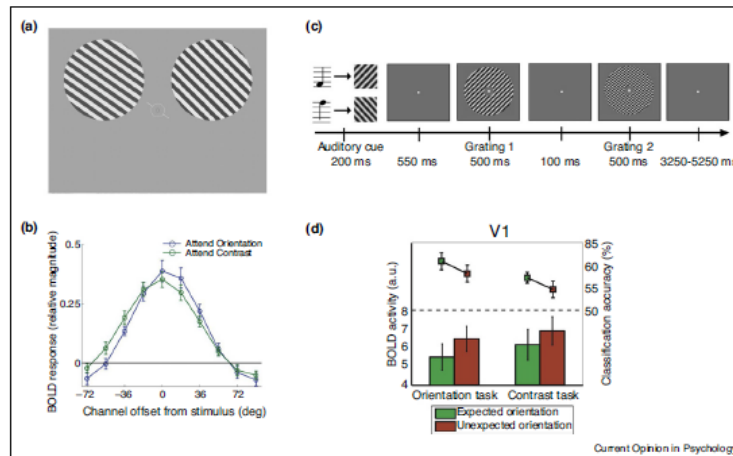
Increased gain modulation of visual responses by attention and expectation. **(a)** Schematic of the experiment design used in Ref. [19*]. Participants fixated on the central cue, while attending to either the orientation or contrast of the gratings in alternating blocks of trials. The orientation of one grating always closely matched the oriented cue line presented at fixation, while the orientation of the remaining grating either matched or mismatched the orientation of the first grating by a small CW or CCW offset. Similarly, the contrast of the second grating either matched or mismatched the contrast of the first grating by a small contrast change. On attend-orientation blocks, the participants had to indicate whether the two gratings were rendered at the same orientation (match trials) or at different orientations (mismatch trials). On attend-contrast blocks, the participants had to ignore differences in orientation and to report whether the contrasts of the two gratings matched or did not match. Additionally, on orientation-mismatch trials, the central cue was presented in green or red to indicate either a CW or CCW rotational offset between the two gratings. **(b)** The orientation selectivity of population responses in V1 [68,69], as measured with fMRI, as participants were performing the orientation discrimination task (i.e. attend-orientation) or the contrast discrimination task (i.e. attend-contrast). Data shown here are shifted such that the 0° channel indicates the cued orientation and positive values on the x-axis indicate responses in orientation channels that were offset in the cued direction, whereas negative values indicate responses in orientation channels offset in the uncued direction. Despite similar overall amplitude of responses in attend-orientation and attend-contrast condition, attention shifts the orientation tuning toward the cued offset when participants attend to the orientation of a grating instead of to the contrast of the grating [19*]. In contrast, responses in neural populations away from the attended feature are relatively muted. **(c)** Schematic of the experiment design used in Ref. [19*]. Each trial began with an auditory cue, which indicated (with 75% validity) the overall orientation of the subsequent gratings (~45° or ~135°). Following the cue, participants saw two consecutive gratings which differed slightly in terms of orientation, contrast, and spatial frequency. In separate blocks, participants judged whether the second grating rotated CW or CCW with respect to the first (i.e. orientation task); or whether the second grating had higher or lower contrast than the first (i.e. contrast task). D. Expected orientations evoke less overall activity in V1 relative to unexpected orientations as measured with the BOLD response (bars). However, MVPA orientation classification accuracy of the grating orientation in V1 was higher for expected relative to unexpected orientations (line plots) [23*] (with permission from the authors).

expected and unexpected stimuli in IT cortex [50]. However, even in these studies, the cueing scheme is set up so that expectation was manipulated by cueing relevant stimuli over a longer time frame whereas attention was cued on a trial-by-trial basis. So, while this manipulation leads to separate sources of top-down information that operate on different time scales, it is not entirely clear that one type of cue solely modulated expectation and the other attention as both cues provided information about what to expect and what features were more likely to be behaviorally relevant.

One way to isolate the effects of expectation from attention on sensory processing is to design an experiment where stimulus regularities are manipulated without using an explicit cue. For example, Rungratsa-meetaweemana *et al.* used a variant of an orientation discrimination task, where targets were either coherently oriented red or blue bars at 0° (horizontal) or 90° (vertical) [54**]. This gave rise to four possible target types: red horizontal, red vertical, blue horizontal, and blue vertical. Each response button was associated with a specific conjunction of color and orientation. The probability that a specific color or orientation was a target feature was independently manipulated on a block-by-block basis such that within each block, targets were presented more frequently in one color (e.g. red; color expectation) or one orientation (e.g. vertical; orientation expectation). Thus, expectations about these sensory features (i.e. color and orientation) were induced through stimulus history without using an explicit cue. By not using an explicit probability cue, this

study minimized the possibility that participants shifted their attention to the expected stimulus features and thus the results are less likely to be influenced by selective attention. That said, it is possible that an implicitly induced expectation about a target feature could lead participants to allocate more attention toward the feature that is most likely to be presented [55]. However, even if participants noticed the expectation manipulation, knowledge about the most likely sensory feature would not provide information about the relevant behavioral response because targets were defined by the conjunction of color and orientation.

Using this behavioral paradigm allowed for a manipulation of expectation about two low-level sensory features (color and orientation) while measuring EEG markers that index early sensory processing and the accumulation of sensory evidence during decision-making (the visual negative potential, or VN, and the centroparietal positive potential or CPP, respectively). Importantly, the paradigm also included an independent manipulation of sensory evidence to validate these markers of sensory processing and to provide a point of comparison for any expectation-related modulations. The behavioral results revealed that expectations about likely sensory features improved the speed and accuracy of decision-making in a manner analogous to increasing the amount of available sensory evidence. However, while manipulations of sensory evidence increased the amplitude of the VN and the amplitude and slope of the CPP, expectations about sensory features had no impact on either of these components despite the robust effect

Figure 2
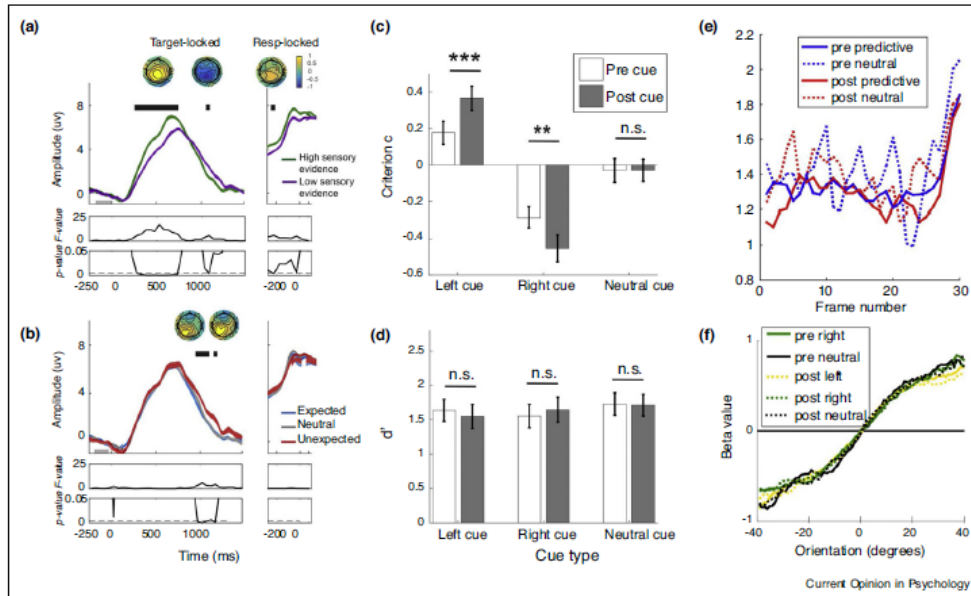
Recent studies that isolate the effects of expectation from attention on sensory processing. **(a)** The CPP is used as an EEG marker of the accumulation of sensory evidence during decision-making and its pre-peak amplitude is shown to be sensitive to manipulations that increase the amount of sensory evidence in the stimulus display. **(b)** Despite the CPP being sensitive to increases in sensory evidence, expectation does not impact the pre-peak CPP amplitude. Instead, violations of expectation modulate the post-peak CPP amplitude which could be associated with later stages of processing after early sensory processing [54**]. **(c)** Behaviorally, predictive (left and right) cues led to criterion shift toward to the cued direction both when presented before and after the gratings. Critically, direct comparisons of the effects of pre-cues and post-cues showed that expectation induced via post-cues had a stronger effect on participants' performance, which must be due to a shift in the decision criterion because the cue was presented after sensory processing of the stimulus was complete [56**]. **(d)** Both pre-cues and post-cues have comparable influence on stimulus sensitivity (d') [56**]. **(e)** A reverse correlation analysis was performed to investigate whether pre-cues or post-cues affected participants' information usage at any time throughout the 30 frames of stimulus presentation. Higher beta values indicate that participants placed more weight on the information provided by a particular stimulus frame. Temporal information usage for predictive (left and right) and neutral cues did not differ by cue time (pre-cues or post-cues), showing that expectation induced via pre-cues and post-cues had similar effects on temporal information usage throughout each trial. Note that noisier plots of neutral-cue condition are due to a smaller number of trials [56**]. **(f)** Feature information usage for predictive (left and right) and neutral cues also did not differ by cue time (pre-cues or post-cues), suggesting that pre-cues and post-cues have the same effect on feature-based information usage (reprinted from Ref. [56**] with permission from the authors).

of expectations on behavior (Figure 2a,b). Instead, expectation modulated the amplitude of posterior alpha and frontal theta oscillations, signals thought to index overall time-on-task and cognitive conflict. Together, these findings suggest that expectations about low-level sensory features, even when the expectations do not provide information about the behavioral relevance of sensory stimuli, primarily operate at post-perceptual stages of information processing.

Another recent study by Bang and Rahnev also converges on the idea that expectations do not impact early sensory processing but instead modulate decision criteria [56**]. Participants performed a discrimination task where they judged whether the overall orientation bias in a series of gratings was tilted left (clockwise) or right (counterclockwise) from vertical. The grating stimuli were either preceded or followed by a predictive cue (i.e. pre-stimulus cue or a post-stimulus cue, respectively) indicating with 66.67% validity whether the overall orientation was more likely to be left or right of vertical. An additional condition was also included where neutral (uninformative) cues were presented. A pre-stimulus cue could impact both sensory signals and later decision processes, whereas a post-stimulus cue could only influence decision processes. By comparing the behavioral effects of pre-stimulus cues and post-stimulus cues, the study could assess the impact of expectation on early sensory processing and on decision-related criterion shifts.

Direct comparisons of pre-cues and post-cues demonstrated similar effects of both cue types on stimulus sensitivity (d'). However, post-cues induced a greater shift in decision criterion (c) compared to pre-cues (Figure 2c,d). To further examine how participants used cue-based information in both the temporal and feature domains, the authors employed a reverse correlation method, in which they compared the impact of predictive and neutral pre-cues and post-cues. The results demonstrated that pre-cueing and post-cueing exerted a similar influence on the use of temporal information and feature-specific information provided by predictive and neutral cues. Since the post-cues could only influence later decisional processes but not early sensory signals, the comparable effects of pre-cues and post-cues suggest that expectations primarily impact decision criteria rather than directly modulating the efficiency of sensory processing (Figure 2e,f). Together with the study by Rungratsameetaweemana *et al.*, these results are more in line with classic theoretical frameworks such as signal detection theory (SDT) and suggest that knowledge about statistical regularities of the sensory environment primarily influence later cognitive operations related to response selection and execution [57–61].

Conclusions

While we argue here that it is premature to assert that expectations about statistical regularities impact early sensory processing, there is substantial evidence that manipulations of expectation have a profound impact

5

on behavior and on responses in higher-order parietal and frontal regions that are thought to be more directly involved in regulating decision-making and behavioral responses (i.e. saccades, reaching movements [62,63]). Saccade-selective neurons in frontal cortex show a pre-stimulus response bias as a function of target probability [64], stimulus-evoked responses in the superior colliculus are mediated based on the certainty associated with a planned saccade [65,66], and disrupting saccade-selective regions in human frontal cortex attenuates the impact of target probability on behavioral performance [67]. This evidence is consistent with the hypothesis that expectations can mediate priors to influence response selection. These findings are also in line with the idea that expected stimuli might exert a larger impact on sensorimotor decision mechanisms via changes in the 'read-out' of sensory-evoked responses rather than affecting the perceptual processing of the sensory signal itself. Moreover, as articulated in Summerfield and de Lange [5**], observers should exploit information about both statistical regularities and behavioral relevance to guide optimal decision making, as both sources of information should support the efficient processing of information to guide behavior. Future studies are needed to more thoroughly explore when and where expectation impacts information processing, and to orthogonally manipulate expectation and attention within the same paradigm to test for differences in temporal dynamics, modulations in different cortical areas, and influences on behavior.

Conflict of interest statement

Nothing declared.

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

- of special interest
- of outstanding interest

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The introduction, in full, is a reprint of the material as it appears in:

Chapter 1:

Expectations do not alter early sensory processing during perceptual decision-making

Expectations Do Not Alter Early Sensory Processing during Perceptual Decision-Making

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Two factors play important roles in shaping perception: the allocation of selective attention to behaviorally relevant sensory features, and prior expectations about regularities in the environment. Signal detection theory proposes distinct roles of attention and expectation on decision-making such that attention modulates early sensory processing, whereas expectation influences the selection and execution of motor responses. Challenging this classic framework, recent studies suggest that expectations about sensory regularities enhance the encoding and accumulation of sensory evidence during decision-making. However, it is possible, that these findings reflect well documented attentional modulations in visual cortex. Here, we tested this framework in a group of male and female human participants by examining how expectations about stimulus features (orientation and color) and expectations about motor responses impacted electroencephalography (EEG) markers of early sensory processing and the accumulation of sensory evidence during decision-making (the early visual negative potential and the centro-parietal positive potential, respectively). We first demonstrate that these markers are sensitive to changes in the amount of sensory evidence in the display. Then we show, counter to recent findings, that neither marker is modulated by either feature or motor expectations, despite a robust effect of expectations on behavior. Instead, violating expectations about likely sensory features and motor responses impacts posterior alpha and frontal theta oscillations, signals thought to index overall processing time and cognitive conflict. These findings are inconsistent with recent theoretical accounts and suggest instead that expectations primarily influence decisions by modulating post-perceptual stages of information processing.

Key words: cognitive control; decision-making; electroencephalography (EEG); expectation; sensory modulation

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Significance Statement

Expectations about likely features or motor responses play an important role in shaping behavior. Classic theoretical frameworks posit that expectations modulate decision-making by biasing late stages of decision-making including the selection and execution of motor responses. In contrast, recent accounts suggest that expectations also modulate decisions by improving the quality of early sensory processing. However, these effects could instead reflect the influence of selective attention. Here we examine the effect of expectations about sensory features and motor responses on a set of electroencephalography (EEG) markers that index early sensory processing and later post-perceptual processing. Counter to recent empirical results, expectations have little effect on early sensory processing but instead modulate EEG markers of time-on-task and cognitive conflict.

Introduction

Selectively attending to relevant sensory inputs (i.e., selective attention) leads to faster and more accurate decisions. In addition,

expectations based on learned statistical regularities in incoming sensory signals or motor responses can also facilitate decision-making, even if the expectations concern features or responses that are irrelevant with respect to current behavioral goals (Summerfield and de Lange, 2014). Selective attention is thought to improve information processing primarily by modulating the re-

sponse properties of neurons in early sensory areas (Desimone and Duncan, 1995; Reynolds and Chelazzi, 2004; Maunsell and Treue, 2006; Serences and Kastner, 2014; Itthipuripat and Serences, 2016). In contrast, classic theoretical frameworks such as signal detection theory (SDT) hold that expectations do not influence early sensory responses, but instead bias later cognitive operations related to response selection and execution (Wald and Wolfowitz, 1949; Green and Swets, 1966; Wolfe, 1998; Berti and Schröger, 2004; Alvarez et al., 2007). Consistent with this idea, a recent behavioral study has shown that stimulus expectations modulated decision criteria without affecting the quality of early sensory signals (Bang and Rahnev, 2017).

Challenging this traditional SDT-based account, recent work suggests that expectations can improve the efficiency of early sensory processing, even when expectations are independent of behavioral goals (Kok et al., 2012a; Wyart et al., 2012b; Summerfield and de Lange, 2014; Cheadle et al., 2015). On this account, expectations increase the precision of information processing by sharpening population-level response profiles in early visual cortex (Lee and Mumford, 2003; Spratling, 2008; Kok et al., 2012a; Jiang et al., 2013). Accordingly, it has been proposed that expectation-related modulations in early visual cortex should directly increase the efficiency of early sensory processing during perceptual decision-making (Summerfield and de Lange, 2014).

However, previous studies examining the impact of expectations on early sensory processing used explicit cues to indicate which stimulus feature had the highest probability of being a target (Wyart et al., 2012b; Cheadle et al., 2015; Kok et al., 2012a, 2016). Importantly, these explicit cues are similar to cues used in other studies to direct the allocation of visual attention to behaviorally relevant spatial locations or features (Motter, 1993; McAdams and Maunsell, 1999; Martínez-Trujillo and Treue, 2004; Scolari et al., 2012, 2014; Itthipuripat et al., 2014a,b; Störmer and Alvarez, 2014; Ester et al., 2016). Therefore, reported expectation effects may actually reflect the operation of the same mechanisms that have been well documented in the selective attention literature (Motter, 1993; McAdams and Maunsell, 1999; Martínez-Trujillo and Treue, 2004).

Here we test the classic SDT account and this new *sensory enhancement* account to better understand how expectations impact early sensory processing (Kok et al., 2012a; Summerfield and de Lange, 2014). We manipulated expectations about two different low-level sensory features (color and orientation). We also included two additional conditions: (1) a manipulation of the amount of sensory evidence available in each stimulus display to validate electroencephalography (EEG) markers of early sensory processing, and (2) an independent manipulation of motor expectation as a point of comparison with feature expectation. Finally, expectations were established based on implicitly learned regularities and we independently manipulated expectations about each component of the task so that statistical regularities in one feature dimension (e.g., color) would not provide information about the relevance of a target defined in the other feature dimension (i.e., orientation). As a result of these design features, the task dissociated manipulations of expectations from the effects of using an explicit cue to provide information about the behaviorally relevant target feature.

Materials and Methods

Participants. Twenty healthy volunteers (8 males; all participants right-handed; mean age = 21.8, SD = 3.3) participated in the experiment. All were neurologically intact and had normal or corrected-to-normal color vision. Participants gave written informed consent and were compen-

sated $15/h for participation. Ethical approval was granted by the Institutional Review Board at the University of California, San Diego. Each participant underwent two EEG recording sessions (sessions were ~2 h each, with 1920 trials collected in total). Three participants were excluded from data analysis for having <70% artifact-free trials in any of the conditions of interest (due to excessive muscle movement and eye movements), leaving 17 participants in the final analyses (see EEG recording and analysis section for details).

Stimuli. Visual stimuli consisted of 200 blue bars and 200 red bars (length = 1.39°, width = 0.18°) displayed in an annulus (outer diameter, 22°; inner diameter, 2.4°) surrounding a black fixation point on a dark gray background of 42.68 ± 2.20 cd/m². Blue and red bars within the annulus flickered at 33.33 Hz (33.33% on–off duty cycle) and 50 Hz, respectively (50% on–off duty cycle; or vice versa) for the duration of the trial, and the location of each bar was randomly reassigned within the aperture at the beginning of each flicker cycle. The combination of color and flicker rate was counterbalanced across trials. At the beginning of each trial, each bar was first randomly assigned to one of eight possible orientations (0–157.5° in 22.5° increments). For a target display, 68.5% of either red or blue lines were assigned a common orientation of either 0° or 90°, whereas all other bars were assigned one of seven remaining orientations. Participants were instructed to report the predominant orientation of these iso-oriented bars via a USB compatible keypad.

Stimuli were presented on a PC running Windows XP using MATLAB (MathWorks) and the Psychophysics Toolbox v3.0.8 (Pelli, 1985; Brainard, 1997). Participants were seated in a sound-attenuated and electromagnetically shielded room (ETS Lindgren) 60 cm from the CRT monitor running at 100 Hz with a gray background of 42.68 ± 2.20 cd/m².

Procedures. Participants performed two sessions of an orientation discrimination task in which feature expectation (i.e., color expectation and orientation expectation) and motor expectation were independently manipulated on a block-by-block basis (Fig. 1). As described, targets were red or blue bars coherently oriented at 0° (horizontal) or 90° (vertical), hence there were four possible target types: red horizontal, red vertical, blue horizontal, and blue vertical targets. Each response button was associated with a specific conjunction of color and orientation. Half of the participants were instructed to map the left button to red horizontal and blue vertical targets and the right button to blue horizontal and red vertical targets. The other half of the participants were given the opposite response-mapping instructions. This stimulus–response mapping was adopted so that we could completely dissociate expectation about sensory features and expectation about motor responses.

To familiarize participants with the task and the response mapping, participants performed a behavioral training session before the first EEG session. During this training session, participants had to complete 10 full blocks of the experimental task, with each block containing four trials from each of the four expectation types (neutral, color expectation, orientation expectation, motor expectation; see the next paragraph). The training session was terminated once participants achieved perfect performance on all blocks, and each block was repeated until participants reached 100% accuracy.

