

NEURO FORUM

Disentangling expectation from selective attention during perceptual decision making

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Simon AJ, Schachtner JN, Gallen CL. Disentangling expectation from selective attention during perceptual decision making. *J Neurophysiol* 121: 1977–1980, 2019. First published March 13, 2019; doi:10.1152/jn.00639.2018.—A large body of work has investigated the effects of attention and expectation on early sensory processing to support decision making. In a recent paper published in *The Journal of Neuroscience*, Rungratsameetaweemana et al. (Rungratsameetaweemana N, Itthipuripat S, Salazar A, Serences JT. *J Neurosci* 38: 5632–5648, 2018) found that expectations driven by implicitly learned task regularities do not modulate neural markers of early visual processing. Here, we discuss these findings and propose several lines of follow-up analyses and experiments that could expand on these findings in the broader perceptual decision making literature.

electroencephalography (EEG); expectation, perceptual decision making, visual processing

Imagine driving down a street when you see a sign indicating that there is a stoplight ahead. The sign was placed there to warn you that you might need to stop soon. You ease off the gas and prepare to brake. When the stoplight comes into view, you notice it is red. Expecting this might be the case because of the earlier sign, you are able to safely bring your car to a stop. Research over the past several decades (Moran and Desimone 1985; Rungratsameetaweemana et al. 2018; Summerfield and Egner 2009) indicates that expectations of an event (e.g., expecting a stoplight) modulate neural processes that lead to more rapid and accurate responses compared with events that occur unexpectedly. First, seeing a sign causes you to anticipate that there will be a stoplight ahead. Next, expecting the stoplight's appearance leads to more efficient visual processing when the red light enters your visual field. Finally, expecting the stoplight allows for more accurate decision making, promoting more rapid response selection and motor execution (e.g., braking) (see Summerfield and Egner 2009 for review).

The cognitive process of making a goal-directed judgment based on sensory information is referred to as perceptual decision making. Importantly, it has been proposed that expectation can facilitate perceptual decision making at both the

behavioral and neural levels (Summerfield and Egner 2009). However, the majority of research that has examined the effects of expectation on perceptual decision making has used tasks that employ explicit cues (e.g., an arrow indicating when or where a target stimulus is likely to appear). Results from these studies suggest that expecting an upcoming stimulus causes an enhanced response in early visual cortex (Gazzaley et al. 2008; Itthipuripat et al. 2014; Moran and Desimone 1985; Summerfield and Egner 2009; Zanto et al. 2011). Recent studies have questioned the mechanistic generalization of expectation-related facilitation on decision making (Bang and Rahnev 2017; Rungratsameetaweemana et al. 2018), namely in the relationship between selective attention and expectation. Specifically, it has been suggested that selective attention allocation induced by an explicit cue can amplify the neural responses to a stimulus in sensory regions; however, expectation of a stimulus alone, in the absence of a cue, may alter later decision processes and not sensory signals themselves (Bang and Rahnev 2017). Thus, it has been proposed that previous studies showing expectancy-related modulations in visual cortex may have been confounded by the presence of explicit cues that engage selective attention processes.

To this end, Rungratsameetaweemana et al. (2018) examined the effects of expectation on sensory processing in the absence of such potential confounds. Here, they used a task that built in implicitly learned regularities to establish expectations about certain stimulus features, rather than utilizing explicit cues. Moreover, they concurrently recorded EEG data to examine the underlying neural processes associated with expectation-related behavior. The orientation discrimination task required participants to identify target stimuli composed of red or blue bars oriented horizontally or vertically. The expectation of a given stimulus was modulated by presenting targets of one feature type (e.g., stimulus color) on 70% of trials within a task block. Thus, over the course of a block, participants would begin to expect the upcoming trial to be the overrepresented feature type. There were three expectation manipulations: color (red or blue), orientation (horizontal or vertical), and motor (left or right button press). In addition, there was a neutral expectancy condition where all target types were presented with equal probability. In their paper, the authors used the term “selective attention” to refer to modulations influenced by processing an explicit cue and used the

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term “expectation” to refer to the neural and behavioral alterations that result from implicitly learning that certain stimuli were more likely to appear on an upcoming trial. For clarity, we will use the same nomenclature when referring to explicitly provoked and implicitly learned expectation.

