Predictive activation of sensory representations as a source of evidence in perceptual
decision-making

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Abstract

Our brains can represent expected future states of our sensory environment. Recent work has shown that, when we expect a specific stimulus to appear at a specific time, we can predictively generate neural representations of that stimulus even before it is physically presented. These observations raise two exciting questions: Are pre-activated sensory representations used for perceptual decision-making? And, are there instances in which we transiently perceive an expected stimulus that does not actually appear? To address these questions, we propose that pre-activated neural representations provide sensory evidence that is used for perceptual decision-making. This can be understood within the framework of the Diffusion Decision Model as an early accumulation of decision evidence in favour of the expected percept. Our proposal makes novel predictions relating to expectation effects on neural markers of decision evidence accumulation, and also provides an explanation for why we do not typically perceive stimuli that are expected, but do not appear.

Keywords: Prediction, Expectation, Decision-Making, MVPA, Perception

We are able to predictively generate neural representations of expected future events. When we expect a specific stimulus to appear at a specific time, neural representations of that stimulus are activated at least 70-90ms earlier compared to when the same stimulus is physically presented, but not expected. Using multivariate decoding applied to time-resolved human MEG/EEG, pre-activation has been demonstrated using probabilistic cueing of visual stimuli (Kok et al., 2017; Aitken et al., 2020), entrainment of expectations according to the trajectory of apparent motion (Blom et al., 2020, Robinson et al., 2020), and structured auditory sequences (Demarchi et al., 2019). These pre-activated neural representations may be enacted via proactive increases in the response gain of feature-selective neurons that are responsive to the expected stimulus (Kok et al., 2014; Myers et al., 2015; Trapp et al., 2016), similar to mechanisms thought to underlie visual imagery (Dijkstra et al., 2018; Robinson et al., 2020).

These findings raise intriguing questions about the role of pre-activated sensory representations in perceptual decision-making and conscious experience. Do pre-activated representations influence our perceptual decision-making? And: when we expect to see one thing and something else appears instead, do we transiently perceive the expected (and pre-activated) sensory representation? To attempt to address these questions, we propose that pre-activated neural representations are utilised as sensory evidence in favour of the expected stimulus, as conceptualised in evidence accumulation models such as the Diffusion Decision Model (DDM, Ratcliff, 1978; Ratcliff & McKoon, 2008; Ratcliff et al., 2016). This early source of decision evidence can potentially account for effects of biased expectations on measures of response times (RTs) and choice proportions in discrete choice decision tasks. It also leads to novel hypotheses relating to neural correlates of evidence accumulation in these tasks. By casting perception as a type of decision, our proposal also offers an explanation for why we do not typically perceive expected stimuli that do not actually appear.

Pre-activated sensory representations as a source of decision evidence

The DDM and similar evidence accumulation models partition perceptual decision-making into multiple serial processes. These models can successfully account for complex patterns of RT distributions and choice proportions across a broad range

of decision-making tasks, based on a small number of variable model parameters (Ratcliff & McKoon, 2008; Ratcliff et al., 2016; Smith, 2016). According to the DDM, there is a (usually fixed) latency between the physical presentation of a stimulus and the conversion of sensory input into a representation that is used for decision-making. This lag is here termed the sensory encoding duration. For discrete choice decisions, sensory evidence in favour of each decision outcome is then gradually accumulated in a noisy fashion. The balance of evidence favouring each option over time can be represented by the trajectory of a hypothetical decision variable (depicted in Figure 1). When the decision variable reaches a set threshold associated with a particular decision outcome, the motor action required to report that decision is initiated.

We propose that pre-activated sensory representations contribute an early source of decision evidence, which onsets at least 70-90ms prior to the evidence that is provided by the physical presentation of a stimulus. As depicted in Figure 1, this early accumulation of evidence is captured by standard versions of the DDM as a systematic shift in the starting point of evidence accumulation toward the threshold corresponding to the expected stimulus, as reported in previous studies (e.g., van Ravenzwaaij et al., 2012; Mulder et al., 2012). This also may sometimes be captured as a combination of changes in the starting point and evidence accumulation rate (e.g., Hanks et al., 2011; Dunovan et al., 2014; Kelly et al., 2019) if evidence associated with the pre-activated representation is temporally integrated with stimulus-driven sensory evidence (discussed in Ratcliff et al., 2016). Our account specifically focuses on the role of pre-activated sensory representations within the broader framework of expectation effects proposed in Summerfield & de Lange (2014).

Importantly, the influence of the resulting starting point shift is hypothesised to be much weaker than the influence of sensory evidence provided by above-threshold stimuli in typical psychophysical experiments. This assumption is based on observations that the magnitudes of pre-activated representations as measured using MEG/EEG are much smaller than the corresponding stimulus-evoked responses (Kok et al., 2017; Blom et al., 2020). This means that the behavioural and perceptual consequences of pre-activated sensory representations are highly dependent on the stimuli that are subsequently presented. When stimuli are clearly discriminable, the reported percept will be determined by the stimulus, and response times will be faster

for expected stimuli (e.g. Mulder et al., 2012; Dunovan et al., 2014; Figure 1 left panel). In situations where stimuli are highly ambiguous, or no decision-relevant evidence is present in the stimulus, the threshold crossed by the decision variable will be more influenced by time-varying noise that occurs during the accumulation of decision evidence. In these instances, the starting point shift associated with pre-activated sensory representations will more substantially bias perceptual reports toward the expected percept (e.g., de Lange et al., 2013, Figure 1 right panel). Observers will also exhibit faster RTs on average when reporting stimuli that were expected, compared to those that were unexpected.