After training, each EEG session was comprised of 16 experimental blocks with 60 trials in each block. This yielded four blocks of trials for each of the four expectation types: neutral, color expectation, orientation expectation, or motor expectation (Fig. 1). In the neutral blocks, all four target types were presented equally often. In the remaining blocks, feature and motor expectations were manipulated orthogonally, such that feature expectation and motor expectation were never manipulated at the same time within the same block. Feature expectation was manipulated by presenting either one color more frequently (i.e., color expectation) or one orientation more frequently (i.e., orientation expectation) than the other value in that feature dimension. For example, on one type of color expectation block, the target would be rendered in red on 70% of the trials and in blue on 30% of the trials. Importantly, on these color expectation blocks, target identity was perfectly balanced such that 50% of the target was horizontal and 50% was vertical. In contrast, on an orientation expectation block, 70% of the targets would be horizontal and 30% of the targets would be vertical, with an equal number of targets composed of blue and red lines. Finally, on a motor expectation block,
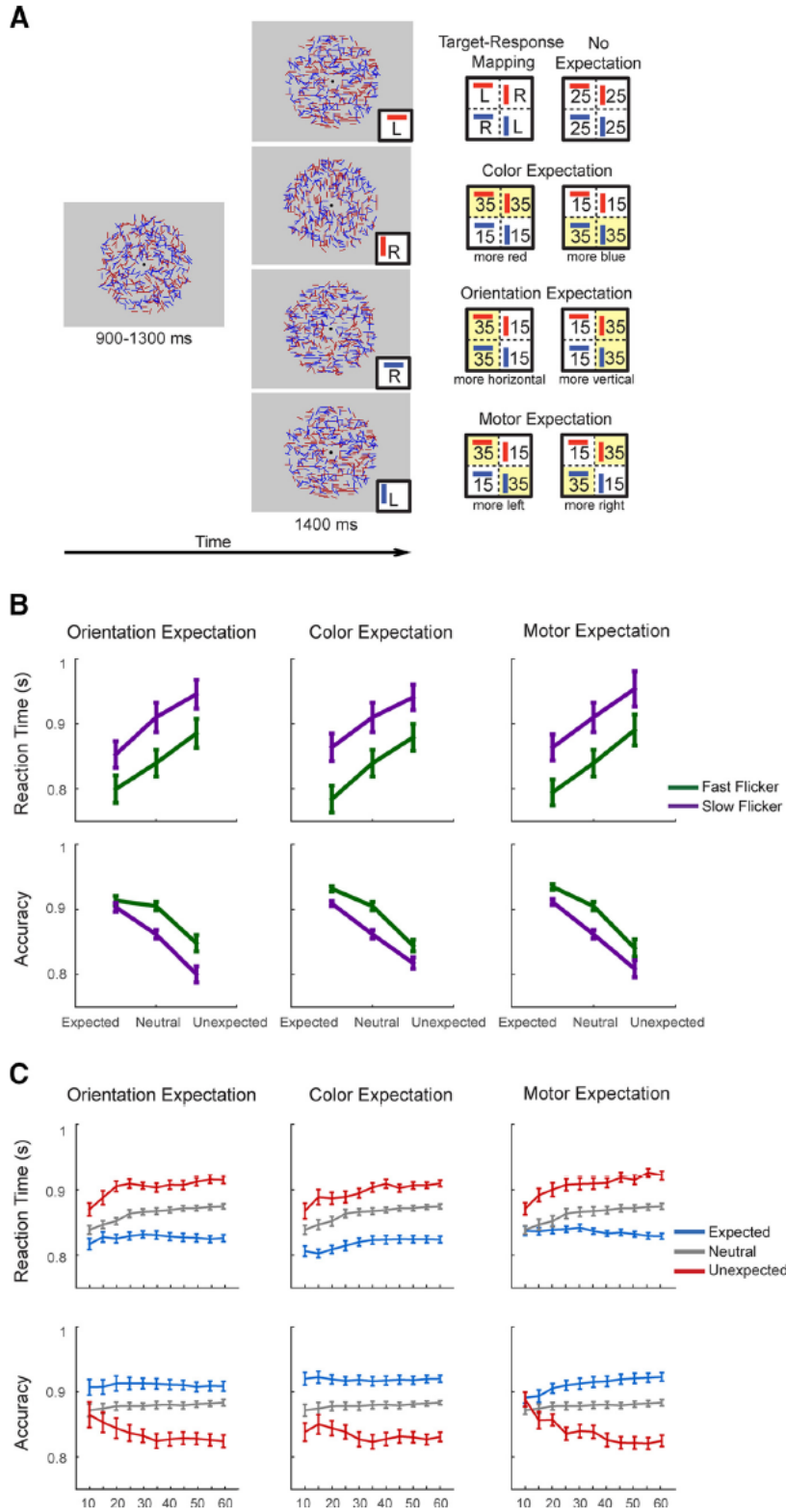
Figure 1. Orientation discrimination task and behavioral results. **A**, Task schematics. Targets were either coherently oriented red or blue bars at 0° (horizontal) or 90° (vertical), and participants indicated the target by pressing the left (L) or right key (R). Each response button was associated with a specific conjunction of color and orientation such that half of the participants were instructed to map the left button to red horizontal and blue vertical targets and the right button to blue horizontal and red vertical targets. There were four expectation types to the task: neutral (no expectation), color expectation, orientation expectation, and

targets associated with the left button (e.g., red horizontal and blue vertical) were presented on 70% of the trials whereas the targets mapped to the right button (e.g., blue horizontal and red vertical) were presented on 30% of the trials. This experimental design thus enabled us to independently manipulate expectation about sensory features (i.e., target color and orientation) and expectation about motor responses. In addition, we could also control expectation within the "feature" domain by separately manipulating expectation about color and orientation of the target stimulus, as both features provided equal amount of information toward decision choices (left/right button press) on each trial. Together, this study design allowed us to examine the effects of feature expectation on information processing during decision-making in the absence of motor expectation and response bias.

Every block started with four practice trials that corresponded to each target type (red horizontal/red vertical/blue horizontal/blue vertical) to ensure that participants understood the assigned stimulus–response mapping. Participants had to provide correct responses for all four practice trials before the main task would proceed; otherwise the practice trials would repeat until participants met criterion performance. In the main task, each trial began with a pre-target display consisting of colored bars flickering at 33.33 and 50 Hz that lasted for 91–127 ms. During this pre-target interval, the

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motor expectation. Expectation types were manipulated on a block-by-block basis. Each target composed of two features: color and orientation, and the expectation status of the target was manipulated in the three expectation conditions by presenting one type of target more frequently than the other target type within the same target feature. That is, for a given block (e.g., color expectation block), one target type (e.g., red target) was expected, whereas the other target type (i.e., blue target) was unexpected. The other target feature (i.e., orientation) was orthogonal to this expectation manipulation, and it was equally likely that the target would be vertical or horizontal. Note that the ratio of expected–unexpected trials within each block is 70:30, such that in a color expectation block where red target is expected, the probabilities of red horizontal target, red vertical target, blue horizontal target, and blue vertical target are 35, 35, 15, and 15% respectively. In the neutral expectation block, the probabilities of each of the four possible targets were 25% accordingly. **B**, Behavioral results. Accuracy was higher on the expected trials than on the unexpected trials in all three expectation types (orientation/color/motor expectation). Accuracy was also higher on trials where stimuli were presented at a fast compared with a slow flicker rate. RTs for correct responses were also shorter for fast flicker-rated stimuli than for slow flicker-rated stimuli. **C**, Performance as a function of the number of cumulative trials in each block (i.e., trial 1–10, 1–15, 1–20, etc. within each block of 60 trials). Data were collapsed across fast and slow flicker rate trials to examine the temporal dynamics of the expectation effects on RTs and accuracy. Across the three expectation types, the effects of expectation on behavior are clearly observed after 20 cumulative trials. Thus, in later EEG analyses where a null effect of expectation is observed, we ran additional analyses after discarding the first 20 trials.

orientation of each bar was pseudorandomly selected from a uniform distribution such that no coherent global orientation signal was present. Following the pre-target interval, the orientation target was presented for 850 ms, followed by a 600 ms post-target display in which the orientation of all bars was again pseudorandomly drawn from a uniform distribution. The post-target display was followed by a feedback display which indicated whether the response on that trial was "too early" (made <85 ms after target onset), "correct", "incorrect", or "too slow" (made after trial offset). The feedback display was presented for 300 ms and immediately followed by an 800–1200 ms blank intertrial interval.

Behavioral analysis. We used a three-way repeated-measures ANOVA with factors for the expectation type (3 levels: color expectation, orientation expectation, and motor expectation), flicker rate (2 levels: fast and slow), and the status of the target (3 levels: expected, neutral, and unexpected) to test the main effects and interactions on the accuracy and reaction times associated with correct trials.

EEG recording and analysis. EEG data were recorded using a 64 + 8 channel BioSemi ActiveTwo system at a sampling rate of 512 Hz. Two reference electrodes were placed at the mastoids. We monitored vertical eye movements and blinks via two pairs of electrodes placed above and below the eyes. Horizontal eye movements were monitored via another pair of electrodes placed near the outer canthi of the eyes. The EEG data were referenced online to the BioSemi CMS-DRL reference, and all offsets from the reference were maintained <20 μV. The data were preprocessed with a combination of EEGlab 11.03.1b (Delorme and Makeig, 2004) and custom MATLAB scripts.

After data collection, we re-referenced the continuous EEG data offline to the mean of the left and right mastoid electrodes and applied 0.25 Hz high-pass and 58 Hz low-pass Butterworth filters (third order). An additional 10 Hz low-pass filter was applied before plotting the data, but all reported statistics were performed on the 58 Hz low-pass filtered data (Luck, 2005; for similar methods, see Hickey et al., 2010; Itthipuripat and Serences, 2016). The data were then segmented into epochs extending from 1500 ms before to 4000 ms after the trial onset. Prominent eyeblink artifacts were first rejected by independent component analysis (Makeig et al., 1996). We then visualized data from each trial and discarded epochs contaminated by residual eye blinks and vertical eye movements (>±80–150 μV deviation from 0, with thresholds chosen for each subject), horizontal eye movements (>±75–100 μV deviation from 0), excessive muscle activity, or drifts. This procedure resulted in the rejection of 12.25% of trials on average (± 1.07% SEM across subjects; ranged from 3.9 to 21.8% of trials). Data from three participants were excluded from further analysis due to the rejection rate of >30% of trials (31.35, 60, and 89%, respectively).

Next, we sorted artifact-free EEG epochs into different experimental conditions based on expectation type (color expectation, orientation expectation, and motor expectation), the status of each target in the context of a given block (expected, neutral, or unexpected), and on the flicker rate of the target (fast or slow). To compute event-related potentials (ERPs), the EEG data from each experimental condition were first baseline-corrected from 200 to 0 ms before the onset of a target or a response. ERPs were then computed by averaging target-locked and response-locked EEG data for each experimental condition. In addition, the EEG data for individual subjects were also wavelet-filtered using a Gaussian filter with a 0.2 factional bandwidth centered on eight frequencies in 1 Hz incremental steps from 4 to 12 Hz, yielding analytic amplitude estimates for oscillatory EEG components in the theta (4–8 Hz) and alpha frequency bands (9–12 Hz; for similar methods, see Canolty et al., 2006; Itthipuripat et al., 2013a). Next, the single-trial alpha and theta data were sorted into different experimental conditions (just like the ERPs). Maximal time-domain SDs of the Gaussian wavelet filters were computed separately for alpha and theta (i.e., alpha: SD = 208 ms; theta: SD = 468 ms). Alpha and theta data were then baseline-corrected across a time window extending 200 ms before their respective time-domain SD (i.e., alpha data were baseline-corrected from 408 to 208 ms before target onset and theta data were baseline-corrected from 668 to 468 ms before target onset).

We then examined the impact of expectation type, flicker rate, and the expectation status of target on two ERP components: the occipital negative-going component recorded from the Oz electrode and the central parietal positive (CPP) component recorded from the central posterior (CPz) electrode. We used three-way repeated-measures ANOVAs with within-subject factors for expectation type (3 levels: color expectation, orientation expectation, and motor expectation), flicker rate (2 levels: fast and slow), and the expectation status of the target (3 levels: expected, neutral, and unexpected) to evaluate the influence of these factors on the amplitude of the ERP components. These ANOVAs were performed on the mean ERP amplitudes across consecutive 50 ms windows from 250 ms before to 1500 ms after target onset for the target-locked data and from 300 ms before to 100 ms after the response onset for the response-locked data. Corrections for multiple comparisons was implemented using the false discovery rate (FDR) method (Benjamini and Hochberg, 1995) based on both target-locked and response-locked data from CPz and Oz electrodes. The impact of expectation type, flicker rate, and expectation on the CPP slope was examined on both target- and response-locked data. The CPP slope was measured as the slope of a straight line fitted to the ERP waveform for each subject, using the interval 200 to 550 ms for the target-aligned CPP and −350 to 0 ms for the response-aligned CPP (for similar methods, see Kelly and O'Connell, 2013). We then performed t tests to examine the impact of flicker rate and a one-way ANOVA to assess the impact of expectation on the CPP slope. In the case of no significant main effects, follow-up one-tailed t tests and Bayes factor analyses were performed on the signals collapsed across consecutive 50 ms windows.

The same ANOVA analyses were then performed on the induced parietal alpha amplitude recorded from the Pz electrode and frontal theta amplitude recorded from the FCz electrode. These electrodes were chosen as they displayed maximum response amplitude in the alpha and theta range respectively. ANOVAs were performed on the mean theta amplitudes across consecutive 50 ms windows from 700 ms before to 1500 ms after target onset for the target-locked data and from 300 ms before to 100 ms after the response onset for the response-locked data. The same ANOVAs were performed on the mean alpha amplitudes from 450 ms before to 1500 ms after target onset for the target-locked data and from 300 ms before to 100 ms after the response onset for the response-locked data. In addition, we performed follow-up one-tailed t tests to compare the impact of flicker rates and a one-way ANOVA to assess the impact of expectation on both ERP components as well as theta and alpha amplitude from each individual expectation type (color expectation/ orientation expectation/motor expectation). Note that corrections for multiple comparisons were computed separately for alpha and theta based on its target-locked and response-locked data from the Pz and FCz electrode respectively. In the case of significant main effects of either flicker rate or expectation, one-tailed follow-up tests were performed on individual expectation type signal amplitudes averaged across significant time windows.

To further examine the impact of expectation, we performed a *post hoc* Bayes factor t tests (Edwards et al., 1963; Wagenmakers, 2007; Rouder et al., 2009) on VN amplitude, CPP slope, and CPP amplitude during the time windows where the effect of flicker rates was significant. We report Bayes factors expressing the probability of the data given H1 (i.e., there was an expectation effect) relative to H0 (i.e., there was no expectation effect). Although Bayes factors are not evaluated against a fixed threshold to determine significance, a Bayes factor >3 is generally considered to indicate positive evidence in favor of H1, whereas a value <0.33 is generally considered evidence for H0.

Results
Behavioral results
In the present study, participants performed an orientation discrimination task in which feature expectation and motor expectation were independently manipulated on a block-by-block basis (Fig. 1). Targets were red or blue bars coherently oriented at 0° (horizontal) or 90° (vertical), and participants indicated the target by pressing the left (L) or right key (R). Each response button was associated with a specific conjunction of color and orientation. Half of the participants were instructed to map the

left button to red horizontal and blue vertical targets and the right button to blue horizontal and red vertical targets (this mapping was reversed for the other half of the participants). There were four main conditions in the task: neutral (no expectation), color expectation, orientation expectation, and motor expectation. Each target was composed of two features: color and orientation, and the expectation status of the target was manipulated by presenting one type of target more frequently than the other target type within the same target feature. That is, for a given block of trials (e.g., a color expectation block), one target type (e.g., red target) was expected, whereas the other target type (i.e., blue target) was unexpected. The other target feature was orthogonal to this expectation manipulation (i.e., it was equally likely that the target would be vertical or horizontal).

We manipulated the flicker rate of the stimuli to manipulate the amount of sensory information being presented per unit time, with more information about the stimuli available as the flicker rate increased. Consequently, participants should have higher accuracy and faster reaction times on trials where stimuli were rendered at a fast compared with a slow flicker rate. In addition, we also predicted better performance when the target feature or its corresponding motor response was expected.

As shown in Figure 1, there was a significant main effect of the flicker rate manipulation on behavioral performance such that participants were faster and more accurate on trials where stimuli were presented at a fast (50 Hz) compared with slow (33.33 Hz) flicker rate (RT: $F_{(1,16)} = 152.73$, $p < 0.001$, accuracy: $F_{(1,16)} = 12.69$, $p = 0.003$). This effect of flicker rate on behavior confirms that our manipulation successfully impacted the amount of sensory evidence available on each trial. Also, shown in Figure 1 was a significant main effect of expectation on both RT and accuracy (expected/neutral/unexpected, RT: $F_{(2,16)} = 97.51$, $p < 0.001$; accuracy: $F_{(2,16)} = 77.26$, $p < 0.001$). *Post hoc t* tests revealed that participants were faster in the expected compared with the neutral ($t_{(16)} = 8.21$, $p < 0.001$) and unexpected conditions ($t_{(16)} = 12.60$, $p < 0.001$). Similarly, accuracy was higher in the expected compared with the neutral ($t_{(16)} = 5.81$, $p < 0.001$) and unexpected conditions ($t_{(16)} = 10.09$, $p < 0.001$). Participants were also faster ($t_{(16)} = 6.64$, $p < 0.001$) and more accurate in the neutral compared with the unexpected conditions ($t_{(16)} = 8.18$, $p < 0.001$). However, there was no significant interaction between expectation and flicker rate on either RT or accuracy (expected/neutral/unexpected vs fast/slow flicker, RT: $F_{(2,16)} = 0.59$, $p = 0.56$; accuracy: $F_{(2,16)} = 1.36$, $p = 0.27$). Finally, there was no main effect of expectation type on RT or accuracy (expectation about color/orientation/motor response, RT: $F_{(2,16)} = 1.01$, $p = 0.38$; accuracy: $F_{(2,16)} = 0.64$, $p = 0.54$), and there was no interaction between expectation type and flicker rate (color expectation/orientation expectation/motor expectation versus fast/slow flicker rate, RT: $F_{(2,16)\text{max}} = 1.20$, $p_{\text{min}} = 0.32$; accuracy: $F_{(2,16)\text{max}} = 0.34$, $p_{\text{min}} = 0.85$).

EEG results
The early visual negative (VN) potential
We used an early visual negative potential (VN), which peaked ~150–300 ms after target onset at the central occipital electrode (Oz) to index the magnitude of early sensory-evoked visual responses. The amplitude of this early sensory ERP increases as the amount of sensory evidence increases (e.g., visual contrast or motion coherence: Johannes et al., 1995; Wyart et al., 2012a; Itthipuripat et al., 2014b, 2017; Loughnane et al., 2016) and we used Oz because the visual stimuli were presented at the center of the screen. We predicted that presenting stimuli at a fast, compared with a slow flicker rate, should lead to an increase in the amount of sensory evidence per unit time and thus greater sensory-evoked re-

sponses as indexed by an increase in VN amplitude. According to the sensory enhancement account, expectation about stimulus features or associated motor responses should also increase the VN amplitude if expectation improves the efficiency of early sensory processing. The classic SDT account, on the other hand, would predict expectation to have no effect on this neural measure of early sensory processing.

Fast flicker rate increases VN amplitude
We analyzed differences in both target-locked and response-locked VN amplitude in sliding 50 ms windows and corrected for multiple comparisons using FDR method based on both target-locked and response-locked data from CPz and Oz electrodes (see Materials and Methods). We found that VN amplitude was significantly larger on fast compared with slow flicker rate trials from 200 to 300 ms after target onset ($F_{(1,16)} = 10.43–20.20$; $p = 0.0004–0.0052$, FDR-corrected threshold = 0.0059; see Fig. 2A, left). This flicker rate effect was consistent across expectation type ($t_{(16)} = -3.98$, -4.65, -4.89 with all p values <0.001 for color expectation, orientation expectation, and motor expectation, respectively; Fig. 2A, right).

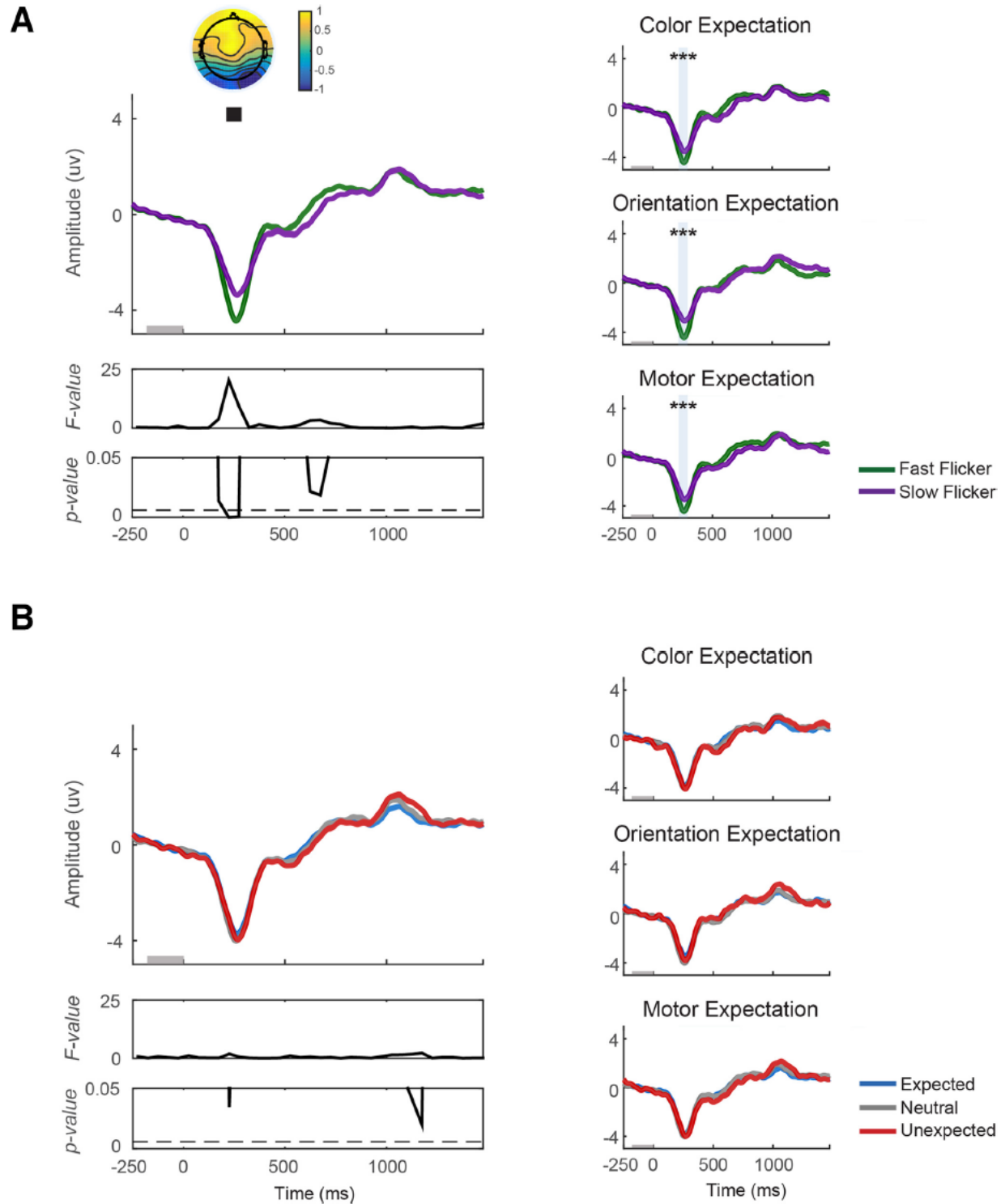### Expectation does not affect VN amplitude
In contrast, expectation had little impact on the VN, with only 1 of 35 time windows showing a trend toward significance that occurred outside the peak window of the VN and did not survive FDR correction ($F_{(2,16)}$ max = 4.45, $p_{\text{min}} = 0.02$, FDR-corrected threshold = 0.0059; Fig. 2B). Note also that during this time window, VN amplitude was marginally higher on unexpected compared with expected trials. This marginal effect is in the opposite direction from that predicted by the sensory enhancement account. A *post hoc* analysis of the Bayes factor indicated either slightly positive or equivocal evidence in favor of the hypothesis that expectation had no effect on VN amplitude ($BF_{10} = 0.33–1.35$ across all comparisons; Table 1).