In a series of analyses, the authors found that the task’s expectancy manipulation led to behavioral performance enhancements, such that participants performed more accurately and responded more quickly when the targets were expected compared with when they were unexpected or neutral. Additionally, this behavioral effect was not specific to any of the expectancy manipulation modalities (e.g., stimulus color versus orientation). They then sought to uncover whether this behavioral facilitation was associated with concurrent neural modulations of early sensory processing, modulations of later cognitive processes related to response selection and execution, or both. The authors focused these neural analyses on 1) the early visual negative (VN) and the prepeak slope and amplitude of the centroparietal posterior positivity (CPP) event-related potential (ERP) components as markers of early visual processing, and 2) on postpeak CPP amplitude, midfrontal theta amplitude, and parietal alpha amplitude as markers of later cognitive processes involved in response selection and execution.

Interestingly, the authors found no evidence for an effect of expectancy on the early visual processing indices (i.e., VN and CPP prepeak slope and amplitude). However, they did observe an effect of expectancy on response selection and execution indices, such that unexpected trials were associated with increased postpeak CPP amplitude, increased midfrontal theta amplitude, and decreased parietal alpha amplitude. As these neural expectation effects were observed preceding a participant’s response, the authors suggested that these measures reflected an involvement of response selection and execution, compared with the earlier time windows related to early visual processing (i.e., shortly after target stimulus onset). The authors interpreted these findings as an indication that expectation does not modulate early sensory processing, but rather that it facilitates perceptual decision making by acting on later response selection processes.

The results of this study provide potentially important new insights into how expectation and selective attention differentially modulate neural activity during perceptual decision making. Here, we discuss several methodological considerations to further support these findings and outline several interesting avenues of future research that integrate this work with other fields, such as aging and cognitive interventions. First, we suggest additional analyses of other visual processing markers that could strengthen the authors’ conclusions. Given that some of the neural results are contrary to previous work, we believe that it would be beneficial to further explore the effects of this expectancy manipulation on additional indices of early visual processing commonly used in the selective attention literature. Second, it is possible that these results could be related to participants’ awareness of the expectancy manipulation. We discuss the implications of awareness, as well as proposing future work that could help elucidate the relationship between awareness and expectancy effects. Third, we examine the role that anticipatory neural processes might play during expectancy-facilitated perceptual decision making. Finally, in addition to these methodological points, we discuss how

understanding the effects of expectations on anticipatory neural processes may deepen our understanding of cognitive changes that occur during the aging process, and how this knowledge can inform the development of novel neurotherapeutic interventions designed to enhance perceptual decision-making abilities.

First, as the authors’ central claim is that expectations do not influence early sensory processing, we believe that it would be extremely valuable to examine other EEG-based markers of visual processing previously shown to be sensitive to expectation manipulations from explicit cues (i.e., “selective attention”). Rungratsameetaweemana et al. (2018) examined two ERP markers that correspond to early visual processing: 1) the amplitude of the VN ERP component to index early evoked responses in visual areas and 2) the CPP to index the accumulation of encoded sensory information over time. Other commonly examined markers of early visual processing that have been shown to be modulated by selective attention demands include the latency of the N1 component (Gazzaley et al. 2008; Zanto et al. 2011) and the amplitude of the P1 component (Itthipuripat et al. 2014). Moreover, the authors calculated the VN component from the central occipital electrode (Oz), a choice that was justified because the stimuli were presented centrally. However, previous work has shown that the P1 and N1 components tend to reach maximum amplitude at lateral posterior electrodes, even when stimuli are presented centrally (Gazzaley et al. 2008). Demonstrating similar null effects of expectation on these additional metrics would further support the authors’ conclusions that implicitly learned expectations do not modulate early visual processing during perceptual decision making.

Second, another methodological point to consider is that the participants’ awareness of the expectancy manipulation could have influenced which neural processes were modulated by expectation. To maintain the implicit nature of the expectancy manipulation throughout the experiment, it would not have been feasible to survey the participants’ awareness of the manipulation during the task. However, assessing awareness after task completion could potentially uncover rich information regarding the nature of how conscious awareness influences expectancy-modulated neural processes. A recent review suggested that the interactions between top-down mechanisms arising from frontoparietal networks and the visual processing stream differ between different states of conscious awareness (Pitts et al. 2018). In particular, there may be a greater degree of communication between frontoparietal and sensory areas when there is heightened awareness of a stimulus or experimental manipulation. Moreover, it has been shown that a greater degree of connectivity between midfrontal and visual cortex was associated with larger modulations of early visual ERP markers during feature processing (Zanto et al. 2010). Taken together, conscious awareness of the expectancy manipulation could be associated with top-down modulations of early sensory ERPs. Thus, future work should assess whether participants’ awareness of such implicitly learned cues contributes to the effects of attention and expectation on modulating early sensory processing as well as later decision and response processes.