Two testable hypotheses can be derived from our proposal. Evidence accumulation dynamics have been traced using the centro-parietal positivity (CPP) event-related potential component (O’Connell et al., 2012), where the shape of this component appears to faithfully trace the trajectory of the hypothesised decision variable in the DDM (Twomey et al., 2015; Kelly et al., 2019). Our account predicts that the onset of CPP amplitude build-up will be earlier in conditions where strong expectations can be formed for a specific stimulus image appearing at a specific time, compared to conditions where such expectations cannot be formed. There is already some evidence to support this hypothesis; earlier CPP build-up onset latencies have been observed for stimuli with predictable onset times (Van Den Brink et al., 2020). Further testing this hypothesis would require manipulations of whether or not image-specific expectations can be formed for upcoming stimuli, for example by including uninformative cue conditions (e.g., de Lange et al., 2013; Kelly et al., 2019).

The magnitude or presence/absence of pre-activated sensory representations is also likely to vary across trials, concurrently with fluctuations in the weighting of an observer’s expectations (e.g., Meyniel et al., 2016). Based on this assumption, we would also predict that this variability should correlate with variation in the magnitude of starting point or drift rate biases as captured in the DDM. When using linear decoding algorithms such as Linear Discriminant Analysis (LDA), the decision value (i.e., the distance from the discriminant axis which separates stimulus categories, not to be confused with the *decision variable* in the DDM) may provide a suitable correlate of the strength of pre-activated neural representations across trials. If pre-activated sensory representations do bias decision-making, then we would

predict starting point or drift rate biases in the DDM to correlate with LDA-derived decision values at time windows during which pre-activated neural representations are detected. Notably, this approach has already been successfully used to predict evidence accumulation model parameters based on stimulus-evoked neural responses (Ritchie & Carlson, 2016; Grootswagers et al., 2017).

Pre-activated sensory representations might also explain choice repetition biases (a type of sequential effect) in discrete choice decisions tasks. Bode et al. (2012) recorded EEG during a piano/chair discrimination task and identified a period of pre-stimulus activity that was predictive of participants' perceptual decisions within the same trial. This decodable EEG activity co-occurred with a shift of the starting point of evidence accumulation in favour of the stimulus category that was reported in the previous trial. Interestingly, they found that this activity was only predictive of participants' choices in conditions with highly ambiguous, 'pure noise' stimuli, and not when decision-relevant information was present in the stimulus. However, it remains to be verified whether this decodable information corresponds to a pre-activation of stimulus category representations in visual cortex, which might also lead to choice history-dependent biases in evidence accumulation rates (Urai et al., 2019), or whether this activity reflects biases in neural activity that correspond to downstream decision-making processes (e.g., de Lange et al., 2013).

Experiments designed to test these hypotheses should be careful to dissociate expectations to see a particular stimulus from expectations to make the motor action required to report the appearance of the expected stimulus. When a stimulus image is consistently associated with the same motor response, as in many previous experiments (reviewed in Gold & Stocker, 2017), building activity in motor cortex can be detected prior to stimulus onset, which can also influence decision-making performance in ways that are consistent with starting point shifts (Donner et al., 2009; de Lange et al., 2013; Kelly et al., 2019). Dissociation between stimulus and motor expectations can be achieved by randomising the motor response associated with each decision outcome across trials (e.g., Bode et al., 2012).

Sensory Evidence Provided by the Stimulus

No Sensory Evidence Provided by the Stimulus

Figure 1. Schematic examples of how pre-activation may induce shifts in the starting point of evidence accumulation, with different consequences depending on the stimulus that is subsequently presented. When strong sensory evidence for a decision is provided by the stimulus, fulfilled expectations lead to earlier decisions and faster responses (top panel). When stimuli are highly ambiguous and do not provide decision-relevant sensory evidence, expectations lead to noticeable biases in choice proportions (bottom panel).

Why we often do not temporarily perceive expected stimuli that fail to appear

By casting perception as a type of decision, our account can also explain why we do not typically perceive stimuli that were expected but never presented to us. The pre-activated representation on its own is not sufficient to shift the decision variable to the threshold necessary to produce a conscious percept, and the path of the decision variable is subsequently largely determined by the influence of the (physically presented) stimulus.

These separable contributions of pre-activation and subsequent stimulation are analogous to the notions of prediction and postdiction in various motion-related illusions, most notably the flash-lag illusion (Nijhawan, 1994; Eagleman & Sejnowski, 2000). In this illusion, the position of a moving object is perceived to lead a physically aligned static flash – an overshoot which has been attributed to predictive motion extrapolation (Nijhawan 1994). However, the illusion is eliminated when the moving object disappears concurrently with the flash (Eagleman & Sejnowski, 2000). This pattern of findings fits with our proposal because pre-activation accelerates the perception of the moving object, leading to motion extrapolation, but only when sensory input that is consistent with the extrapolation is subsequently available (e.g. Figure 1, left panel). When the expected sensory input fails to arrive, preactivation alone is insufficient to drive a conscious percept. Interestingly, our proposal predicts that in situations with highly noisy or ambiguous stimuli, this pre-activation may manifest as a decision bias in favour of motion extrapolation (Figure 1, right panel). This is consistent with recent findings that the flash-lag illusion persists when the moving object disappears concurrently with the flash in cases where both are presented on a background of dynamic noise (Nakayama & Holcombe, 2019).

Conclusion

We have argued that the consequences of pre-activated sensory representations can be potentially accounted for using mathematically-formalised evidence accumulation model frameworks. Testing the hypotheses derived from our proposal will allow us to better understand how prior knowledge can influence our perception and decision-making, and how these influences affect downstream computations that

are critical for perceptual decision-making (e.g., Summerfield & de Lange 2014; Gold & Stocker, 2017).

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