We then examined the interaction between flicker rate and expectation on the amplitude of the VN and found that although one time window showed a trend toward an increased VN amplitude on fast-flickered expected trials, none survived correction for multiple-comparison ($F_{\text{max}} = 4.66$, $p_{\text{min}} = 0.02$, only one time window had a p value <0.05, FDR-corrected threshold <0.001).

Excluding the first 20 trials following a change in expectation type does not influence the null effects of expectation on the VN
We next examined whether these null effects of expectation on the VN could be caused by a failure of participants to build an expectation until the end of each experimental block. To evaluate this account, we first examined the time course of expectation effects on behavioral accuracy and RT. We found that expectation had a relatively fast impact on RT and accuracy early in each block (Fig. 1C). Specifically, after excluding the first 20 trials following a change in expectation types, we found significant effects of flicker rate and expectation on RT (flicker rate: $F_{(1,16)} = 125.29$, $p < 0.001$; expectation: $F_{(2,16)} = 118.29$, $p < 0.001$) and accuracy (flicker rate: $F_{(1,16)} = 11.19$, $p = 0.0004$; expectation: $F_{(2,16)} = 77.22$, $p < 0.001$) across expectation type.

Moreover, we replicated our main findings with respect to VN amplitude after discarding the first 20 trials from each experimental block (Fig. 3). VN amplitude was greater on fast compared with slow flicker rate trials from 200 to 300 ms after target onset ($F_{(1,16)} = 4.99–11.01$; $p = 0.004–0.04$, FDR-corrected threshold = 0.0043; Fig. 3A, left). This effect was consistent across expectation type ($t_{(16)} = -3.76$, -4.84, -6.52 with all p values < 0.001 for color expectation, orientation expectation, and motor expectation, respectively; Fig. 3A, right). In contrast, manipulations of expected target features did not impact the VN amplitude ($F_{(2,16)\text{max}} = 3.36$, $p_{\text{min}} = 0.05$, FDR-corrected threshold = 0.0043; Fig. 3B). A *post hoc* analysis of the Bayes factor indicates either slightly positive or equivocal evidence in favor of the hypothesis that expectation had no effect on VN amplitude ($BF_{10} = 0.25–0.48$ across all comparisons). Finally, we examined an interaction effect between flicker rate and expectation on CPP amplitude and found that no time window survived correction for multiple comparisons ($F_{\text{max}} = 5.92$, $p_{\text{min}} = 0.007$, FDR-corrected threshold <0.001). Together, these results demonstrate that even though the VN is a sensitive marker of the amount of sensory

14

Figure 2. Expectation does not affect early VN amplitude. VN amplitude was computed on data from all trials of each block. *A*, VN plotted from 250 ms before target onset to 1500 ms after target onset. VN plotted as a function of flicker rate (fast/slow) and (*B*) as a function of the expectation status of the target (expected/neutral/unexpected). Left, VN collapsed across expectation type (color/orientation/motor). Right, VN from individual expectation type. Fast flicker rate induced a significantly more negative VN from 200 to 300 ms after target onset. Significant main effect of flicker rate, ***$p < 0.001$.

Table 1. Bayes factor analyses of flicker rate and expectation status of the target

Neural measures	Flicker rate comparison		Expectation comparisons	
	Fast vs slow flicker rate	Expected vs unexpected	Expected vs neutral	Neutral vs unexpected
VN amp, tg-locked, 200 to 300 ms	$t = -5.51, p < 0.001, BF_{10} = 545.62$	$t = 0.91, p = 0.38, BF_{10} = 0.36$	$t = 2.06, p = 0.06, BF_{10} = 1.35$	$t = -0.81, p = 0.43, BF_{10} = 0.33$
CPP slope	$t = 3.52, p = 0.003, BF_{10} = 15.34$	$t = 0.48, p = 0.64, BF_{10} = 0.28$	$t = -1.64, p = 0.12, BF_{10} = 0.76$	$t = 1.85, p = 0.08, BF_{10} = 1.01$
CPP amp, tg-locked, 200 to 750 ms	$t = 7.36, p < 0.001, BF_{10} = 11,528$	$t = -0.93, p = 0.37, BF_{10} = 0.36$	$t = -0.001, p = 1.00, BF_{10} = 0.25$	$t = -0.64, p = 0.53, BF_{10} = 0.30$
CPP amp, resp-locked, −300 to −200 ms	$t = 3.75, p = 0.002, BF_{10} = 23.55$	$t = -1.10, p = 0.29, BF_{10} = 0.42$	$t = -0.47, p = 0.65, BF_{10} = 0.27$	$t = -0.53, p = 0.60, BF_{10} = 0.28$
−100 to 0 ms	$t = 3.45, p = 0.003, BF_{10} = 13.69$	$t = 0.18, p = 0.86, BF_{10} = 0.25$	$t = -0.60, p = 0.56, BF_{10} = 0.29$	$t = 0.81, p = 0.43, BF_{10} = 0.33$

evidence available in the display, manipulating expectations about target features or motor responses has a negligible impact on its magnitude.

The centro-parietal positive potential (CPP)

The CPP recorded from the CPz electrode is an established ERP marker thought to track a running sum of sensory evidence over time (Squires et al., 1973, 1975a,b; O'Connell et al., 2012; Kelly and O'Connell, 2013; Itthipuripat et al., 2015; Loughnane et al., 2016; Twomey et al., 2015). Thus, we predicted an increase in CPP amplitude and slope before its peak when stimuli were rendered at a fast flicker rate. The *sensory enhancement* account would also predict this pattern of results when the feature of the target or its associated motor response is expected. On the other hand, the classic SDT account would not predict any expectation-related modulations of either the amplitude or slope of the pre-peak CPP.

Fast flicker rate increases the pre-peak amplitude and decreases the post-peak amplitude of the CPP

We found a significant increase in CPP amplitude on trials where stimuli were rendered at a fast compared with slow flicker rate (Fig. 4A, left). The increases in the amplitude of the CPP were most pronounced from 200 to 750 ms after target onset ($F_{(1,16)} = 10.43$–47.74; $p = 0$–0.0052, FDR-corrected threshold = 0.0059); and from 300 to 200 ms and from 100 to 0 ms before response onset ($F_{(1,16)} = 13.21$–13.36; $p = 0.0021$–0.0022, FDR-corrected threshold = 0.0059; $F_{(1,16)} = 10.08$–12.36; $p = 0.0029$–0.0059, FDR-corrected threshold = 0.0059, respectively; Fig. 4A, left). *Post hoc t* tests revealed that the effects of flicker rate on CPP amplitude were consistent across expectation type (from 200 to 750 ms after target onset: $t_{(16)} = 5.49$, 4.27, 6.98 with all $p < 0.001$ for color expectation, orientation expectation, and motor expectation, respectively; from 300 to 200 ms before response onset: $t_{(16)} = 2.36$, 1.04, 5.55 with $p = 0.02$, 0.16, and < 0.001 for color expectation, orientation expectation, and motor expectation, respectively; from 100 to 0 ms before response onset: $t_{(16)} = 2.76$, 1.56, 3.99 with $p = 0.01$, 0.07, and < 0.001 for color expectation, orientation expectation, and motor expectation, respectively; Figure 4A, right). In addition, after the peak of the target-locked CPP, there was a significant decrease in CPP amplitude from 1050 to 1100 ms after target onset ($F_{(1,16)} = 11.57$; $p = 0.004$, FDR-corrected threshold = 0.0059), suggesting that decision-making associated with the faster flicker rate target required less processing time as evidenced by the earlier offset of the post-peak CPP amplitude. *Post hoc t* tests revealed that the flicker rate effect during this time window was consistent across expectation type ($t_{(16)} = -2.78$, −2.19, −2.07 with $p = 0.01$, 0.02, 0.03 for color expectation, orientation expectation, and motor expectation, respectively).

Expectation does not impact the pre-peak amplitude of CPP but violations of expectation modulates the post-peak amplitude of CPP

We next evaluated the impact of expectation on CPP amplitude. We found no effect of expectation on target-locked CPP amplitude before the peak or on response-locked CPP amplitude. A *post hoc* Bayes factor analysis was generally consistent with these null results ($BF_{10} = 0.25$–0.42; Table 1). While there was no effect of expectation on target-locked CPP amplitude before the peak amplitude, expectation did have an impact on the amplitude of the CPP after the peak amplitude from 950 to 1200 ms after target onset ($F_{(2,16)} = 11.53$–17.08; $p = 0$–0.0002, FDR-corrected threshold = 0.0059; Fig. 4B, left). During this interval, the amplitude of the CPP was higher on unexpected compared with neutral ($t_{(16)} = -5.17$, $p < 0.001$) and expected trials ($t_{(16)} = -5.08$, $p < 0.001$). Follow-up repeated-measures one-way ANOVAs also showed that this expectation effect was consistent across expectation type ($F_{(2,16)} = 3.65$, 13.77, 8.15 with all $p < 0.05$ for color expectation, orientation expectation, and motor expectation, respectively; Fig. 4B, right). Finally, we examined the interaction between flicker rate and expectation on the amplitude of CPP and found that no time window survived correction for multiple comparisons (target-locked: $F_{max} = 3.17$, $p_{min} = 0.06$; response-locked: $F_{max} = 0.78$, $p_{min} = 0.46$, FDR-corrected threshold < 0.001).

### Fast flicker rate increases the CPP slope but expectation does not

We then more directly examined the rise-time (or slope) of the target-locked CPP, which was computed over an interval from 200 to 550 ms after target onset (see Materials and Methods). We found a higher slope when targets were rendered at a fast compared with slow flicker rate (mean slopes ± 1 SEM = $0.032 ± 0.003$ and $0.027 ± 0.004 \mu V/ms$ for fast and slow flicker rate, respectively; $t_{(16)} = 3.52$, $p = 0.003$). *Post hoc t* tests also revealed that the effect of flicker rate on CPP slope was consistent across expectation type ($t_{(16)} = 2.46$, 2.82, 2.67 with all $p < 0.05$ for color expectation, orientation expectation, and motor expectation respectively). Given this demonstration of the CPP's sensitivity to changes in sensory evidence, we tested whether expectation also impacted the efficiency of early sensory processing in a manner similar to increasing the amount of sensory evidence. However, unlike the flicker rate effect, we found no effect of expectation on the slope of the CPP (mean slopes ± 1 SEM = $0.029 ± 0.004$, $0.031 ± 0.004$ and $0.028 ± 0.004 \mu V/ms$ for expected, neutral, and unexpected conditions, respectively; $F_{(2,16)} = 1.91$, $p = 0.16$), and this was true for all manipulations of expectation type ($F_{(2,16)} = 2.67$, 1.86, 1.75 with $p = 0.08$, 0.17, 0.19 for color expectation, orientation expectation, and motor expectation, respectively). Further, *post hoc* Bayes factor analysis indicated either slightly positive or equivocal evidence in favor of the hypothesis that expectation had no effect on CPP slope ($BF_{10} = 0.28$–1.01; Table 1).

Excluding the first 20 trials following a change in expectation type does not influence the effects of expectation on the CPP

Discarding the first 20 trials from each block following a change in expectation type did not influence the CPP effects reported above (Fig. 5). The amplitude of pre-peak CPP was greater on fast compared with slow flicker rate trials from 250 to 750 ms after target onset and from 250 to 200 ms before response onset (target-locked: $F_{(1,16)} = 11.01$–33.05; $p < 0.001$–0.0043; response-locked $F_{(1,16)} = 11.50$; $p = 0037$, FDR-corrected threshold = 0.0043, respectively; Fig. 5A, left). These flicker rate effects were consistent across expectation type (from 250–750 ms after target onset: $t_{(16)} = 5.38$, 2.40, 4.68 with all $p < 0.05$ for color expectation, orientation expectation and motor expectation, respectively; from 250 to 200 ms before response onset: $t_{(16)} = 2.11$, −0.02, 4.77 with $p = 0.03$, 0.51, and < 0.001 for color expectation, orientation expectation, and motor expectation, respectively; Figure 5A, right). In addition, the post-peak amplitude of the CPP was lower on fast compared with slow flicker rate trials from 1050 to 1100 ms after target onset ($F_{(1,16)} = 11.11$; $p = 0.004$, FDR-corrected threshold = 0.0043). This decrease
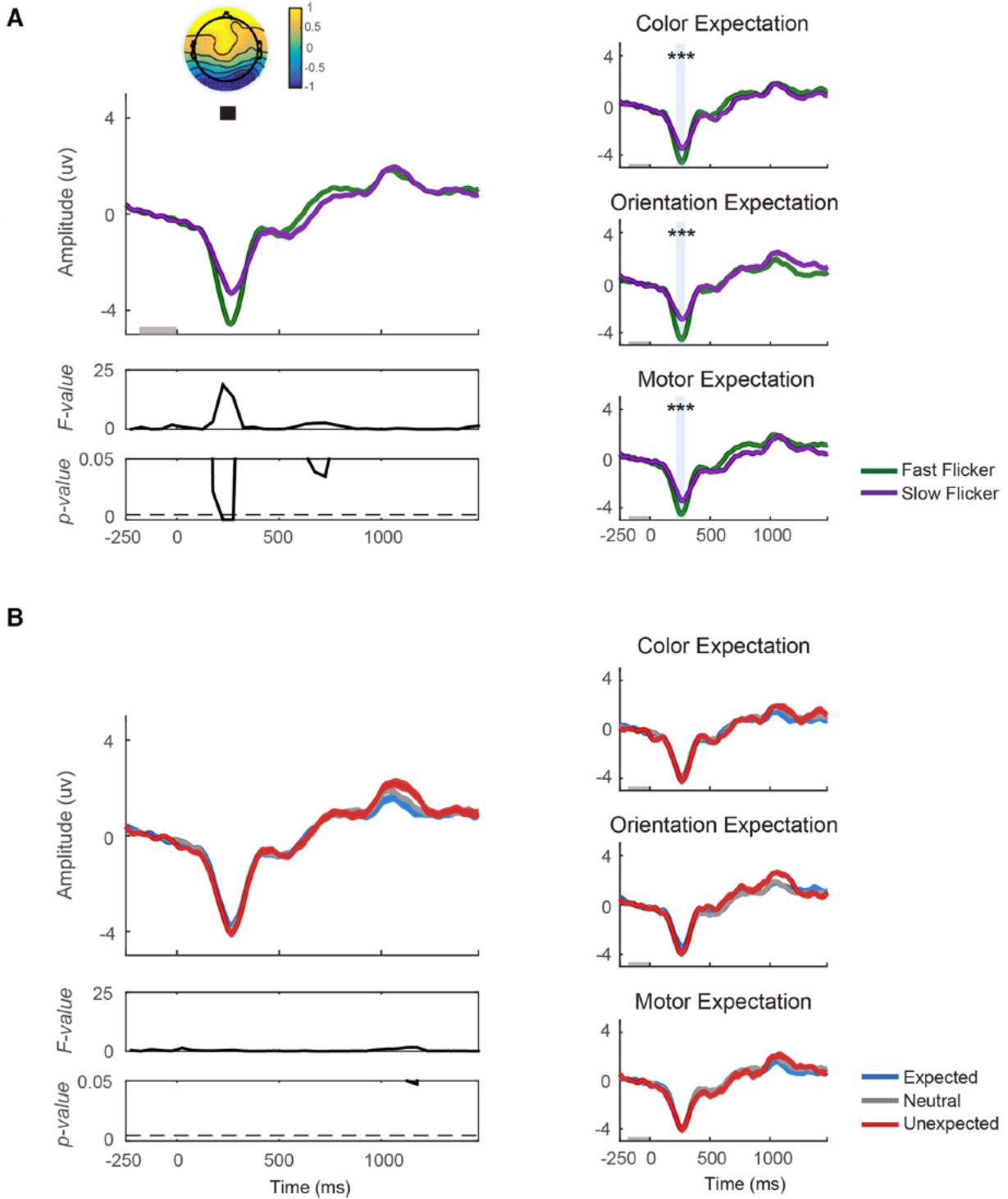
Figure 3. Excluding the first 20 trials following a change in expectation types does not influence the null effect of expectation on the VN. VN amplitude was computed on data after the first 20 trials from each block were discarded. Similar to Figure 2, VN was plotted from 250 ms before target onset to 1500 ms after target onset. *A*, VN was plotted as a function of flicker rate (fast/slow) and (*B*) as a function of expectation status of the target (expected/neutral/unexpected). Left, VN collapsed across expectation type (color/orientation/motor expectation). Right, VN from individual expectation type. Fast flicker rate induced a significantly more negative VN from 200 to 300 ms after target onset. Significant main effect of flicker rate, ***$p < 0.001$.
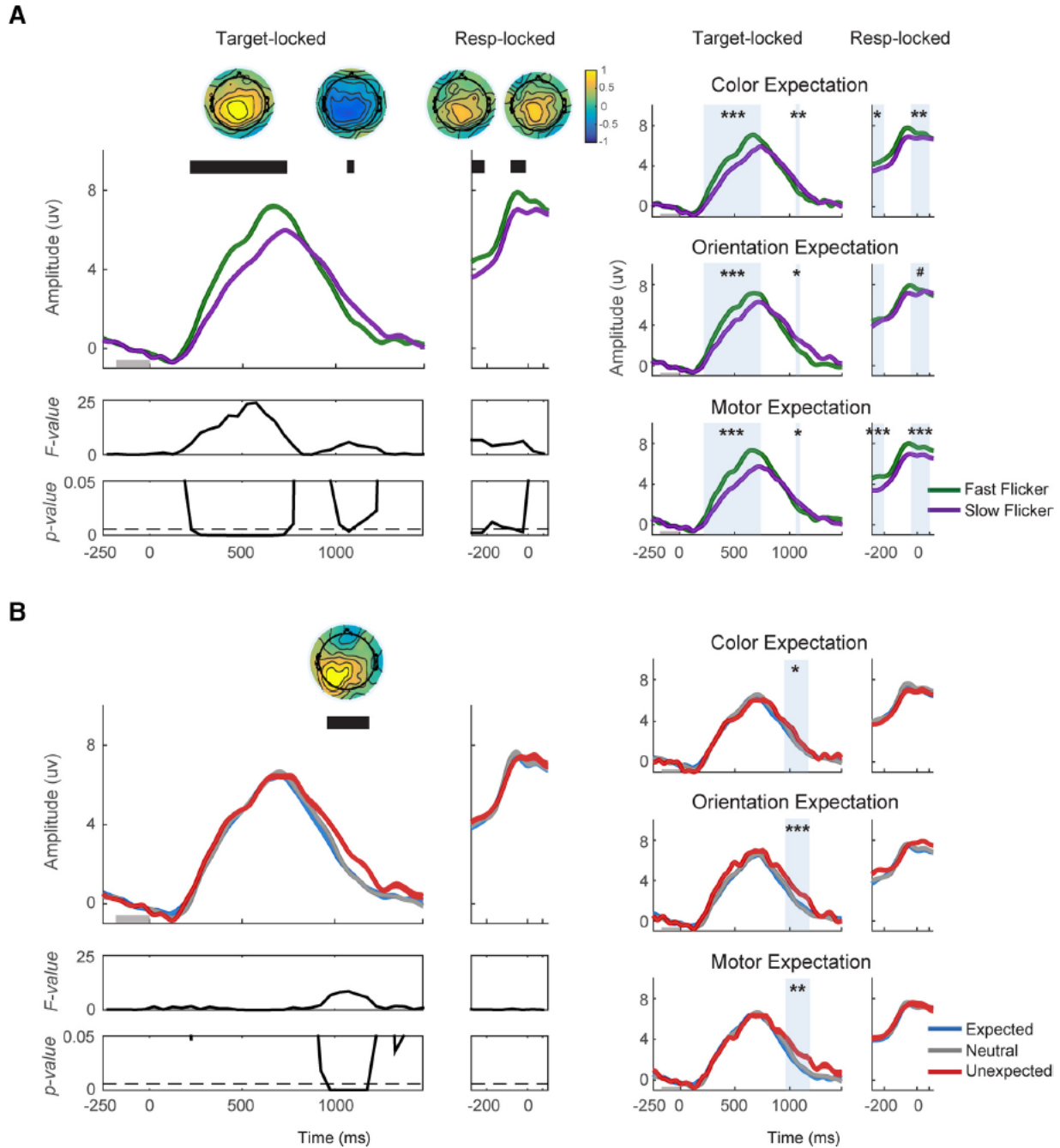
Figure 4. Expectation does not impact the pre-peak CPP amplitude but violations of expectation modulate the post-peak CPP amplitude. CPP amplitude and slope were computed on data from all trials of each block. *A*, Target-locked CPP was plotted from 250 ms before target onset to 1500 ms after target onset, whereas response-locked CPP was plotted from 300 ms before response onset to 100 ms after the onset. CPP was plotted as a function of flicker rate (fast/slow) and (*B*) as a function of expectation status of the target (expected/neutral/unexpected). Fast flicker rate induced higher CPP amplitude from 200 to 750 ms after target onset, and from 300 to 200 and from 100 to 0 ms before response onset. Additionally, after the peak of the target-locked CPP, the CPP amplitude dropped faster on trials where stimuli were presented at the fast flicker rate from 1000 to 1100 ms after target onset. The effect of expectation on the CPP amplitude emerged from 950 to 1200 ms after target onset where the CPP amplitude was lower for unexpected compared with neutral and expected trials. Significant main effects of flicker rate and expectation: #*p* < 0.1, *p < 0.05, **p < 0.01, and ***p < 0.001.

in post-peak CPP amplitude with the fast flicker targets was consistent across expectation type ($t_{(16)}$ = −3.03, −2.24, −1.93 with p = 0.004, 0.02, 0.04 for color expectation, orientation expectation, and motor expectation, respectively).