Third, it is also likely that prestimulus, anticipatory neural activity is important during perceptual decision making (Summerfield and Egner 2009). Top-down signaling occurring dur-

ing prestimulus, anticipatory phases of a trial (e.g., via enhanced baseline firing rates for anticipated stimuli) could result in higher initial levels of evidence for a particular stimulus and thus a behavioral enhancement (Summerfield and Egner 2009). Furthermore, it has been demonstrated that interactions between prestimulus posterior alpha power and poststimulus midfrontal theta power subserved optimal performance during a perceptual discrimination task (Cohen and van Gaal 2013). This latter finding is especially interesting in the context of the midfrontal theta findings from the Rungratsameetaweemana et al. (2018) study. In particular, the authors found that midfrontal theta power increased during unexpected trials, which they interpreted to reflect increased cognitive effort required to successfully detect more novel targets. However, as Rungratsameetaweemana et al. (2018) did not examine prestimulus, anticipatory neural markers in their analyses, it remains unknown whether expectations in the absence of external cues modulate anticipatory alpha as well. For example, it is possible that expectancy-driven prestimulus neural activity (e.g., posterior alpha) mediates the observed expectancy effects on midfrontal theta. Uncovering this relationship would further connect the authors' study to the anticipatory neural activity literature and could potentially shed light on whether anticipatory processes are deployed by expectation in addition to selective attention.

While Rungratsameetaweemana et al. (2018) and others have demonstrated facilitatory effects of selective attention and expectation on behavior in healthy young adults, there is also evidence of age-related declines in perceptual decision making; however, the physiological bases of these declines remains relatively underexplored (Dully et al. 2018). Uncovering the role of anticipatory neural activity in expectation-related perceptual decision making could help inform research efforts aimed to elucidate the neural mechanisms that underlie impairments associated with aging. For example, one study showed that anticipatory neural processes during selective attention diminish with aging, leading to a negative impact on task performance (Zanto et al. 2011). However, the effect of aging on expectancy-driven perceptual decision making (i.e., implicit expectation rather than explicit cues) remains unknown. Thus, future work should explore whether there are age-related deficits in expectancy-mediated decision making, and whether these deficits are driven by altered anticipatory neural activity (e.g., prestimulus posterior alpha), later decision-related neural processes (e.g., midfrontal theta), or both.

Nevertheless, there is evidence that training can enhance neural processes that facilitate perceptual decision-making abilities (Diaz et al. 2017), albeit in the absence of a selective attention or expectancy manipulation. Interestingly, the neural markers modified by training in this particular study map on to some of those examined by Rungratsameetaweemana et al. (2018) (e.g., the CPP). Future experiments could examine how training influences underlying neural metrics important for expectancy-mediated perceptual decision making as well as subsequent behavioral enhancements. Additionally, given the relationship between response-related cognitive processes and anticipatory neural activity during perceptual decision making (Cohen and van Gaal 2013), it is plausible that anticipatory neural processes might also be a suitable target for improving these abilities. Finally, given that there is a large body of work examining the effects of training on enhancing cognition in

older populations, this line of work could potentially identify suitable neural targets for cognitive interventions that improve deficits in decision-making processes in older adults.

In this Neuro Forum, we first outlined several methodological points for future lines of work relating to Rungratsameetaweemana et al.'s (2018) findings, focusing how the authors' results could influence research investigating the link between awareness and attention and the role of anticipatory neural activity in expectation and perceptual decision making. Furthermore, we also discussed integrating these findings with other fields, focusing on the relationships between perceptual decision making and aging as well as cognitive training interventions. In addition to shedding light on important distinctions between expectation and selective attention, Rungratsameetaweemana et al.'s (2018) work has the potential to impact broad areas of research, spanning cognitive and translational neuroscience.

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DISCLOSURES

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AUTHOR CONTRIBUTIONS

A.J.S. and J.N.S. drafted manuscript; A.J.S., J.N.S., and C.L.G. edited and revised manuscript; A.J.S., J.N.S., and C.L.G. approved final version of manuscript.

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