Similar to the null result obtained when we included all trials, we found no effect of expectation on the pre-peak target-locked CPP ampli-

tude or on response-locked CPP amplitude. *Post hoc* Bayes factor analysis was generally consistent with these null results (BF_{10} = 0.25–0.34). Instead, expectation had an impact on the post-peak amplitude of the CPP from 950 to 1100 ms and from 1150 to 1200 ms after target onset (950–1100 ms: $F_{(2,16)}$ = 6.97–11.74; p = 0–0.0002; 1150–1200 ms; $F_{(2,16)}$ = 11.53–17.08; p = 0–0.0002; FDR-corrected threshold = 0.0043, respec-
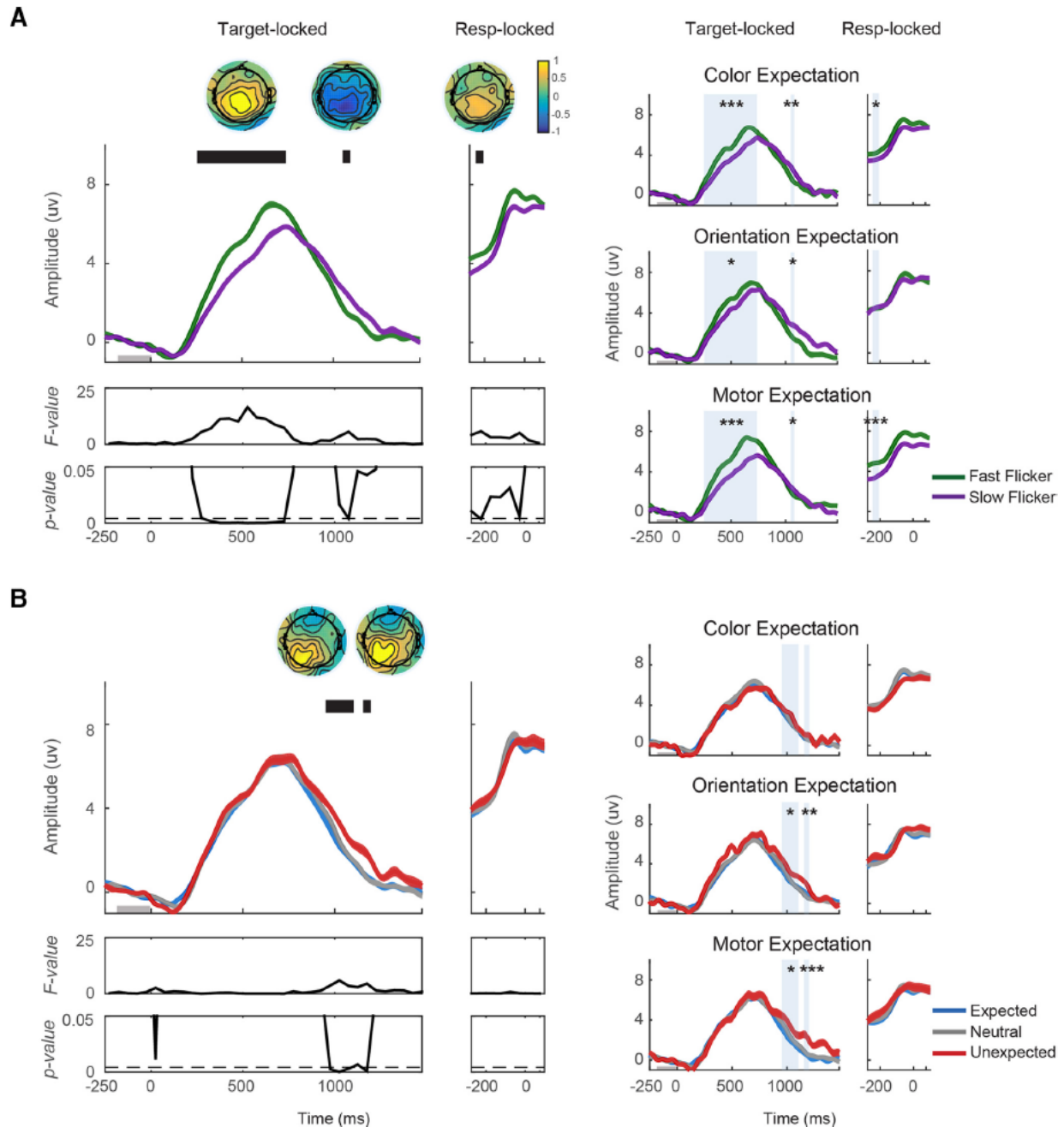
Figure 5. Excluding the first 20 trials following a change in expectation types does not influence the CPP effects. The amplitudes and slopes of the CPP were recomputed after the first 20 trials from each block were discarded. Similar to Figure 4, CPP was plotted from 250 ms before target onset to 1500 ms after target onset, whereas response-locked CPP was plotted from 300 ms before response onset to 100 ms after response onset. *A*, CPP was plotted as a function of flicker rate (fast/slow) and (*B*) as a function of the expectation status of the target (expected/neutral/unexpected). The faster flicker rate induced higher CPP amplitude from 250 to 750 ms after target onset, and from 250 to 200 before response onset. Additionally, after the peak of the target-locked CPP, the CPP amplitude dropped faster on trials where stimuli were presented at a fast flicker rate from 1050 to 1100 ms after target onset. The effects of expectation on the CPP amplitude emerged from 950 to 1100 ms and from 1150 to 1200 ms after target onset where the CPP amplitude was lower for unexpected compared with neutral and expected trials. Significant main effects of flicker rate and expectation: $*p < 0.1$, $**p < 0.05$, $***p < 0.001$.

tively; Fig. 5*B*, left). During these intervals, the amplitude of the CPP was higher on unexpected compared with neutral and expected trials (950–1100 ms: $t_{(16)} = -3.26$, $p < 0.01$; $t_{(16)} = -3.56$, $p < 0.01$, respectively; 1150–1200 ms: $t_{(16)} = -3.52$, $p < 0.01$; $t_{(16)} = -2.89$, $p < 0.01$, respectively). Further, this expectation effect was consistent across nearly all expectation types (950–1100 ms: $F_{(2,16)} = 2.33$, 5.19, 4.84 with $p = 0.11$,

0.01, 0.01 for color expectation, orientation expectation, and motor expectation, respectively; 1150–1200 ms: $F_{(2,16)} = 0.27$, 7.66, 9.10 with p's = 0.76, 0.002, <0.001 for color expectation, orientation expectation, and motor expectation, respectively; Fig. 5*B*, right). In addition, we examined the interaction between flicker rate and expectation on the amplitude of the CPP and found that no time window survived correction

for multiple comparisons (target-locked: $F_{max} = 3.33$, $p_{min} = 0.05$; response-locked: $F_{max} = 0.29$, $p_{min} = 0.75$, FDR-corrected threshold < 0.001).

Finally, discarding the first 20 trials from each block following a change in expectation types did not influence the effects of flicker rate and expectation on the CPP slope. We found a higher slope when targets were rendered at a fast compared with slow flicker rate (mean slopes ± 1 SEM = 0.031 ± 0.004 and 0.025 ± 0.004 μV/ms for fast and slow flicker rates, respectively; $t_{(16)} = 4.17$, $p < 0.001$). This flicker rate effect was consistent across expectation types ($t_{(16)} = 2.97, 2.59, 2.65$ with all $p < 0.05$ for color expectation, orientation expectation, and motor expectation, respectively). Similar to what we previously reported when all trials were included, there was no effect of expectation on the slope of the CPP (mean slopes ± 1 SEM = $0.027 \pm 0.004, 0.029 \pm 0.003$ and 0.028 ± 0.004 μV/ms for expected, neutral, and unexpected conditions, respectively; $F_{(2,16)} = 0.33$, $p = 0.72$), and this was true across expectation type ($F_{(2,16)} = 1.55, 2.01, 0.02$ with $p = 0.23, 0.15, 0.98$ for color expectation, orientation expectation, and motor expectation, respectively). Further, *post hoc* Bayes factor analysis indicated slightly positive or equivocal evidence in favor of the hypothesis that expectation had on effect on CPP slope (BF$_{10}$ = $0.26 - 0.43$), as Bayes factor revealed no substantial evidence in favor of H1.

Together, the lack of expectation effects on the CPP slope and the significant post-peak expectation-related modulation of CPP amplitude suggest that expectation did not directly impact the efficiency of early sensory processing during perceptual decision-making. Instead, violations of expectation may slow down decision-making by affecting processing after sensory evidence has already been accumulated.

Parietal alpha activity
The duration of poststimulus reductions in alpha amplitude over parietal cortex has been previously established as an index for alertness and task engagement (von Stein et al., 2000; Fries et al., 2001; Sauseng et al., 2005; Klimesch et al., 2007; Rihs et al., 2007; Hanslmayr et al., 2008; Busch et al., 2009; Kelly et al., 2009; Mathewson et al., 2009; Zhang et al., 2010; Foxe and Snyder, 2011; Bosman et al., 2012). If expectations primarily impact total time on task without modulating early sensory processing, then alpha modulations should build over the course of the trial and track response times.

Flicker rate does not affect parietal alpha activity
First, we examined the effect of flicker rate on alpha amplitude. We found that a few time windows showed a trend but did not survive correction for multiple comparisons (target-locked: $F_{max} = 9.92$, $p_{min} = 0.01$, FDR-corrected threshold = 0.002; response-locked: $F_{max} = 2.62$, $p_{min} = 0.13$, FDR-corrected threshold = 0.002; Fig. 6A, left). Overall, this result suggests that parietal alpha does not reflect the efficiency of early sensory processing.

Violations of expectation induces reductions in parietal alpha amplitude
We found significant expectation effects on alpha amplitude from 800 to 1150 ms following target onset ($F_{(2,16)} = 7.52 - 10.48$; $p = 0.0003 - 0.002$, FDR-correct threshold = 0.002; Fig. 6B, left). During these time windows, alpha amplitude was significantly lower in the unexpected compared with the expected condition ($t_{(16)} = 3.42$, $p = 0.002$) and the neutral condition ($t_{(16)} = 2.71, p = 0.008$). Follow-up one-way ANOVAs showed that these expectation effects were consistent across expectation type ($F_{(2,16)} = 6.57, 3.94, 9.21$ with $p < 0.01$, < 0.05, < 0.001 for color expectation, orientation expectation, and motor expectation, respectively; Fig. 6B, right). Note that the expectation effect on the alpha activity emerged after the CPP peaked. This suggests that the violations of expectation occurred only after early sensory processing had been completed, thus violations of expectation may induce surprise, higher vigilance and more prolonged task engagement (Zimmer et al., 2010; cf. Talsma et al., 2012; Wessel and Aron, 2017).

Frontal theta activity
Last, we examined the amplitude of frontal theta activity, which has been previously used to index multiple attributes of executive function in the prefrontal cortex, including novelty detection, conflict-monitoring, error detection, response inhibition, and working memory (D'Esposito et al., 1995; Carter et al., 1998; Curtis and Esposito, 2003; Kane and Engle, 2003; Ridderinkhof et al., 2004; Cavanagh et al., 2011, 2012; Itthipuripat et al., 2013b; Aron et al., 2004, 2014, Botvinick et al., 1999, 2001, 2004; Cavanagh and Frank, 2014; Wessel and Aron, 2017). According to the classic SDT account, unexpected targets or motor responses should lead to higher theta amplitude because unexpected events put greater demands on several aspects of executive functions including novelty detection and conflict monitoring. In contrast, the sensory enhancement account would not predict an expectation effect on this neural measure of post-sensory processing.

*Fast flicker rate increases frontal theta amplitude*
We found significant increases in frontal theta amplitude on trials with a fast compared with slow flicker rate over a temporal window extending from 400 to 900 ms after target onset ($F_{(1,16)} = 10.76 - 20.95$; $p = 0.0003 - 0.005$, FDR-correct threshold = 0.007; Fig. 7A, left). This flicker rate effect was consistent across nearly all expectation conditions ($t_{(16)} = 1.64, 3.60, 2.43$ with $p = 0.06$, < 0.01, 0.05 for color expectation, orientation expectation, and motor expectation, respectively; Fig. 7A, right). This is consistent with the idea that presenting more sensory information per unit time leads to an earlier and stronger engagement of frontal executive control processes.

Violation of expectation increases frontal theta amplitude
The effect of expectation on frontal theta activity was found from 300–50 ms before response onset ($F_{(2,16)} = 5.90 - 7.98$; $p = 0.002 - 0.007$, FDR-correct threshold = 0.007; Fig. 7B, left). During these time windows, theta amplitude was significantly higher in the unexpected compared with the expected ($t_{(16)} = -3.17$, $p = 0.003$) and the neutral condition ($t_{(16)} = -1.97, p = 0.03$). Follow-up ANOVAs showed that these expectation effects were consistent across most expectation types ($F_{(2,16)} = 3.07, 9.71, 3.46$ with $p = 0.06$, < 0.001, < 0.05 for color expectation, orientation expectation, and motor expectation, respectively; Fig. 7B, right). These results are consistent with the notion that violations of expectation engaged the frontal executive control network, which in turn led to the slowing of motor responses.

Discussion
Expectations about likely sensory features and motor responses can modulate the speed and accuracy of decision-making. According to classic accounts, expectation about a motor response should reduce the amount of evidence needed to trigger a decision (i.e., introduce a response bias; Wald and Wolfowitz, 1949; Green and Swets, 1966; Ratcliff, 1978; Voss et al., 2004; Macmillan and Creelman, 2005; Bogacz et al., 2006; Ratcliff et al., 2016). However, the impact of expectations about sensory features on decision-making is controversial. Some accounts hold that expectation about low-level sensory features such as color, orientation, and motion direction improves sensory encoding by modulating the quality of sensory responses in early visual cortex (Lee and Mumford, 2003; Spratling, 2008; Kok et al., 2012b, 2014). If modulations of sensory responses in visual cortex impact decision-making, they should do so by increasing the efficiency of sensory processing (Diederich and Busemeyer, 2006; Summerfield and de Lange, 2014; Cheadle et al., 2015; Forstmann et al., 2016). However, previous studies of the effect of expectation on sensory processing often used an explicit cue that provided information about a relevant stimulus feature. However cues about the relevance of an impending target lead to the deployment of selective attention, which is well known to influence early sensory responses (Moran and Desimone, 1985; Hillyard and Anllo-Vento, 1998; McAdams and Maunsell, 1999; Treue and Martínez Trujillo, 1999; Reynolds et al., 2000; Martínez-Trujillo and Treue, 2002; Cohen and Maunsell, 2009; Störmer et al., 2009; Scolari et al., 2012; Anderson et al., 2013; Itthipuripat et al., 2014a,b, 2017;
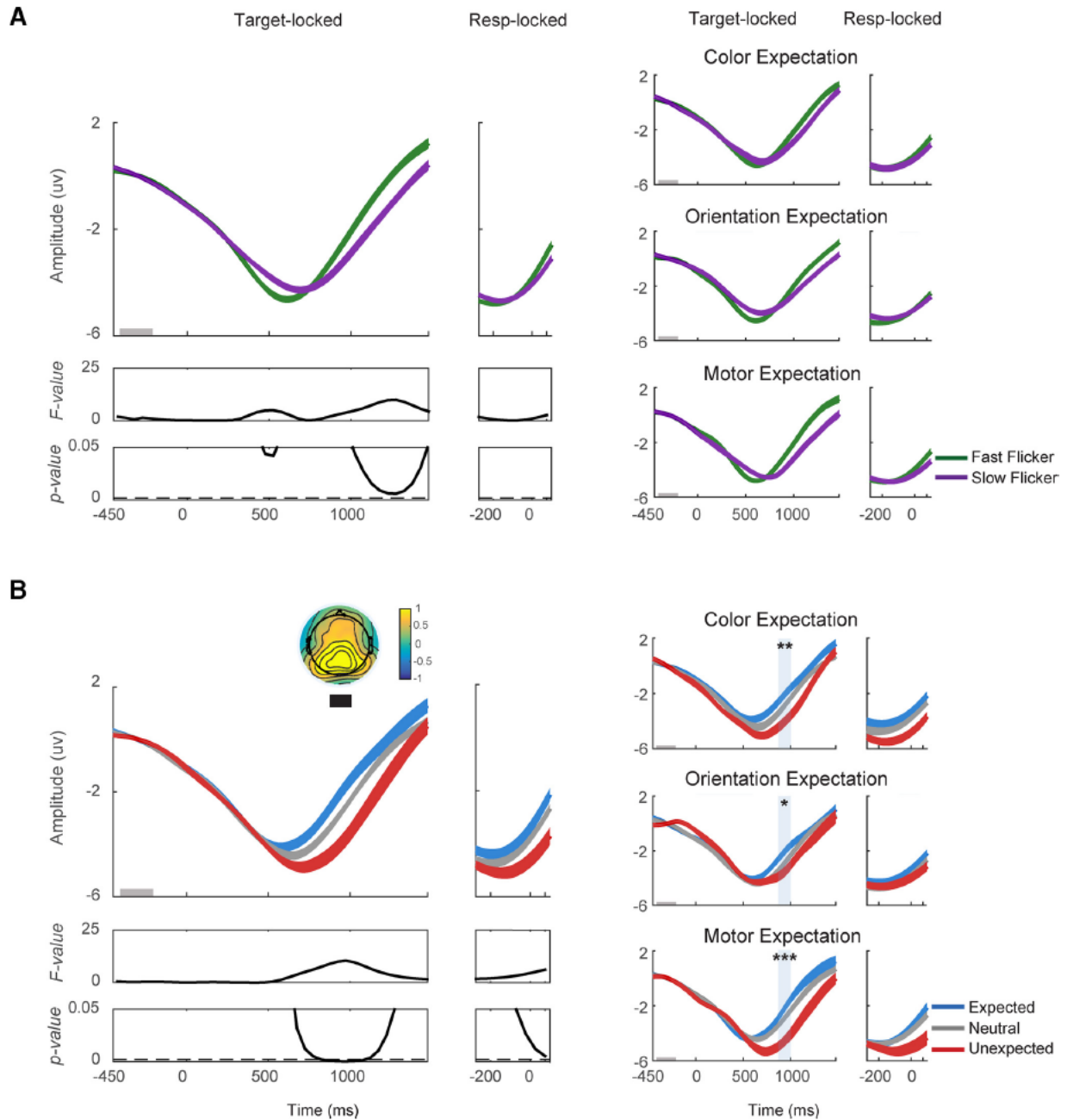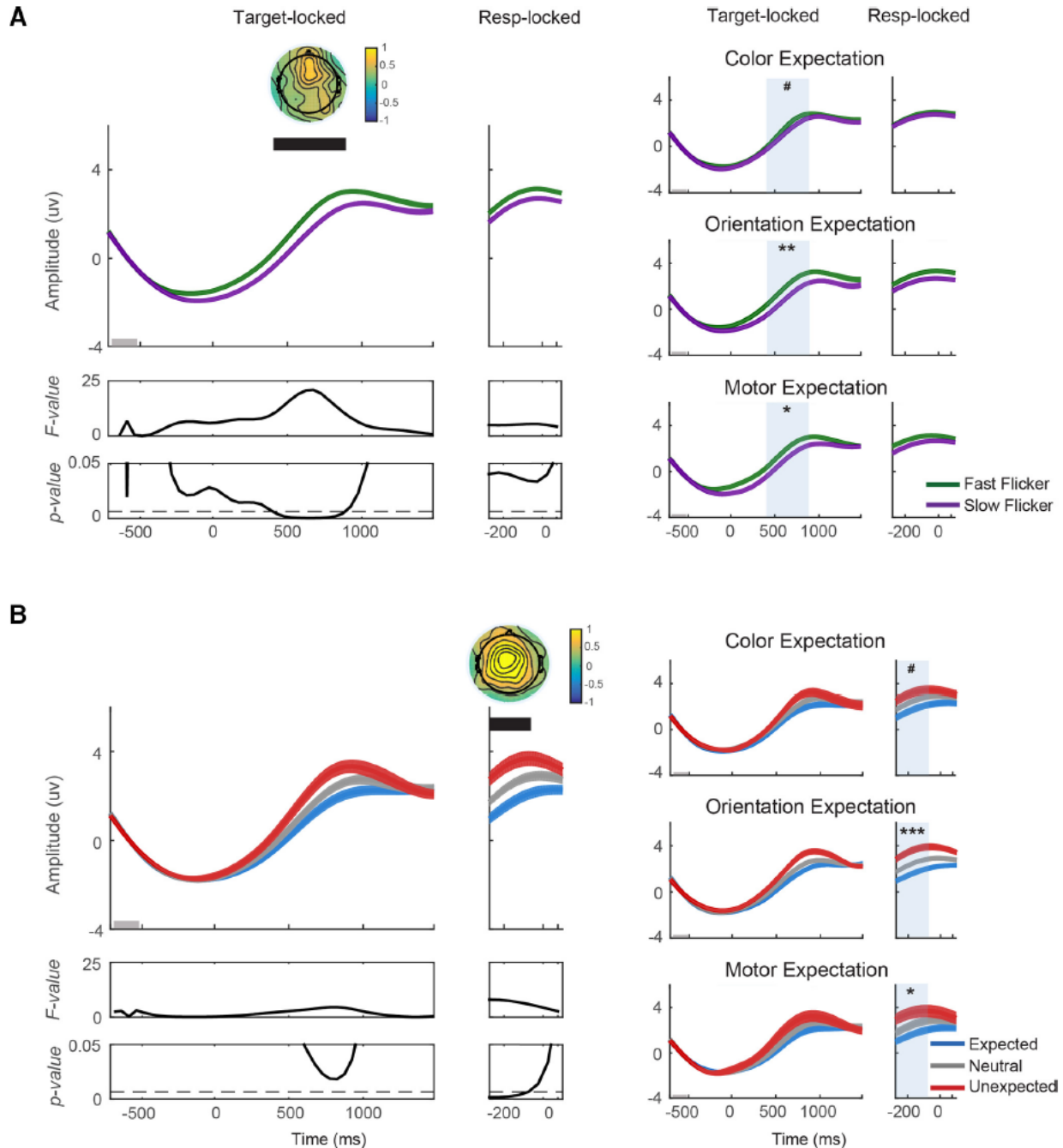
Figure 6. Violations of expectation induce reductions in parietal alpha amplitude. *A*, Target-locked alpha was plotted from 450 ms before target onset to 1500 ms after target onset, whereas response-locked alpha plotted from 300 ms before response onset to 100 ms after the onset. The parietal alpha amplitude was plotted as a function of flicker rate (fast/slow; *B*) as a function of the expectation status of the target (expected/neutral/unexpected). Expectation had an effect on parietal alpha amplitude from 800 to 1150 ms after target onset such that alpha amplitude was higher on expected trials during this period. Significant main effects of flicker rate and expectation: *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$.

Saproo and Serences, 2014; Störmer and Alvarez, 2014). As an alternative to this sensory enhancement account, violations of expectation might influence behavior by interfering with later stages of response selection and response execution, thus leading to slower overall responses.

Here we tested these accounts by orthogonally manipulating expected and relevant feature (e.g., expectation was about target color, but target was defined by orientation). In addition, we also independently manipulated amount of available sensory evi-

dence and motor expectation. We found that increasing the amount of sensory evidence led to faster and more accurate responses, as did manipulations of expectation with a comparable magnitude. Moreover, manipulations of sensory evidence increased the amplitude of the VN and the amplitude and slope of the CPP. However, feature and motor expectation had no impact on either of these components. This suggests that even though expectation impact behavior, it does not directly modulate early sensory processing. Note that although interpreting null ef-

21

Figure 7. Violations of expectation increase frontal theta amplitude. *A*, Target-locked theta was plotted from 700 ms before target onset to 1500 ms after target onset, whereas response-locked theta was plotted from 300 ms before response onset to 100 ms after the onset. The frontal theta amplitude was plotted as a function of flicker rate (fast/slow; *B*) as a function of the expectation status of the target (expected/neutral/unexpected). The theta amplitude was higher on trials where stimuli were rendered at the fast flicker rate from 400 to 900 ms after target onset. In addition, theta amplitude was higher on unexpected trials from 300 to 50 ms before response onset. Significant main effects of flicker rate and expectation: $^\#p < 0.1$, $^*p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$.

fects is often difficult, the lack of expectation effects on the VN and the CPP cannot be easily explained as a simple lack of sensitivity. We reported comparable effects of flicker rate and expectation on RT and accuracy, yet only found an impact of flicker rate on the VN and the CPP. Furthermore, we found no interaction effects between these two factors on performance or on ERP components.

Note that we did not assess participant's awareness of the expectation manipulation at the end of each block as we wanted to keep the block-by-block manipulation implicit throughout the experiment. We also did not ask participants to report their awareness after the very last block because each participant performed two sessions of the task and we felt that a single response about which feature occurred more frequently in the last block of

22

Session 2 would not be a robust indication of their overall perception of the experimental manipulation. That said, if the participants were aware of the expectation manipulation, our observed null effects of expectation on VN and CPP would be even more compelling.

The lack of expectation-related modulations of early sensory responses in our dataset stands in contrast to other recent reports. Using fMRI, one previous study reported that expectation about the orientation of an imperative stimulus improved the quality of stimulus representations in human primary visual cortex (V1; Kok et al., 2012a). However, the design of that study did not clearly disentangle expectations about selective attention to relevant sensory features (the auditory cue used to convey information about expectation also indicated the relevant stimulus feature i.e., an oriented stimulus rendered at 45 or 135°). Note that this was not the case in the present study, because expectation was always built on one feature (e.g., color) without providing additional information about overall target relevance since the target feature (i.e., orientation) was equally likely across expected and unexpected trials. In addition, fMRI lacks the time resolution necessary to establish whether early modulations in V1 influence behavior. Related experiments also provide behavioral evidence that expectation may selectively enhance sensitivity to low-level stimulus features (Wyart et al., 2012a; Cheadle et al., 2015). Although consistent with a sensory enhancement account, it is notoriously difficult to use behavioral evidence alone to distinguish between early sensory processing and a reweighting, or selective readout, of sensory information during decision-making (Palmer et al., 1993; Shimozaki et al., 2012; cf. Eckstein et al., 2002, 2013, Law and Gold, 2008, 2009).

Finally, complementing the present report, another recent study also provides evidence that expectations do not impact early sensory signals but instead affect later cognitive processes by shifting decision criteria (Bang and Rahnev, 2017). This study manipulated expectations by using pre-cues, post-cues and a reverse correlation method to examine the effects of expectation on a perceptual decision process. Their results demonstrate that both pre- and post-cueing expectations about the stimuli affected decision criteria but not early sensory processing. In line with this finding, Mulder et al., 2012 manipulated the prior probability of a specific direction of motion and used fMRI to examine the effect of expectation on decision-making. Although expectation improved performance, modeling of the behavioral data combined with fMRI data suggest that this effect was likely due to a shift in the starting point of sensory accumulation processes rather than a change in the drift rate (i.e., rate of sensory evidence accumulation). Given the lack of temporal resolution in fMRI, the present EEG data provide complementary and more direct evidence that manipulations of expectation do not affect early sensory processing during decision-making.

Although expectation did not impact the amplitude of the VN or the slope or peak-amplitude of the CPP, expectation did lead to a decrease in CPP amplitude after the peak amplitude. In addition, expectation influenced the pattern of alpha/theta oscillatory signals previously used to index task effort and cognitive control. Parietal alpha power showed a sustained decrease on trials in which targets were presented on unexpected features or when unexpected motor responses were required. This is consistent with the notion that violations of expectation require more and prolonged task engagement (Zimmer et al., 2010; Talsma et al., 2012; Wessel and Aron, 2017). Further, we found an increase in frontal theta ampli-

tude when the target appeared on unexpected features and when an unexpected motor response was required. This pattern is consistent with the hypothesis that unexpected stimuli require greater executive control during later stages of decision-making and response planning and execution (Cavanagh et al., 2012; Cavanagh and Frank, 2014). For instance, frontal theta, which is thought to be generated from medial frontal cortex, has been implicated in novelty detection and the resolution of response conflict that can cause motor slowing (Botvinick et al., 2001, 2004; Wessel et al., 2012; Cohen and Donner, 2013; Zavala et al., 2014; Voytek et al., 2015; Wessel and Aron, 2017). In sum, our findings suggest that expectations about low-level sensory features, even when the expectations do not provide information about the behavioral relevance of sensory stimuli, primarily impact later decision- and response-related processing. These findings are in line with earlier reports that unexpected stimuli and motor responses lead to global cognitive interruption and motor suppression (Alvarez et al., 2007; Eckstein, 2011; Wessel et al., 2016; Wessel and Aron, 2013, 2017). This suggests that violations of expectation about sensory features influence global networks that modulate late-stage processes including choice evaluation, conflict resolution, and/or motor execution. In the context of the present design, this interpretation is consistent with the fact that participants do not know whether stimuli being presented are "expected" or "unexpected" until they have already integrated sufficient evidence (i.e., the temporal sensory accumulation has reached the associated decision threshold). This situation mirrors real world decision-making in the sense that the importance of learned regularities in the environment, independent of additional information about their behavioral relevance, is not known until a target of visual search is detected. That said, beyond the broad distinctions between relatively early sensory processing and later decision-related processing, the present EEG measures do not reveal the specific neural mechanisms that are impacted by violations of expectation. In addition, the optimal means of using prior expectations during decision-making likely depend on the structure of the task as well as overall difficulty levels (Mulder et al., 2012). Finally, given the well documented effects of selective attention to relevant features on early visual processing, simultaneously and orthogonally manipulating both attention and prior expectations during the same task is a critical future direction.

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25

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Chapter 2:

Differential temporal dynamics of top-down control

on probabilistic perceptual decision making

2.1 Introduction

To maximize the efficiency of sensory processing, our visual system relies on foreknowledge to prioritize the processing of relevant or expected features. For example, knowledge of statistical regularities in the environment can lead to faster recognition of objects when they are encountered in an expected context (e.g., a bird in a backyard) than when they are encountered in unlikely context (e.g., a bird in a washing machine; Biederman, Glass and Stacy, 1973; Biederman, Mezzanotte and Rabinowitz, 1982; Geisler, 2008; Summerfield and de Lange, 2014; Rungratsameetaweemana *et al.*, 2018). In addition, knowledge about the current task goals can also support faster and more accurate processing of relevant over irrelevant items a mechanism referred to as selective attention (Carrasco, 2011; Rungratsameetaweemana and Serences, 2019; Summerfield et al., 2008). Importantly, these two types of "top down" modulatory factors are potentially dissociable, as the probability that a stimulus will be encountered in a specific context is not necessarily linked to its behavioral relevance (Firestone and Scholl, 2015, 2014; Lupyan, 2017, 2015; Newen and Vetter, 2017; Summerfield and de Lange, 2014; Summerfield and Egner, 2009; Summerfield and Tsetsos, 2015).

Over the last several decades, numerous studies have demonstrated that attention improves the efficiency of perceptual processing by modulating the gain of neural populations with respect to current task demands (Carrasco, 2011; Desimone and Duncan, 1995; Reynolds and Chelazzi, 2004; Serences and Kastner, 2014). Expectation, in contrast, has only recently been explicitly investigated as a potentially separable mechanism that might also bias early sensory processing (Summerfield and de Lange, 2014; Summerfield and Egner, 2009). Initial reports regarding the influence of expectation on sensory processing suggest that expected stimuli evoke a more precise feature-selective pattern of responses in primary visual cortex, leading to more efficient processing (Kok et al. 2012; Kok et al. 2013; Wyart et al. 2012; Summerfield & de Lange 2014; Cheadle et al. 2015).

Expectation and attention can be dissociated by adopting a Bayesian account of perceptual inference that takes into account the precision of existing beliefs (i.e. prior) as well as the precision of the sensory information (i.e. the likelihood function). Specifically, expectation about stimulus regularities should modulate the precision of priors while attention based on behavioral relevance of the stimulus should modulate the precision of the likelihood function. Based on the Bayesian framework, attention and expectation should also have the strongest influence on perception when sensory evidence is weak and prior knowledge about both

stimulus identity and relevance is needed to supplement sensory information (Chalk et al., 2010; de Lange et al., 2018; Sterzer et al., 2008; Summerfield and de Lange, 2014). Thus, while both expectation and attention clearly impact overall behavioral performance, it is possible that these two factors differentially influence information processing and decision making at different processing stages and at different time scales.

To investigate these questions, the strength of prior knowledge (expectation) and the behavioral relevance of competing stimuli (attention) have to be independently manipulated. Several recent studies have at least partially achieved this goal by inducing expectation without using an explicit probability cue that carried information about the behavioral relevance of the target. These reports showed that expectations did not impact early sensory processing but instead modulated later cognitive operations including response criteria as well as the selection and execution of motor responses (Bang and Rahnev, 2017; Rungratsameetaweemana et al., 2018). However, these studies did not manipulate attention and little is known about the temporal dynamics of attention and expectation, interactions between these factors, or about their interaction with the strength of sensory evidence to influence different stages of sensory processing and decision making.

The present study examined these questions be devising a continuous orientation discrimination task where expectation, attention, and stimulus strength were manipulated orthogonally. Each trial started with an attention cue to indicate whether participants had to monitor one (focused attention) or two patches (divided attention) of flickering bars to detect a target coherent orientation. Expectation was implicitly manipulated on a block-by-block basis such that the targets on each block were predominantly presented at one orientation. Stimulus strength was manipulated through the coherence level of the flickering bares that defined the target coherent orientation. Participants reported the coherent orientation using a flight simulator joystick which enabled a continuous measure of responses over time. Electroencephalography (EEG) was concurrently recorded while participants performed the task. With this experimental design, we were able to 1) isolate the impact of stimulus strength, attention, and expectation on behavior; 2) examine the temporal dynamics of these factors behaviorally through response trajectories and response error across time as well as neurally through EEG markers of early sensory processing and steady-state visually evoked potentials (SSVEP) which track processing of feature-specific information during decision making.

2.2   Methods

2.2.1   Participants

Thirteen healthy volunteers (seven males; all participants right-handed; mean age = 20.5, SD = 2.3) participated in the experiment. All were neurologically intact and had normal or corrected-to-normal color vision. Participants provided written informed consent and were compensated $10 per hour for participation. Ethical approval was granted by the Institutional Review Board at the University of California, San Diego. Each participant underwent 4 behavioral sessions (sessions were approximately 1.5 hours each, with 5376 trials collected in total).

2.2.2   Stimuli

For each of four test sessions, participants completed a block of practice trials (n = 120 trials), a block of calibration trials (n = 120 trials), and 20 test blocks (n = 120 trials each block). For the practice trials and the main task, stimuli consisted of 200 red bars and 200 blue bars displayed in an annulus (outer diameter, 22°; inner diameter, 2.4°) that surrounded an attention of either red, blue, or green on a dark gray background of 42.68 ± 2.20 cd/m^2 (Fig. 2.1). Red and blue bars within the annulus were flickered either at 30 Hz or 40 Hz for the duration of the trial such that on a trial where the red bars were flickered at 30 Hz, the blue bars would be flickered at 40 Hz and vice versa. Each bar was randomly re-plotted on each 83 ms frame. During coherent motion, 32% (low coherence) or 54% (high coherence) of either the red or blue bars were randomly selected on each frame to be displaced in one of 5 possible orientation (15-159° with 36° increments), while the remaining bars were assigned one of 4 other motion directions. Participants were instructed to report the coherent orientation of these flickering bars via a USB compatible 360° flight simulator joystick.

For the calibration block, stimuli consisted of 400 black bars displayed in an annulus like the practice trials but without an attention cue. On each trial, 100% of the bars (i.e., 100% coherence) were formed a coherent orientation in one of the five possible orientations (15-159° with 36° increments). Participants reported the motion direction of coherent orientation using the flight simulator joystick.

Stimuli were presented on a PC running Windows XP using MATLAB (MathWorks, Natick, MA) and the Psychophysics Toolbox (version 3.0.8; (Brainard, 1997; Pelli, 1985)).

Participants were seated 60 cm from the CRT monitor running at 100 Hz with a gray background of 42.68$\pm$2.20 cd/m^2.

2.2.3 Procedures

Participants performed an orientation variant of a random-dot motion task (RDMs; Williams & Sekular, 1984; Britten et al., 1993; Churchland, Kiani, & Shadlen, 2008; Forstmann et al., 2010), such that stimulus strength (coherence levels), selective attention, and expectation about target coherent orientations could be manipulated. Participants completed 4 test sessions: each of which consisted of practice trials, calibration trials, and test trials. For 6 locks of test trials, each trial began with a display consisting of a fixation point surrounded by an annulus of flickering randomly oriented red and blue bars. After 400-800 ms, the fixation point was replaced by an attention cue, either red, blue, or green. A red or blue cue informed participants of the color of a forthcoming target coherent orientation such that participants could monitor either the red or blue bars (focused attention). A green cue did not provide information about the color of the target coherent orientation and thus participants had to monitor both red and blue bars for a coherent orientation (divided attention). After 600-1000 ms, the red and blue flickering bars were presented for 800 ms, such that a proportion of either red or blue bars formed a coherent orientation at one of the 5 possible orientations. The remaining bars were randomly assigned to the other 4 directions. Note that the attention cue was always valid such that on focused attention trials, the coherent orientation was represented by red bars on half the trials (red attention cue) and by blue bars (blue attention cue) on half the trials. The target display was followed by a 500-ms of a display of a fixation point surrounded by randomly oriented red and blue bars. Each trial ended with a blank intertrial-interval (ITI) that lasted for 666.7-1000 ms. Participants indicated the target coherent orientation by moving the flight simulator joystick its maximal distance in a direction matching the coherent orientation. After making a response, participants turned the joystick to the center in preparation for the next trial. Responses were considered valid when they occurred in the interval between target onset and ITI offset. Together, this study design allowed us to simultaneously investigate the effects of feature expectation and selective attention on information processing during decision-making.

To familiarize participants with the task and the joystick, practice trials were given at the beginning of each session. There were a total of 120 trials from all coherence levels (high/low coherence level), attention conditions (focused/divided), orientations (15-159° with 36° increments), and target color conditions (red/blue). After training, participants performed a block of calibration trials. The purpose of the calibration trials was to estimate how each participant

represented each orientation. These estimates were used to compute performance accuracy on the test trials. Participants reported coherent orientations consisting of 100% coherent bars using the flight simulator joystick. In each session, participants completed one block of 120 trials (24 of each of the 5 possible orientations).

2.2.4 Behavioral Analysis

On each trial, we first identified the final coordinate of the joystick at maximum distance from starting point and used that coordinate to compute the final angle response on each trial (i.e., final response). We then computed an absolute error between this final response and the presented coherent orientation (i.e., final response error) on each trial. Any trials with missed responses and responses that were too early were discarded from further analysis.

We then examined the impact of coherence level (low/high), attention (focused/divided), and expectation (expected /unexpected) on response trajectories and response errors across time. Response trajectory is a measure of a temporal integration of sensory information from the onset of target presentation leading up to a decision choice. Response trajectory was computed as a cumulative distance the joystick was moved from the center across time (Fig. 2.2, left panel). A response trajectory with a steeper slope represents a faster, more efficient processing of sensory information. In order to examine performance accuracy, we computed response errors by calculating the difference between the presented coherent orientation and the joystick response angle at each time point. This analysis was performed on the behavioral data aligned to the onset of target coherent orientation (Fig. 2.2, middle panel) as well as on the data aligned to the peak of response trajectories (Fig. 2.2, right panel).

2.2.5 EEG Recording and Analysis

EEG data were recorded using a 64+8 channel BioSemi Active Two system at a sampling rate of 1024 Hz. Two reference electrodes were placed at the mastoids. We monitored vertical eye movements and blinks via two pairs of electrodes placed above and below the eyes. Horizontal eye movements were monitored via another pair of electrodes placed near the outer canthi of the eyes The EEG data were referenced online to the BioSemi CMS-DRL reference, and all offsets from the reference were maintained <20 uV. The data were preprocessed with a combination of EEGlab 11.03.1b (Delorme and Makeig, 2004) and custom MATLAB scripts.

After data collection, the continuous EEG data were re-referenced off-line to the mean of the left and right mastoid electrodes and applied 0.25 Hz high-pass and 58 Hz low-pass

Butterworth filters (third order). An additional 10 Hz low-pass filter was applied before plotting the data, but all reported statistics were performed on the 58 Hz low-pass filtered data (Luck, 2005; for similar methods, see Hickey, Chelazzi and Theeuwes, 2010; Itthipuripat and Serences, 2015). The data were then visualized from each trial and discarded epochs contaminated by residual eye blinks and vertical eye movements (≥ ±80-150 μV deviation from 0, with thresholds chosen for each participant), horizontal eye movements (≥ ±75-100 μV deviation from 0, with thresholds chosen for each participant), excessive muscle activity, or drifts. This procedure resulted in the rejection of 13.5% of trials on average (± 1.32% SEM across participants; ranged from 3.2% to 22.1% of trials). Data from two participants were excluded from further analysis due to the rejection rate of more than 30% of trials. Finally, the data were temporally aligned to the onset of a target.

Next, artifact-free EEG epochs were sorted into different experimental conditions based on coherence level of target orientation (high or low), on attention directed to target stimuli (focused or divided), on the flicker frequency of target stimuli (30 Hz or 40 Hz), and on the status of each coherent orientation in the context of a given block (expected or unexpected). Due to the uneven number of expected and unexpected trials, we first performed resampling with replacement on data in each experimental bin (e.g., focused attention and divided attention) such that the size of each bin after resampling was equal to the that of the smallest experimental bin (i.e., unexpected condition). To compute event-related potentials (ERPs), the target-aligned EEG data were averaged for each experimental condition. The ERPs were baseline-corrected from 200 before the onset of an attention cue to the onset of an attention cue.

To compute steady-state visually evoked potentials (SSVEPs), the non-baseline-corrected EEG data from each experimental bin for each participant were used to compute Fourier coefficients at frequencies of 30 and 40 Hz (the two stimulus frequencies). The resulting 30 and 40 Hz SSVEPs were then baseline-corrected across a time window extending 200 ms before their respective time-domain SD (i.e., 30-Hz SSVEP data were baseline-corrected from 262.5 to 62.5 ms before cue onset and 40-Hz SSVEP data were baseline-corrected from 245.9 to 46.9 ms before cue onset). The SSVEPs were then extracted from the central occipital (Oz) electrode where the SSVEP signal peaked across both center frequencies of 30 Hz and 40 Hz. Finally, amplitude of 30 and 40Hz SSVEPs was normalized by its respective maximal amplitude to account for differences across frequency level.

Next, we examined the impact of target coherence, attention directed to target stimuli, and the expectation status of target coherent orientation on the SSVEPs and on four ERP components recording from the centro-parietal (CPz), parietal (Pz), parieto-occipital (POz), and occipital (Oz) electrodes.

2.2.6 Statistical Procedures

2.2.6.1 Behavioral Analysis

All reported confidence intervals (CIs) were computed by resampling the data with replacement (i.e., bootstrapping) for 1,000 iterations for each bootstrapping procedure. Note that this method constrains the resolution of our p-values to a lower limit of $p \leq 0.001$. We generated permuted null distributions of response trajectories and response errors for each participant, and condition, and for each time point.

For tests comparing a bootstrapped distribution against zero, *p* values were computed by conducting two one-tailed tests against 0 (e.g., mean(difference in response trajectories < 0) and mean(difference in response trajectories > 0) and doubling the smaller *p* value.

2.2.6.2 EEG Analysis

We examined the impact of coherence level, attention, and expectation on four ERP components: the occipital component recorded from the Oz electrode, the parieto-occipital component recorded from the POz electrode, the parietal component recorded from the Pz electrode, and the centro-parietal component recorded from the CPz electrode. To evaluate the influence of our manipulations on the amplitude of the ERp components, we used 1) three-way repeated-measures ANOVAs with within-subject factors for target coherence (2 levels: low and high coherence), attention (2 levels: focused and divided attention), and expectation status of the target coherent orientation (2 levels: expected and unexpected orientation); and 2) paired t-tests within-manipulation comparisons. These ANOVAs and paired t-tests were performed on the mean ERP amplitudes across consecutive 50 ms windows from 200 ms before to 1000 ms after target onset. Corrections for multiple comparisons were implemented using the false discovery rate (FDR) method (Benjamini and Hochberg, 1995) based on data from all four electrodes of interest.

The same ANOVA analyses and t-tests were then performed on the normalized SSVEP amplitude recorded from the Oz electrode. This electrode was chosen as it displayed maximum response amplitude at 30 Hz and 40 Hz. ANOVAs were performed on the target-aligned SSVEP

response across consecutive 50 ms from 1) 500 ms before to target onset to target onset; 2) target onset to 500 ms after target; and 3) 500 ms to 1000 ms after target onset. Corrections for multiple comparison were computed separately for each of these three windows.

2.3   Results

The main goal of the present study was to orthogonally manipulate and examine the effects of stimulus strength, changes in the distribution of selective attention, and expectation about stimulus regularities on perceptual decision making. We used trajectories of behavioral responses and response errors as behavioral markers of sensory and post-sensory decision-related processes, respectively. Further, we used ERPs from the centro-parietal to occipital electrodes and SSVEPs as neural markers of sensory encoding and early processing of sensory information during perceptual decision making. If prior expectation improves decision making by enhancing the efficiency of early sensory processing, we expect to see increased ERP and SSVEP responses over visual cortex. However, if expectation improves decision making by primarily modulating decisional and response-related processes, we expect to see little impact of expectation on ERP and SSVEP responses. With our experimental setup, we were able to directly test this hypothesis as well as to future investigate and compare the temporal dynamics of expectation with those of stimulus strength and attention both behaviorally and neurally.

2.3.1   Behavioral results

High target coherence and focused attention enhanced early sensory processing as indexed by trajectories of behavioral responses. The response trajectory indicated the distance the joystick had moved from the center at each time point (0 to 1300 ms after the onset of coherent orientation). Notably, this measure represents a temporal integration of sensory information about the coherent orientation as participants accumulate evidence that eventually leads to a decision choice. The coherence level of the target orientation displays (high/low) affected response trajectories from 675 to 1200 ms after the onset of coherent orientation (high > low coherence; all resampled $p < 0.05$; Fig. 2.2a). Similar to high target coherence, focused attention also enhanced the amplitude of response trajectories but its effect emerged much earlier in time (266.7 to 966.7 ms after the onset of coherent orientation; all resampled $p < 0.05$; Fig. 2.2b). Response trajectories were not modulated by manipulations of expectation (Fig. 2.2c). Fig 2.2d summarizes the effects of target coherence, attention and expectation. Fig. 2.2e

shows the p values for each condition and at each time point (500 ms before the onset of coherent orientation to 1300 ms after the onset; all resampled $p < 0.05$).

Expectation modulates biases baseline responses error. Response errors were computed as the absolute difference at each time point between the participant's response orientation and the calibrated orientation for that participant (see **Methods**). The amplitude of the response errors at each time point indexes the accuracy of the orientation judgment of participants, which primarily reflects response-related operations. The coherence level of the target orientation affected performance accuracy such that high orientation coherence decreased responses errors from 541.4 to 1300 ms after the onset of coherent orientation and from 225 ms before peaked response to 250 ms after peaked response (resampled $p < 0.05$; fig. 2.2f). Similarly, focused attention also led to lower response errors from 691.7 to 716.7 ms after target onset (resampled $p < 0.05$; fid. 2g). In contrast, expectation enhanced baseline performance accuracy such that response errors were lower when the target coherent orientation was expected. This effect was observed from 500 ms before target onset to 833.3 ms after target onset (resampled $p < 0.05$; fig. 2.2h). Additionally, response errors were lower on expected trials from 500 ms to 133.3 ms before the peaked responses (resampled $p < 0.05$; fig. 2.2h). Fig 2.2i summarizes the effects of target coherence, attention and expectation. Fig. 2.2j shows the p values for each condition and at each time point (left panel: 500 ms before the onset of coherent orientation to 1300 ms after the onset; right panel: 500 ms before to 250 ms after the peaked response; all resampled $p < 0.05$).

2.3.2 EEG results

Expectation does not modulate the efficiency of early sensory processing. We used ERPs recorded from the centro-parietal (Cpz), parietal (Pz), parieto-occipital (POz), and occipital (Oz) electrode to index the magnitude of early sensory processing during a perceptual decision making task. We analyzed the effects of target coherence, attention, and expectation on the amplitude of target-aligned ERPs in sliding 50 ms windows and corrected for multiple comparison using FDR method based on target-aligned data from CPz, Pz, POz, and Oz electrodes (see **Methods**). Manipulations of target coherence and attention directed to target coherent orientation influenced ERPs across all four electrodes at different time scales. Focused attention induced early changes in the ERP responses across all channels (CPz: target onset to 500 ms after target onset; $t_{(12)} = 3.24\text{-}5.01$; $p = 0.0003\text{-}0.0071$; Cz: target onset to 450 ms after target onset; $t_{(12)} = 3.17\text{-}4.67$; $p = 0.0005\text{-}0.0081$; POz: target onset to 100 ms and 150 to 250 ms after target onset; $t_{(12)} = 4.04$; $p = 0.0016$; Oz: target onset to 50 ms after

37

target onset; $t_{(12)}$ = 3.70; p = 0.0031, FDR-corrected threshold = 0.0106; Fig. 2.3b). The effect of orientation coherence occurred later in time (CPz: 450 to 1000 ms; $t_{(12)}$ = 3.34-4.54; p = 0.0007-0.0058; Cz: 500 to 850 ms and 900 to 1000 ms; $t_{(12)}$ = 3.01-4.59; p = 0.0006-0.0109; POz: 950 to 1000 ms; $t_{(12)}$ = 3.19-3.29; p = 0.0065-0.0077; Oz: 400 to 450 ms after target onset; $t_{(12)}$ = 3.03; p = 0.0105, FDR-corrected threshold = 0.0123; Fig. 2.3a). ERP responses were not affected by manipulations of expectation.

We assessed SSVEPs from three different time windows: i) from 500 ms before target onset to target onset; ii) from target onset to 500 ms after target onset; and iii) fron 500 ms to 1000 ms after target onset. High orientation coherence increased SSVEP amplitude from 200 ms to 250 ms after target onset ($t_{(12)}$ = 3.85; p = 0.0023; FDR-corrected threshold = 0.0023; Fig. 2.4a). Manipulations of attention also affected SSVEP responses such that focused attention enhanced SSVEP amplitude from 250 ms to 50 ms before the onset of coherent orientation ($t_{(12)}$ = 3.40-4.44; p = 0.0008-0.0053; FDR-corrected threshold = 0.0053; Fig. 2.4b). In contrast, expectation had no effects on SSVEP responses. Notably, this pattern of results was similar to what was observed in ERPs with the early modulation of focused attention that was followed by the effects of orientation coherence. In addition, the lack of expectation effects was consistent on both the ERP and SSVEP responses.
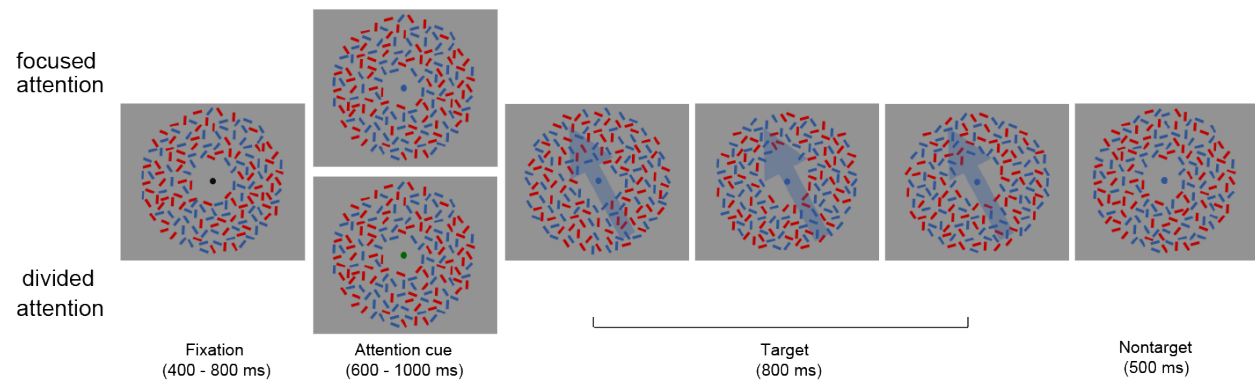
2.4   Discussion

In past studies, expectation was manipulated in a way that likely induced a shift in attention, making it difficult to attribute any observed effects on early sensory processing to expectation per se or to some combination of expectation and attention. For example, a recent study used fMRI and a task where expectation about a target orientation (45° or a 135°) was manipulated by an explicit cue presented at the beginning of each trial (Kok et al., 2012). This cue provided information about what target feature to expect on each trial, but simultaneously provided information about which target feature was relevant to performing the behavioral task. Similar arguments can be made regarding other studies that examined the influence of expectation on decision making (Kok et al. 2013; Kok et al. 2016; Kok et al. 2017; St. John-saaltink et al. 2015; Lange et al. 2013; Jiang et al. 2013; Cheadle et al. 2015; Summerfield & Egner 2016). A few studies have taken a further step to examine how expectations about stimulus regularities interact with attention to modulate information processing, it is difficult to interpret their findings due to a possible conflation of these two top-down signals as a result of the use of explicit probabilistic cues (Jiang et al., 2013; Wyart et al., 2012). Therefore, the selective role that expectations play in early sensory processing, and also how expectations

interact with attention to modulate the overall flow of information through the visual system remains unclear.

The present study investigated these questions by devising a continuous orientation discrimination task where expectation about coherent orientation was manipulated such that one (expected) orientation was presented as a target more frequently than other (unexpected) orientations. Stimulus strength and the degree of attention being afforded to the relevant stimulus were also orthogonally controlled for. As a result, the impact of expectation could directly be compared to the effects of stimulus strength and to the effects of selective attention. Specifically, we directly tested whether expectation about stimulus probabilities improved decision making by enhancing the efficiency of early sensory processing. Behaviorally, we showed that expectation did not impact response trajectories—a behavioral measure that primarily reflects sensory processing and temporal integration of sensory information leading up to a decision choice. In contrast, response trajectories were modulated by stimulus strength and attention such that high orientation coherence and focused attention increased the amplitude of response trajectories. Specifically, the effect of attention occurred earlier in time compared to the effect of orientation coherence. These temporal dynamics were also observed in our ERP and SSVEP results suggesting early processing of sensory information in our decision-making task is sequentially modulated by selective attention and stimulus strength leading up to a decision choice. Once a decision choice has been triggered, the response-related operations to execute a motor response is modulated by prior expectation such that the response associated with a more probable choice is preferred and thus will take less time to execute.

Taken together, our behavioral results reveal that prior expectation improves perceptual decision making as by shifting baseline response errors and thus increasing performance accuracy without impacting early processing of sensory information. This evidence for a selective role of expectation on decisional and response-related processes was consistent with the lack of expectation effects on the neural markers for sensory processing of information throughout the visual cortex.

focused
attention

divided
attention

| Fixation
(400 - 800 ms) | Attention cue
(600 - 1000 ms) | Target
(800 ms) | Nontarget
(500 ms) |

Figure 2.1: Experimental paradigm and analysis overview. A trial began with a fixation point (400 to 800 ms) and was followed by an attention cue (600 to 1000 ms) to indicate the color of the bars that would represent coherent orientation (target). A red (blue) attention cue indicated that coherent orientation would be represented with red (blue) bars (focused attention condition). A green attention cue indicated that coherent orientation would be represented with either red or blue dots, i.e., the participant had to discern which color of bars was in coherent orientation (divided attention). Coherent orientation was presented for 800 ms during which the participant could start beginning to make a response by moving the joystick from the starting point in the directions that match the perceived coherent orientation.

Figure 2.2: Response trajectories and response errors. Target-aligned response trajectories (left) and target-aligned response errors (middle) were plotted from the onset of coherent orientation (0 ms) to 1000 ms after onset. Response-aligned response errors (right) were plotted from 500 ms before target onset to 1250 ms after target onset. Response trajectories and response errors were plotted **a,** as a function of orientation coherence (high/low), **b**, as a function of attention (focused/divided), and **c,** as a function of expectation (expected/unexpected). **d,** Differences in response trajectories and response errors for each manipulation condition were plotted together with the associated p values (**e**). The amplitude of response trajectories was higher on trials with high orientation coherence versus trials with low coherence from 675 to 1200 ms after the onset of coherent orientation (resampled $p < 0.05$; **a**). Focused attention led to a greater amplitude of response trajectories in comparison to divided attention from 266.7 to 966.7 ms after target onset (resampled $p < 0.05$; **b**). Response trajectories were not modulated by manipulations of expectation (**c**). Response errors were lower when coherent orientation was presented at a high coherence than at a low level from 541.4 to 1300 ms after target onset and from -225 ms before peaked response to 250 ms after peaked response (resampled $p < 0.05$; **f**). Response errors were lower when attention was focused than when attention was divided from 691.7 to 716.7 ms after target onset (resampled $p < 0.05$; **g**). Expectation reduced baseline response errors (i.e., prior to and at the onset of coherent orientation), and this effect lasted from 500 ms before target onset to 833.3 ms after target onset (resampled $p < 0.05$; **h**). Additionally, response errors were lower on expected trials from 500 ms to 133.3 ms before the peaked responses (resampled $p < 0.05$; **h**). For **e**, the legend is the same as in (**d**). Error bars for each of the three measures indicate 95% CIs computed by resampling the data distribution.
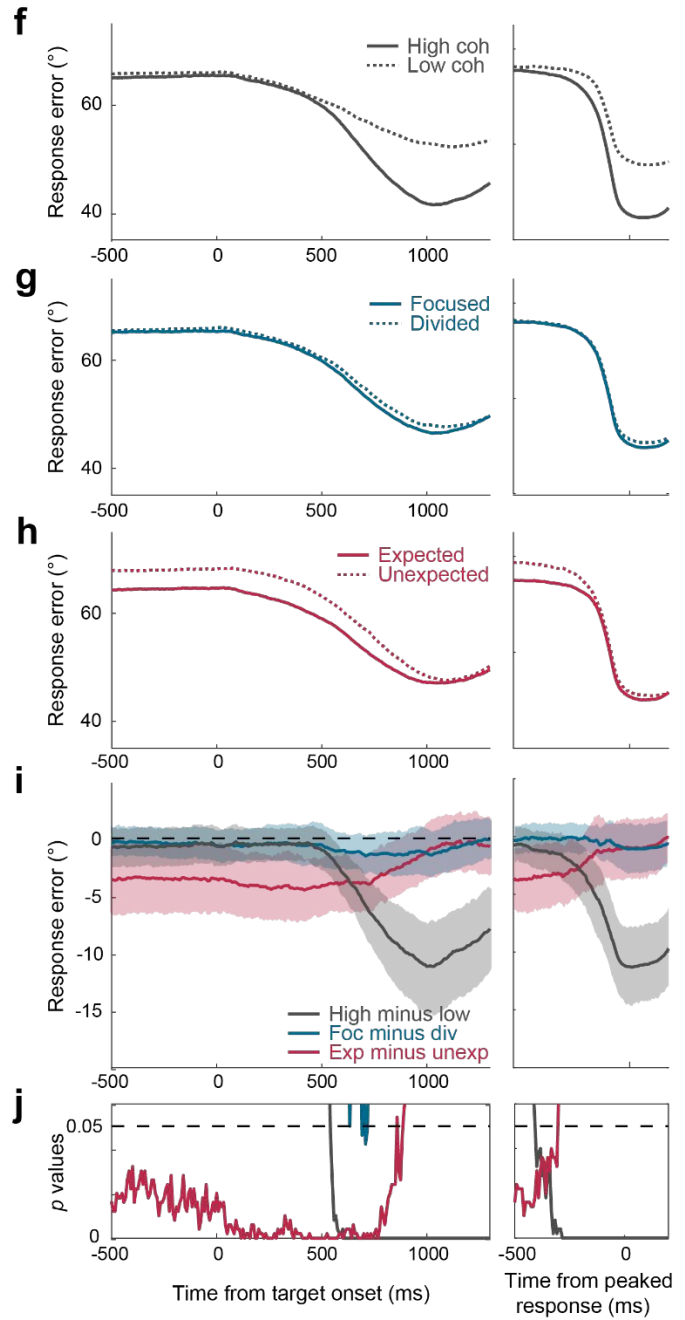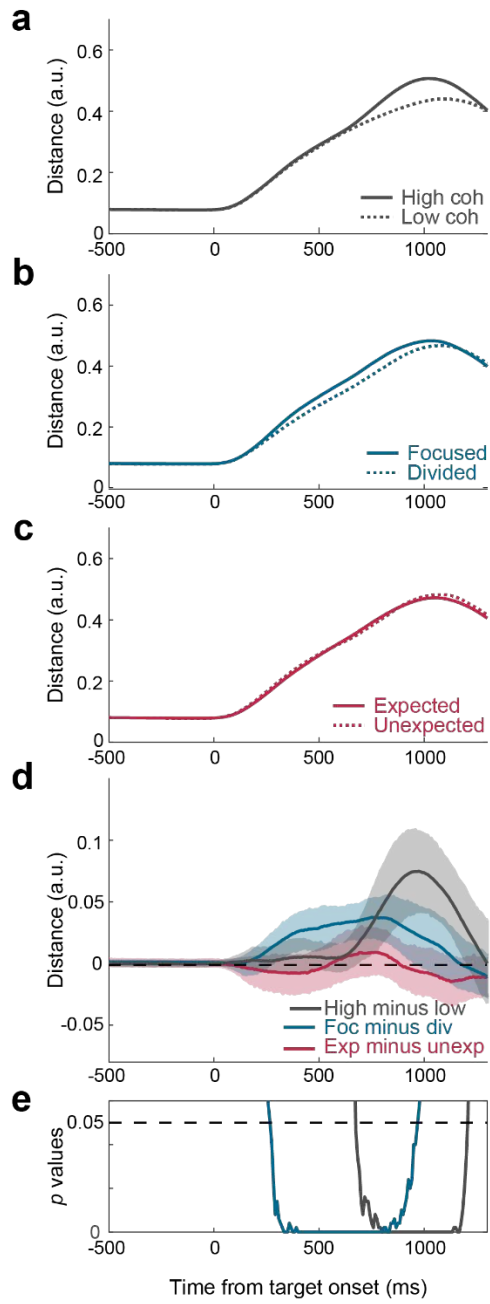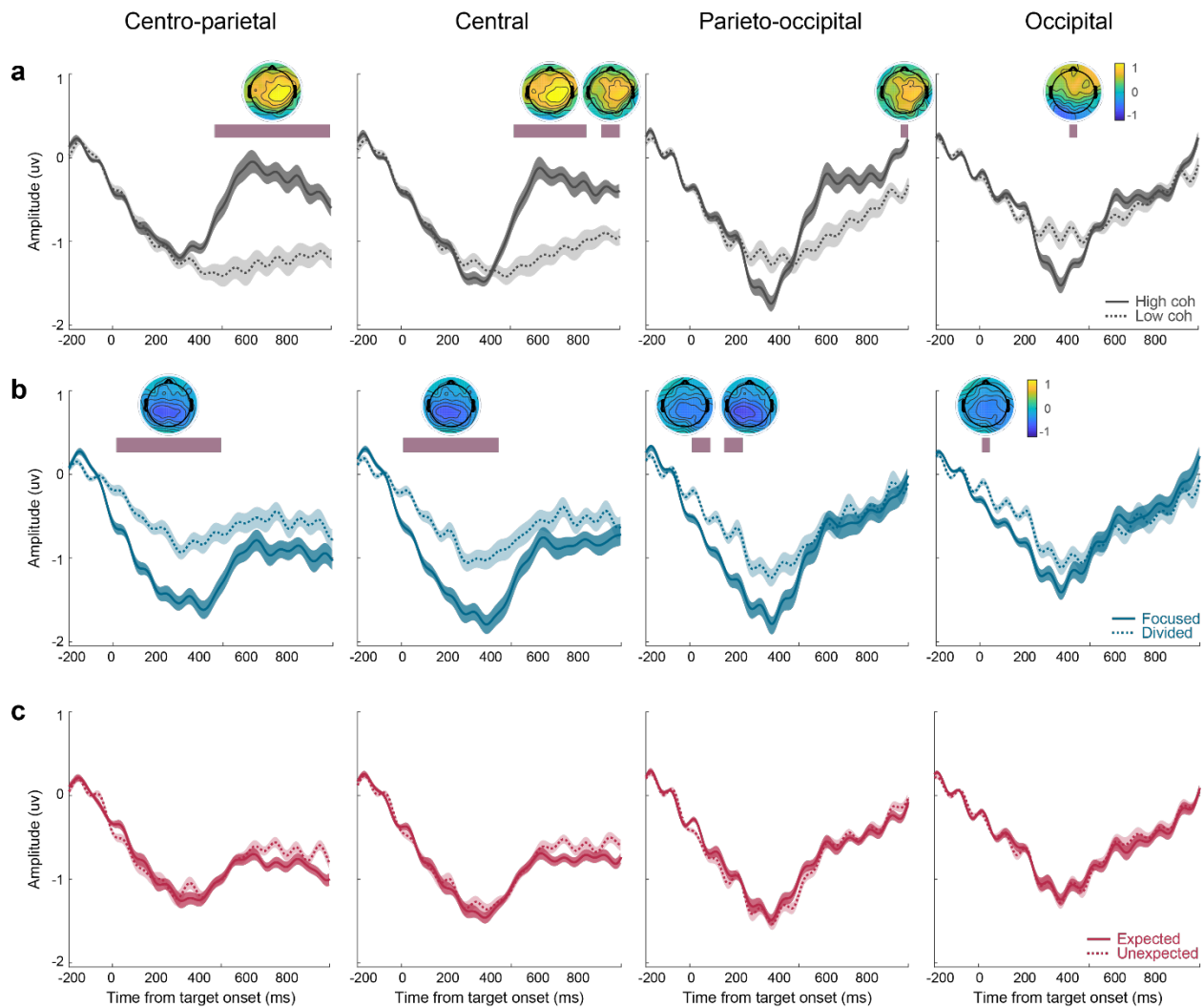
Figure 2.3: Event-related potentials (ERPs) as a function of orientation coherence, attention, and expectation. Amplitude of ERPs was computed from all trials of each manipulation condition recorded from centro-parietal (CPz), central (Cz), parieto-occipital (POz), and occipital (Oz) electrode. ERPs are plotted from 200 ms before target onset to 1000 ms after target onset **a**, as a function of orientation coherence (high/low), **b**, as a function of attention (focused/divided), and **c**, as a function of expectation (expected/unexpected). Focused attention induced early changes in the ERP responses across all channels (CPz: target onset to 500 ms after target onset; Cz: target onset to 450 ms after target onset; POz: target onset to 100 ms and 150 to 250 ms after target onset; Oz: target onset to 50 ms after target onset), whereas the effect of orientation coherence occurred later in time (CPz: 450 to 1000 ms; Cz: 500 to 850 ms and 900 to 1000 ms; POz: 950 to 1000 ms; Oz: 400 to 450 ms after target onset). ERP responses were not affected by expectation.
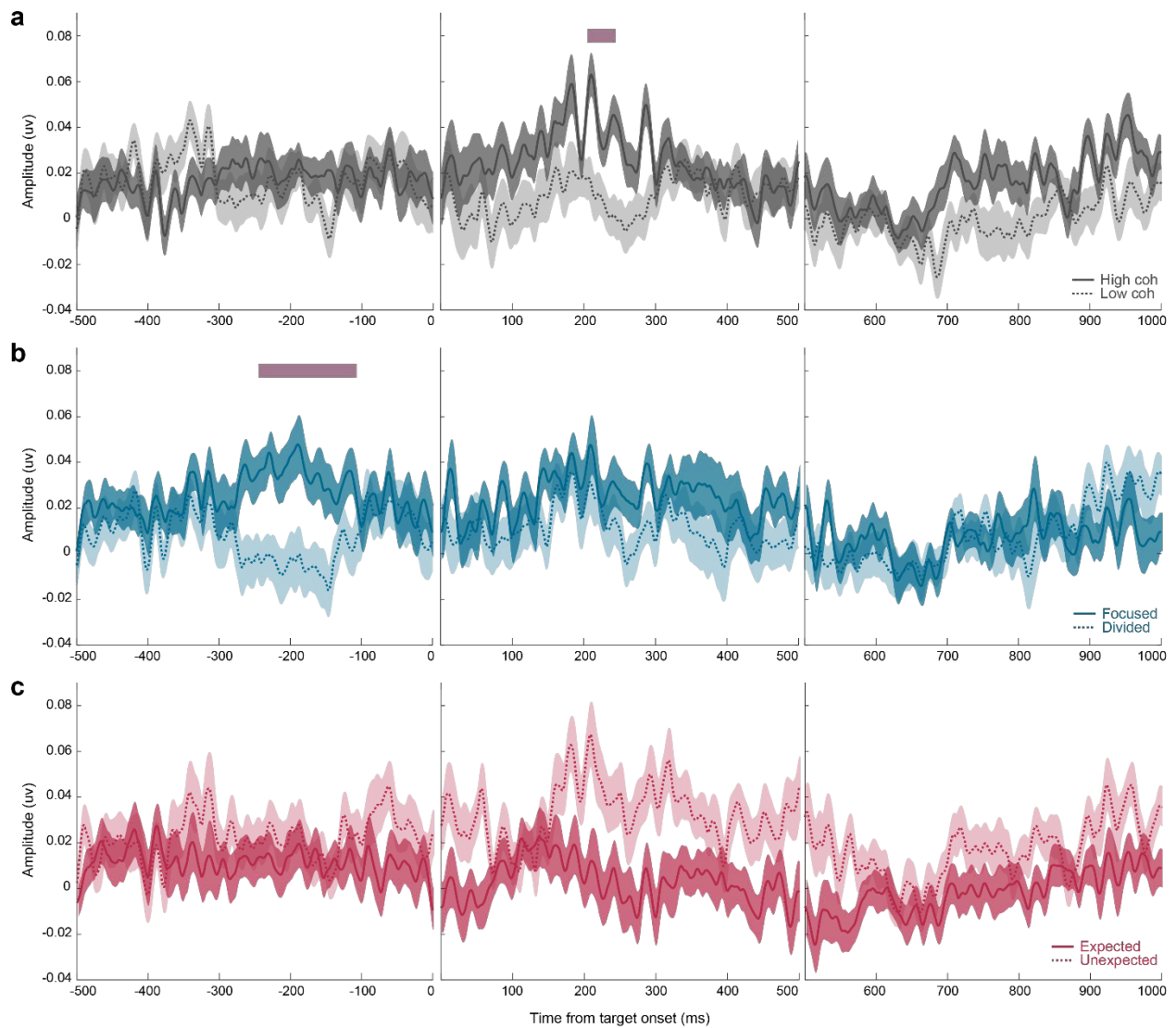
Figure 2.4: Steady state visually evoked potentials (SSVEPs) as a function of orientation coherence, attention, and expectation. Normalized amplitude of SSVEPs was computed from all trials of each manipulation condition recorded from Oz electrode. SSVEPs are plotted in three windows: (left), 500 ms before target onset to target onset; (middle), target onset to 500 ms after target onset; and (right), 500 ms to 1000 ms after target onset. SSVEPs are plotted **a**, as a function of orientation coherence (high/low), **b**, as a function of attention (focused/divided), and **c**, as a function of expectation (expected/unexpected). Focused attention led to higher SSVEP amplitude from 250 ms to 50 ms before the onset of coherent orientation. High orientation coherence increased SSVEP amplitude from 200 ms to 250 ms after target onset. Expectation had no effects on SSVEP responses.

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Chapter 3:

Preserved capacity for learning statistical regularities

and directing selective attention after hippocampal

lesions

Preserved capacity for learning statistical regularities and directing selective attention after hippocampal lesions

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Prior knowledge about the probabilistic structure of visual environments is necessary to resolve ambiguous information about objects in the world. Expectations based on stimulus regularities exert a powerful influence on human perception and decision making by improving the efficiency of information processing. Another type of prior knowledge, termed top-down attention, can also improve perceptual performance by facilitating the selective processing of relevant over irrelevant information. While much is known about attention, the mechanisms that support expectations about statistical regularities are not well-understood. The hippocampus has been implicated as a key structure involved in or perhaps necessary for the learning of statistical regularities, consistent with its role in various kinds of learning and memory. Here, we tested this hypothesis using a motion discrimination task in which we manipulated the most likely direction of motion, the degree of attention afforded to the relevant stimulus, and the amount of available sensory evidence. We tested memory-impaired patients with bilateral damage to the hippocampus and compared their performance with controls. Despite a modest slowing in response initiation across all task conditions, patients performed similar to controls. Like controls, patients exhibited a tendency to respond faster and more accurately when the motion direction was more probable, the stimulus was better attended, and more sensory evidence was available. Together, these findings demonstrate a robust, hippocampus-independent capacity for learning statistical regularities in the sensory environment in order to improve information processing.

expectation | memory | hippocampus

Visual input provides inherently ambiguous information about objects in the world (1). Prior knowledge about the probabilistic structure of the world plays a critical role in resolving this ambiguity (2). Thus, expectations about statistical regularities can improve the efficiency of decision making (3–16). For example, we learn from past experience that certain objects are more likely to be seen in particular contexts. Thus, when presented with an image of a gym, people are better at recognizing and processing information about a treadmill than a piano (17, 18).

A second factor that is based on prior knowledge, termed top-down attention, can also improve perceptual performance by facilitating the processing of information that is immediately relevant in the context of current behavioral goals (19–21). Attention sharpens the quality of relevant information by increasing the responsiveness of neurons in early visual cortex to task-relevant signals (22–24). Thus, when looking for your car in a parking lot, knowledge about its color, shape, and size can improve search by selectively facilitating the processing of potentially relevant target features. Critically, these 2 types of prior knowledge (expectation and top-down attention) are different, because expectations about what stimuli will be encountered in a given context can be entirely independent of what stimuli are attended based on behavioral relevance.

While much is known about attention, the process by which expectation about statistical regularities is acquired and used to guide behavior is not well-understood. The hippocampus has been implicated as a key structure involved in or perhaps necessary for the learning of statistical regularities (25, 26). In one study, controls were faster on a visual search task when search displays were repeated than when they were novel, but amnesic patients did not exhibit this advantage (25). There is some ambiguity about what damage was responsible for this impairment, because MRI scans were available for only 2 of the 4 patients tested and these indicated damage extending well beyond the hippocampus. In a subsequent study (27), patients with hippocampal damage confirmed by MRI performed similar to controls, that is, patients, like controls, searched repeated displays faster than novel displays. An impairment was observed only in a patient with damage extending beyond the hippocampus to include the parahippocampal gyrus and lateral temporal cortex.

In another study (26), a patient with large lesions of the medial temporal lobe viewed a long sequence of stimuli that contained a repeating pattern of 12 items. Unlike controls, the patient failed to learn the pattern. However, knowledge was assessed by asking

Significance

The hippocampus is important for many kinds of learning and memory. We explored the role of the hippocampus in the learning of statistical regularities. We administered a motion discrimination task where expectation about stimulus regularities, the degree of attention afforded to the relevant stimulus, and the amount of available sensory information were manipulated. Although modestly slower overall, patients with bilateral damage to the hippocampus performed similar to controls, exhibiting a normal tendency to respond faster and more accurately when the motion direction was more probable, when the stimulus was better attended, and when more sensory evidence was present. These findings show that the ability to acquire expectations based on regularities of a sensory environment can be independent of the hippocampus.

participants to explicitly report or recognize the repeating pattern. These measures are unlikely to be representative of the patient's knowledge, as memory-impaired patients can exhibit knowledge about the regularities in sequences indirectly through performance, despite an inability to verbally report declarative knowledge about the sequence (28). In the same way, patients can successfully acquire skills or habits even when they are unable to express knowledge about the task itself (29–31). Notably, in a serial reaction time task, hippocampal patients and controls learned a 12-item sequence of 4 button presses guided by visual cues (28). Reaction time improved as participants practiced the sequence and came to anticipate the order in which the cues appeared. Critically, both groups markedly slowed their reaction times when the sequence was unexpectedly changed, thereby demonstrating that they had learned the sequence. Nevertheless, the patients were unable to verbally report the sequence or to recognize it. These considerations point out the utility of indirect, performance-based measures to assess knowledge about statistical regularities and raise doubts about the importance of the hippocampus in acquiring such information.

The present study examined the contribution of the hippocampus to the learning of statistical regularities more directly by devising a motion discrimination task in which expectation was manipulated by presenting one (expected) motion direction more frequently than other (unexpected) directions. Four memory-impaired patients with bilateral damage to the hippocampus, as well as controls, reported the direction of motion by moving a joystick from the starting point to an end point along a trajectory from 0 to 360° (Fig. 1). We also included 2 additional conditions: (*i*) a manipulation of the amount of sensory information (high versus low motion coherence) available in each stimulus display, and (*ii*) a manipulation of top-down attention (focused versus divided). Manipulating the amount of sensory information allowed us to parametrically assess interactions between the strength of sensory signals with top-down attention and expectation. Notably, sensory and attentional processes are thought to be independent of hippocampal function on the basis of findings from patients such as H.M. and E.P. (25–28). Accordingly, the manipulations of sensory information and attention serve as control or baseline conditions against which to evaluate the ability of patients to form and use expectations about statistical regularities.

Results

Response Trajectories. The response trajectory indicated how far the joystick had moved from the center at each time point (0 to 1,500 ms). The coherence level of the motion displays (high/low coherence) affected controls and patients similarly (Fig. 2*A*). For controls, the trajectory amplitudes were different from 567 to 1,408 ms after stimulus onset (high > low coherence). For patients, the trajectory amplitudes were different from 633 to 1,225 ms after stimulus onset (high > low coherence) (all resampled $P < 0.05$).

Manipulations of attention (focused/divided) also affected controls and patients similarly (Fig. 2*B*). For controls, the trajectory amplitudes were different from 550 to 1,392 ms after stimulus onset (focused > divided). For patients, the trajectory amplitudes were different from 600 to 1,492 ms after stimulus onset (focused > divided) (all resampled $P < 0.05$).

Expectation (expected/unexpected) also affected controls and patients similarly (Fig. 2*C*). For controls, the trajectory amplitudes were different from 508 to 892 ms after stimulus onset (expected > unexpected) and also from 1,400 to 1,500 ms after stimulus onset (unexpected > expected). This effect was not visually remarkable in Fig. 2*C*, but is clear in Fig. 2*D*. For patients, the trajectory amplitudes were different from 567 to 1,017 ms after stimulus onset (expected > unexpected) and also from 1,258 to 1,500 ms after stimulus onset (unexpected > expected). Fig. 2*D* summarizes the effects of coherence level, attention, and expectation. Fig. 2*E* shows the *P* values for each condition and
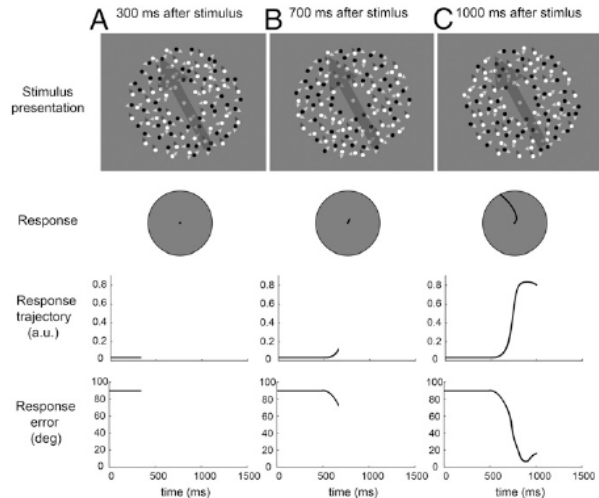

Fig. 1. Sample trial. A trial began with an attention cue (1,000 to 1,500 ms) to indicate the color of the dots that would represent coherent motion. A white (black) attention cue indicated that coherent motion would be represented with white (black) dots. A blue attention cue indicated that coherent motion would be represented with either white or black dots, that is, the participant had to discern which color of dots was in coherent motion. (*A*) At 300 ms after stimulus onset (motion direction 112° in this case, as indicated by the arrow), the participant has not yet begun a response, and the black dot represents the stationary joystick. The response trajectory, which is the distance that the joystick has moved from the center, remains close to 0, and the response error is approximately at chance (90°). (*B*) At 700 ms after stimulus onset, the participant has accumulated some information about the direction of coherent motion and begun a response, trying to match the movement of the joystick to the direction of motion. The response error shows the difference between the direction of the participant's response and the target motion direction at each time point. (*C*) At 1,000 ms after stimulus onset, the participant has moved the joystick its maximal distance. The response trajectory reaches its maximum at this time, and the response error is now close to 0.

at each time point (0 to 1,500 ms) (all resampled $P < 0.05$). There were no interactions between coherence levels, attention, and expectation on response trajectories for either controls or patients.

Patients performed similar to controls across all 3 manipulations of coherence level, attention, and expectation. Each patient performed within the 95% confidence intervals of the control group in all conditions (*SI Appendix*). Note that the onset of these effects was delayed in patients compared with controls (coherence level: 567 ms [controls] vs. 633 ms after stimulus onset [patients]; attention: 550 ms [controls] vs. 600 ms [patients]; expectation: 508 ms [controls] vs. 567 ms [patients]; all resampled $P < 0.05$). As this effect was similar across manipulations of bottom-up sensory information and top-down factors like attention and expectation, this slowing likely reflects a modest impairment in the ability of patients to exploit available perceptual information in the service of decision-making tasks (27, 28, 32).

Response Errors. Response errors were computed as the absolute difference at each time point between the participant's response angle and the calibrated angle for that participant. The magnitude of the response errors, before and after the onset of the joystick movement, indexed the accuracy of the direction judgment of participants.

The coherence level of the presented motion directions (high/low coherence) affected controls and patients similarly (Fig. 3*A*). For controls, the magnitude of the response errors was different
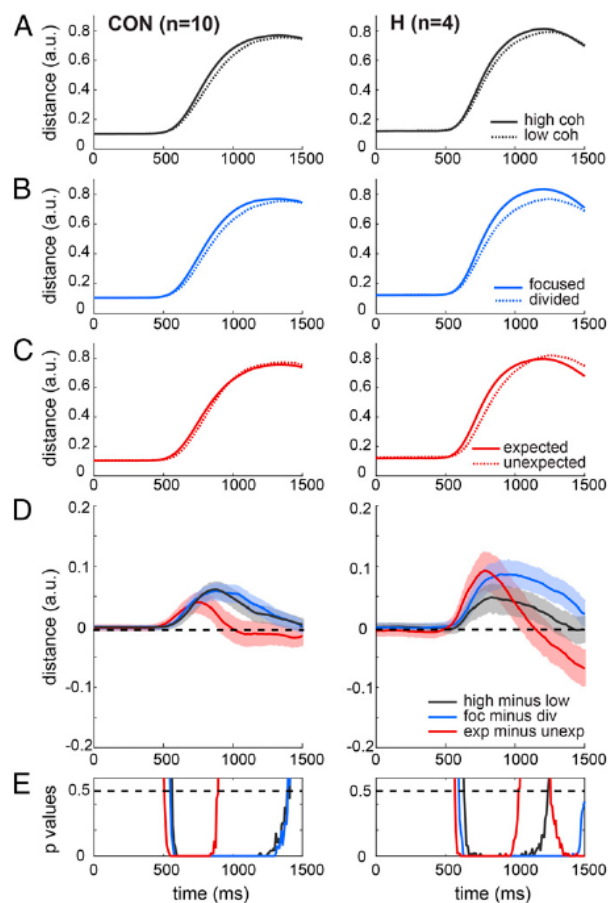
Fig. 2. Response trajectories. Response trajectories for controls and patients with hippocampal lesions were plotted from the onset of coherent motion (0 ms) to 1,500 ms after onset. (A–C) Response trajectories were plotted (A) as a function of coherence level (high/low), (B) as a function of attention (focused/divided), and (C) as a function of expectation (expected/unexpected). (D and E) Differences in response trajectories for each manipulation condition were plotted together with the associated P values. From 567 to 1,408 ms in controls, and from 633 to 1,225 ms in patients (A), the joystick had moved farther when coherent motion was presented at a high coherence than at a low level (resampled $P < 0.05$). From 550 to 1,392 ms in controls, and from 600 to 1,492 ms in patients (B), the joystick had moved farther when attention was focused than when attention was divided (resampled $P < 0.05$). From to 508 to 892 ms in controls, and from 567 to 1,017 ms in patients (C), the joystick had moved farther when coherent motion was presented in the expected direction than in the unexpected direction (resampled $P < 0.05$). In addition, from 1,400 to 1,500 ms in controls, and from 1,258 to 1,500 ms in patients (C), the joystick had moved farther when coherent motion was presented in the unexpected direction than in the expected direction (resampled $P < 0.05$). For E, the legend is the same as in D. Error bars for each of the 3 measures indicate 95% CIs computed by resampling the data distribution.

from 642 to 1,100 ms after stimulus onset (high < low coherence). For patients, the magnitude of the response errors was different from 733 to 1,050 ms after stimulus onset (high < low coherence) (all resampled $P < 0.05$).

Attention (focused/divided) also affected controls and patients similarly (Fig. 3B). For controls, the magnitude of the response errors was different from 567 to 1,133 ms after stimulus onset (focused < divided). For patients, the magnitude of the response errors was different from 775 to 817 ms after stimulus onset (focused < divided) (all resampled $P < 0.05$).

Expectation (expected/unexpected) also affected controls and patients similarly (Fig. 3C). For controls, the magnitude of the response errors was different from 0 to 708 ms after stimulus onset (expected < unexpected). For patients, the magnitude of the response errors was different from 0 to 1,067 ms after stimulus onset (expected < unexpected) (all resampled $P < 0.05$). Fig. 3D summarizes the effects of coherence level, attention, and expectation. Fig. 3E shows the P values for each condition and at each time point (0 to 1,500 ms). There were no interactions between coherence levels, attention, and expectation on response errors for either controls or patients. Each patient performed within the 95% confidence intervals of the control group in all conditions (SI Appendix).

Discussion

We examined the contribution of the hippocampus to the ability to learn statistical regularities by devising a motion discrimination task where expectation about motion direction was manipulated such that one (expected) direction was presented more frequently than other (unexpected) directions. We also asked if patients with lesions to the hippocampus would benefit as much as controls from the effects of focused versus divided attention and from the effects of strong versus weak sensory evidence. Despite a modest slowing in response initiation across all task conditions, patients performed similar to controls. Both controls and patients exhibited a similar benefit of expectation on response accuracy and speed beginning immediately after stimulus onset (Figs. 2C and 3C), both groups responded more quickly and more accurately when attending to 1 color of dots versus 2 colors (Figs. 2B and 3B), and both groups responded more quickly and more accurately when the sensory evidence was strong (high coherence) than when it was weak (low coherence) (Figs. 2A and 3A). Together, these findings indicate that the ability to learn statistical regularities, selectively attend to behaviorally relevant stimuli, and perform better when given stronger sensory evidence is intact after bilateral hippocampal lesions.

The present study used a continuous decision task, such that performance could be assessed at all time points from stimulus onset to response offset. Participants reported the direction of motion by moving a flight simulator joystick along a path (0 to 360°) to match the perceived direction of moving dots. Knowledge about the statistical regularities of motion direction was indirectly assessed by measuring how far the joystick had moved and how accurate the response was at each time point. These indirect, performance-based measures were used because hippocampal patients have been shown to acquire skills and habits even when they do not have explicit knowledge about the task itself (28), and even when they are unaware that they have been tested before (29–31).

Expectation about statistical regularities improves information processing and behavior in a variety of perceptual tasks (2, 14–16, 33–35). Past work suggested that the hippocampus might be critical in the learning of statistical regularities (25, 36) in light of its importance for many forms of learning and memory. In our study, however, patients successfully learned about statistical regularities, and they were able to exploit expectations as well as controls. Our results are in line with an earlier study that tested hippocampal patients in a serial reaction time task. In that study, participants learned a sequence of button presses guided by visual cues (28). Reaction time for both controls and patients improved as they practiced the sequence and successfully learned the order in which the lights would appear. Like controls, patients slowed their reaction times when the sequence of lights unexpectedly changed. Despite this evidence for implicit knowledge about the learned sequence, the patients were unable to verbally report the sequence or to recognize it among 4 choices. A similar finding was reported in an earlier study of statistical learning in which a patient with large medial temporal lobe lesions attempted to learn a repeating pattern of 12 items (26).

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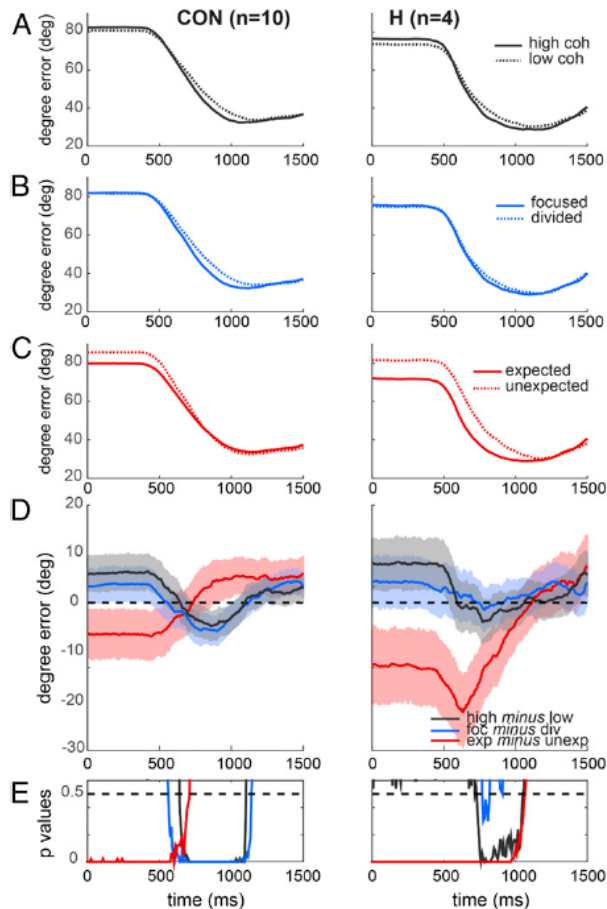
Fig. 3. Response errors. Response errors for controls and patients with hippocampal lesions were plotted from the onset of coherent motion (0 ms) to 1,500 ms after onset. (A–C) Response errors were plotted (A) as a function of coherence level (high/low), (B) as a function of attention (focused/divided), and (C) as a function of expectation (expected/unexpected). (D and E) Differences in response trajectories for each manipulation condition were plotted together with the associated P values. From 642 to 1,100 ms in controls, and from 733 to 1,050 ms in patients (A), response errors were lower when coherent motion was presented at a high coherence than at a low level (resampled $P < 0.05$). From 567 to 1,133 ms in controls, and from 775 to 817 ms in patients (B), response errors were lower when attention was focused than when attention was divided (resampled $P < 0.05$). (C) Expectation reduced baseline response errors (i.e., at the onset of coherent motion; 0 ms), and this effect lasted until 708 and 1,067 ms after stimulus onset in controls and patients, respectively (resampled $P < 0.05$). For E, the legend is the same as in D. Error bars for each of the 3 measures indicate 95% CIs computed by resampling the data distribution.

As in Reber and Squire (28), this patient also failed to exhibit knowledge of the sequence when asked for an explicit report of the repeating sequence or when asked to recognize it. However, the patient was not tested using indirect, performance-based measures that might have revealed implicit knowledge about the sequence.

One way in which our task differed from previous tasks is in the nature of the information needed to be learned and used to support performance. To benefit from statistical learning in our task, participants had to form knowledge about the direction of motion that had the highest probability of being presented in each test block. It is possible that the statistical learning of other kinds of information (such as spatial locations) might yield different results.

With the current task, we cannot determine if the effects of expectation on response error reflect response bias or changes in perceptual sensitivity or both. However, recent work has demonstrated that response bias (i.e., expectation about motor responses) affects information processing in the same manner as expectation about stimulus features such as stimulus color and orientation (34, 35). In addition, there is an effect of response error at 0 ms (i.e., stimulus onset), consistent with an important role for response bias. Thus, we argue that the effects on response errors are primarily driven by changes in response bias that occurred due to learned expectations about the motor responses associated with each of the expected coherent motion directions.

In the present study, patients also benefited as much as controls from manipulations of attention and the amount of available sensory evidence. These findings are consistent with a sizeable literature showing that patients with hippocampal lesions perform well on tests of intelligence and perceptual function (37–41). That said, previous work has not specifically examined the importance of the hippocampus for the top-down deployments of selective attention. Thus, the intact performance reported here, though not surprising, demonstrates directly that the hippocampus is not necessary to exploit attentional cues in order to determine behavioral relevance.

In summary, we evaluated statistical learning, attention, and processing of sensory evidence in memory-impaired patients with circumscribed hippocampal lesions. Patients and controls performed similarly in all respects. Thus, patients exhibited a normal tendency to perform faster and more accurately when the stimulus was probable, behaviorally relevant, and provided stronger sensory evidence. These findings demonstrate a robust capacity for acquiring expectations about statistical regularities in the sensory environment that can operate independent of the hippocampus.

Methods

Participants. Four memory-impaired patients participated with bilateral lesions thought to be limited to the hippocampus (CA fields, dentate gyrus, and subicular complex) (Table 1). Patients D.A. and G.W. became amnesic in 2011 and 2001, respectively, following a drug overdose and associated respiratory failure. K.E. became amnesic in 2004 after an episode of ischemia associated with kidney failure and toxic shock syndrome. L.J. (the only female) became amnesic during a 6-mo period in 1988 with no known precipitating event. Her memory impairment has been stable since that time.

For the 4 patients, the average score per passage for delayed recall (30 min) of 2 short prose passages was 1.0 segment (25 segments per passage). The average score for delayed recall (10 min) of a complex diagram was 5.4 (maximum score 36). Paired-associate learning of 10 unrelated noun–noun pairs summed across each of 3 successive trials was 3.8 pairs (30 pairs total) (Table 2). On these same tests, 11 controls scored 20.2 for the prose passages, 18.3 for the diagram, and 24.1 for paired-associate learning (42).

Estimates of medial temporal lobe (MTL) damage were based on quantitative analysis of magnetic resonance (MR) images from 19 age-matched, healthy males for K.E. and G.W., 11 age-matched, healthy females for patient L.J. (43), and 8 young healthy males for D.A.; patients D.A., K.E., L.J., and G.W. have an average bilateral reduction in hippocampal volume of 35, 49, 46, and 48%, respectively (all values are at least 2.9 SDs from the control mean). On the basis of 2 patients (L.M. and W.H.) with similar bilateral volume loss in the hippocampus for whom detailed postmortem neurohistological information was obtained (44), the degree of volume loss in these four patients may reflect nearly complete loss of hippocampal neurons. That is, patients L.M. and W.H. had a nearly complete loss of hippocampal neurons, despite exhibiting considerable sparing of hippocampal volume as measured by MRI. Apparently, neuronal death need not lead to disappearance of all hippocampal tissue, perhaps because the tissue can be supported to some extent by glia and white matter.

The volume of the parahippocampal gyrus (temporopolar, perirhinal, entorhinal, and parahippocampal cortices) is reduced by −5, 11, −17, and 10%, respectively (all values within 2 SDs of the control mean). Minus values indicate volumes that were larger for a patient than for controls. These values are based on published guidelines for identifying the boundaries of the parahippocampal gyrus (45, 46). Eight coronal magnetic resonance

Table 1. Characteristics of memory-impaired patients

Patient	Age, y	Education, y	WAIS-III IQ	WMS-R				
				Attention	Verbal	Visual	General	Delay
D.A.	34	12	95	104	90	91	90	56
K.E.	76	13.5	108	114	64	84	72	55
L.J.	81	12	101	105	83	60	69	<50
G.W.	58	12	108	105	65	86	70	<50

WAIS-III, Wechsler Adult Intelligence Scale III; WMS-R, Wechsler Memory Scale Revised. The WMS-R does not provide numerical scores for individuals who score <50. The IQ score for D.A. is from the WAIS-IV.

images from each patient, together with detailed descriptions of the MTL lesions, can be found elsewhere (47).

Ten healthy controls (3 female) also participated (mean age 64.9 ± 13.5 y; mean education 14.3 ± 1.8 y). All procedures were approved by the Institutional Review Board at the University of California, San Diego, and both patients and controls gave written informed consent prior to participation.

Stimuli. In each of 2 ~1-h test sessions, participants completed a block of calibration trials ($n = 60$ trials), a block of practice trials ($n = 104$ trials), and 5 test blocks ($n = 104$ trials for each block).

For the calibration trials, stimuli consisted of 400 black dots (diameter 0.18°) displayed in an annulus (outer diameter 22°; inner diameter 2.4°) on a dark gray background (luminous intensity 42.68 ± 2.20 cd/m^2; Fig. 1). Black dots within the annulus were flickered at 33 Hz for the duration of the trial, and each dot was randomly replotted on each frame. On each trial, 100% of the dots (i.e., 100% coherence) were coherently moved in one of the 5 possible motion directions (46 to 334° with 72° increments). Dot stimuli moved at a speed of 100 pixels per ms. Participants were instructed to report the motion direction of these moving dots via a USB-compatible flight simulator joystick. The purpose of the calibration trials was to estimate how each participant represented each motion direction. These estimates were used to compute performance accuracy on the test trials.

For the practice and test trials, stimuli consisted of 200 black dots and 200 white dots (diameter 0.18°) displayed in an annulus, as in the calibration trials, but surrounding an attention cue of either black, white, or blue. Black and white dots within the annulus were flickered at 33 Hz for the duration of the trial, and each dot was randomly replotted on each frame. During coherent motion, either 50% (low coherence) or 70% (high coherence) of the black (or white) dots was randomly selected on each frame to be displaced in one of 5 possible motion directions (46 to 334° with 72° increments), while the remaining dots were assigned one of 5 other motion directions. Dot stimuli moved at a speed of 100 pixels per ms. Participants were instructed to report the motion direction of the moving dots via a USB-compatible 360° flight simulator joystick.

Stimuli were presented on a PC with Windows XP using MATLAB (MathWorks) and the Psychophysics Toolbox [version 3.0.8 (48, 49)]. Participants were seated 60 cm from the CRT monitor running at 100 Hz with a gray background of 42.68 ± 2.20 cd/m^2.

Procedure. Participants performed a version of the random dot motion task (50–52), such that the amount of sensory evidence (coherence levels), selective attention, and expectation about target direction could be manipulated. Participants completed 2 test sessions, each of which consisted of calibration trials, practice trials, and 5 blocks of test trials as described above. Each test trial began with a display consisting of an attention cue, either black, white, or blue. A black or white cue informed participants to monitor either the black or white dots (focused attention), and the blue cue informed participants to monitor both black and white dots (divided attention) to determine which color of dots displayed coherent motion. After 1,000 to 1,500 ms, black and white moving dots were presented for 2,000 ms, such that a proportion, either 50% (low coherence) or 70% (high coherence) of either black or white dots, formed coherent motion in one of the 5 possible directions. The remaining dots were randomly assigned to the other 4 directions. Note that the attention cue was always valid such that on focused-attention trials the coherent motion was represented by black dots on half the trials and by white dots on half the trials. For each test block of 104 trials, half of the test trials were focused-attention trials and the other half were divided-attention trials, yielding a total of 520 trials for focused- and divided-attention conditions for each participant in each of the 2 test sessions. Presentation of the moving dots was followed by a 500- to 800-ms blank intertrial interval (ITI). For each test block, expectation about motion

direction was manipulated such that one (expected) direction (out of 5 possible directions) was presented on 69.2% of trials (72 trials per block), whereas the other (unexpected) directions were presented equally on the remaining 30.8% of trials (32 trials per block). The expected motion direction differed from one test block to another such that each of the 5 possible motion directions was assigned as the expected direction in just one block per session. Participants indicated the target motion direction by moving the flight simulator joystick its maximal distance in a direction matching the coherent motion. After making a response, participants returned the joystick to the center in preparation for the next trial. Responses were considered valid when they occurred in the interval between stimulus onset and ITI offset. In summary, each participant was given 1,040 trials. All 3 factors of interest (attention, expectation, and coherence levels) were manipulated orthogonally such that each participant was given a total of 520 focused-attention trials (260 of which were low-coherence trials and the other 260 high-coherence trials), 520 divided-attention trials (260 of which were low-coherence trials and the other 260 high-coherence trials), 720 expected trials, and 320 unexpected trials.

To familiarize participants with the task and the joystick, practice trials were given at the beginning of each session. There were a total of 104 practice trials from all attention conditions (focused/divided), coherence levels (high/low coherence level), motion directions (46 to 334° in 72° increments), and target color conditions (black/white). After practice, participants performed a block of calibration trials. Participants reported coherent motion consisting of 100% coherent dots using the flight simulator joystick. In each session, participants completed one block of 60 calibration trials (12 of each of the 5 possible motion directions).

Data Analysis. We first estimated how each participant responded to each of the 5 motion directions (46 to 334° in 72° increments) by computing circular medians of the participant's responses to each motion direction on the calibration trials (mean responses across controls and patients were 41.3, 127.5, 169.1, 250.6, and 303.5° for the motion directions of 46, 117, 189, 261, and 333°, respectively). These calibrated angles were later used as participant-specific baselines to compute performance accuracy on the test trials for each participant.

For each test trial in the main task, we first computed at each time point how far the joystick had moved from the center (response trajectory). We next identified the coordinate of the joystick at its maximum distance from the starting point and used that value to compute the angle in degrees from the starting point to the end point. We then computed the difference between the response angle at each time point and the calibrated response at each time point (response error). Response errors could be recorded even before the joystick began moving toward the end point, based on the direction in which the joystick was oriented. Test trials where responses were either made after the response deadline or where the response errors were at the joystick's maximal distance were more than 150° were excluded from further analysis.

We also examined the effect of coherence level (low/high), attention (focused/divided), and expectation (expected/unexpected) on response trajectories

Table 2. Neuropsychological scores for memory-impaired patients

Patient	Prose recall, segments	Diagram recall	Paired-associate learning, pairs
D.A.	3	9	13
K.E.	0.5	4.5	2
L.J.	0	5	0
G.W.	0.5	3	0

and response errors across time. Finally, we asked whether each patient's performance conformed to control performance by comparing response trajectories and response errors of each patient with the control averages.

Statistical Procedures. Due to the small number of participants (10 controls and 4 patients), a bootstrapping procedure was performed to assess significant differences between conditions and to establish 95% confidence intervals. Specifically, each of the bootstrapping iterations was performed by resampling with replacement at the level of individual trials and computing means for each comparison of interest. All reported confidence intervals (CIs) were computed based on 1,000 bootstrapping iterations for each comparison. Note that this method constrains the resolution of P values to a lower limit of $P \leq 0.001$. We generated permuted null distributions of response trajectories and response errors for each participant, each condition, and each time point. For tests comparing a bootstrapped distribution against 0, P values were computed by conducting 2 one-tailed tests against 0 (e.g., mean[difference in response trajectories < 0] and mean[difference in response trajectories > 0] and doubling the smaller P value).

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Supplementary Information for

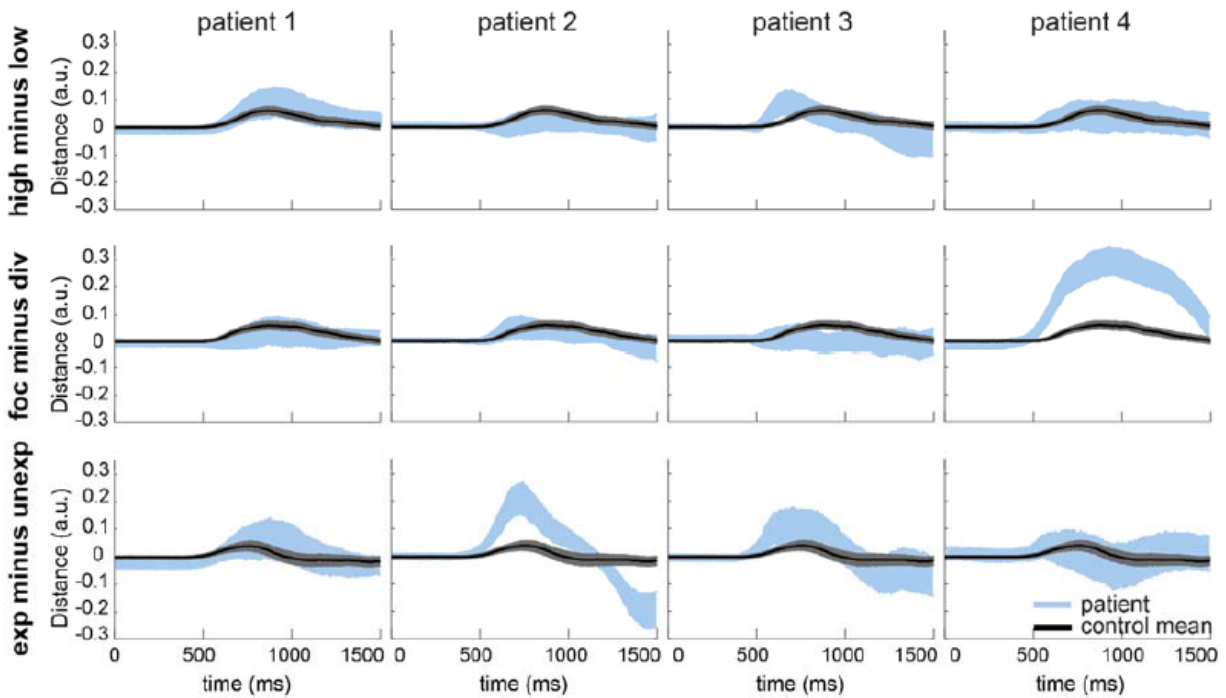Preserved capacity for learning statistical regularities and directing selective attention after hippocampal lesions

Nuttida Rungratsameetaweemana, Larry R. Squire, John T. Serences

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Figs. S1 to S2

Fig. S1. Response Trajectories of Individual Patients

Response trajectories of each patient were plotted together with the control averages. The 95% confidence intervals (CIs) for each patient (in blue) and the CIs of the control group averages (in grey) were plotted as a function of (A) coherence level (high minus low coherence), (B) attention (focused minus divided), and (C) expectation (expected minus unexpected trials). First, we computed the difference in response trajectories between high and low coherence condition separately for controls and patients. This effect of coherence was delayed in patients compared to controls (i.e., 66 ms), and this delay was then used to shift the patient data here to aid visual inspection. Each patient performed within or outside (in the direction of larger effects) the 95% confidence intervals of the control group in all conditions (compare to Fig. 2D).

58
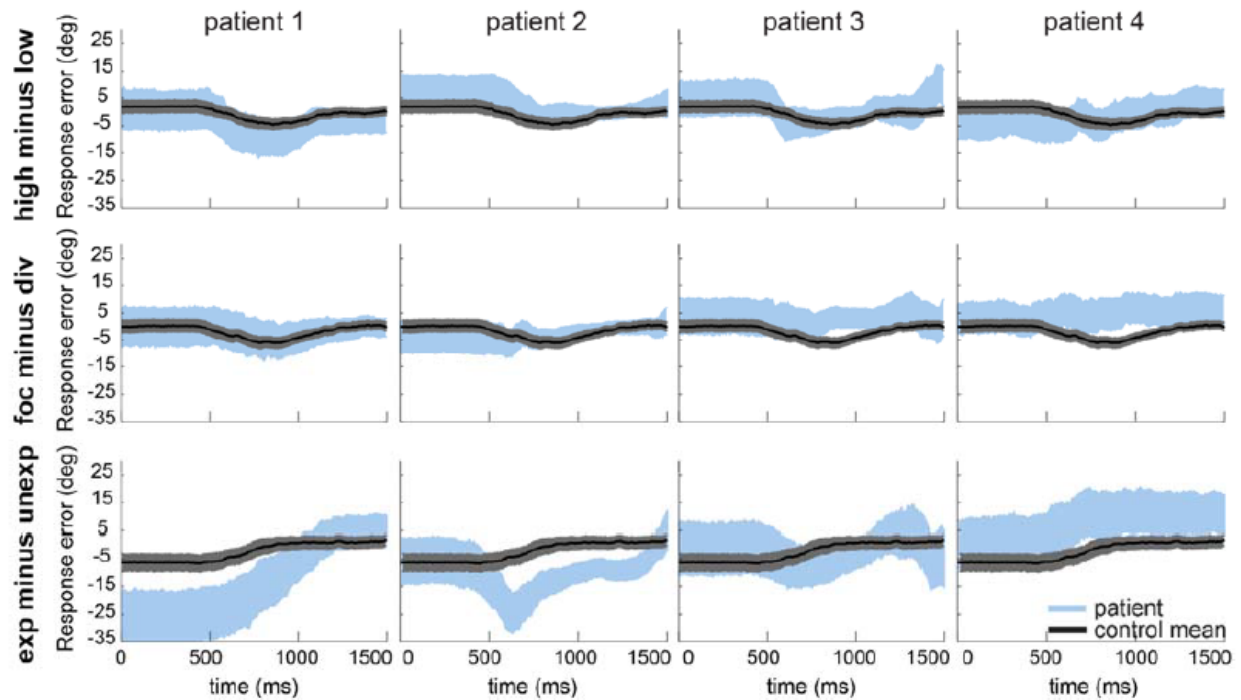
Fig. S2. Response Errors of Individual Patients

Response errors of each patient were plotted together with the control averages. The 95% confidence intervals (CIs) for each patient (in blue) and the CIs of the control group averages (in grey) were plotted as a function of (A) coherence level (high minus low coherence), (B) attention (focused minus divided), and (C) expectation (expected minus unexpected trials). Each patient performed within or outside (in the direction of larger effects) the 95% confidence intervals of the control group in all conditions (compare to Fig. 3D).