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Viewpoint

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, do 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 sometimes perceive stimuli that are expected, but do not appear.

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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 70–90 ms 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). Indeed, such expectation-related effects have been conceptualised as a form of ‘involuntary imagery’ whereby a neural representation of the expected stimulus is automatically generated following an associated cue stimulus (Pearson, 2019). Although expectation related pre-activation and imagery are hypothesized to be enacted via similar mechanisms, we treat each as distinct phenomena in this paper.

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:

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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, which in turn influences the accumulation of decision evidence 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 sensory 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 sometimes perceive expected stimuli that do not actually appear.

1. 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 et al., 2016; Ratcliff & McKoon, 2008; 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 Fig. 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 sensory information that is utilised as decision evidence, which onsets at least 70–90 ms prior to the evidence that is provided by the physical presentation of a stimulus. 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 (depicted in Fig. 1; e.g., van Ravenzwaaij et al., 2012; Mulder et al., 2012), a shift in the evidence accumulation rate (i.e., the drift rate; Hanks et al., 2011; Yon et al., 2020), or a combination of both effects (e.g., Dunovan et al., 2014; Kelly et al., 2020). Exactly which effects are observed may depend on how pre-activated sensory evidence is integrated with subsequent stimulus-driven sensory input (discussed below, see also 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 and de Lange (2014).

Importantly, the influence of the resulting changes in starting point and/or drift rate are 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 largely determined by the stimulus, and response times will be faster on average for expected stimuli (e.g., Mulder et al., 2012; Dunovan et al., 2014, Fig. 1 left panel). Pre-activation may also lead to an earlier perceived onset of sensory events and altered judgements of event durations (e.g., Haggard et al., 2002; Press et al., 2014), however this idea remains speculative. 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 frequently bias perceptual reports toward the expected percept (e.g., de Lange et al., 2013, Fig. 1 right panel). Observers will also exhibit faster RTs on average when reporting stimuli that were expected, compared to those that were unexpected. More generally, effects of pre-activated representations on observed choice proportions will depend on the relative quality of stimulus-driven sensory evidence compared to the combined magnitudes of internal and external noise in the decision process (for discussion of these concepts see Ratcliff et al., 2018; Turner et al., 2020).

Here we have assumed that pre-activated representations as measured using MEG/EEG co-occur with increased pre-stimulus firing rates of feature-selective neurons that prefer the expected stimulus, as found in paired association learning tasks (Sakai & Miyashita, 1991; Erickson & Desimone, 1999; Schlack & Albright, 2007; reviewed in Albright, 2012). These firing rate increases are presumably treated in the same way as stimulus-driven sensory input by downstream decision-making circuits. How pre-activated sensory representations are combined with subsequent stimulus-driven sensory input likely depends on how decision-relevant sensory information is integrated over time. Contemporary implementations of the DDM specify a process whereby sensory input is temporally integrated to form a representation in visual short-term memory, which determines the (average) drift rate within a trial (see Smith et al., 2004, 2013; Ratcliff et al., 2016). This is akin to models which specify that the drift rate smoothly increases over time and reaches an asymptote within the duration of the temporal integration window (e.g., Smith & Lilburn, 2020). The length of the temporal integration window depends on the decision-relevant stimulus features. In stimulus brightness discrimination tasks drift rates increased with longer presentation durations up to approximately 100 ms (Ratcliff, 2002), whereas the integration window was estimated to be around 400–450 ms for dot motion discrimination tasks (Watamaniuk & Sekuler, 1992, reviewed in; Smith

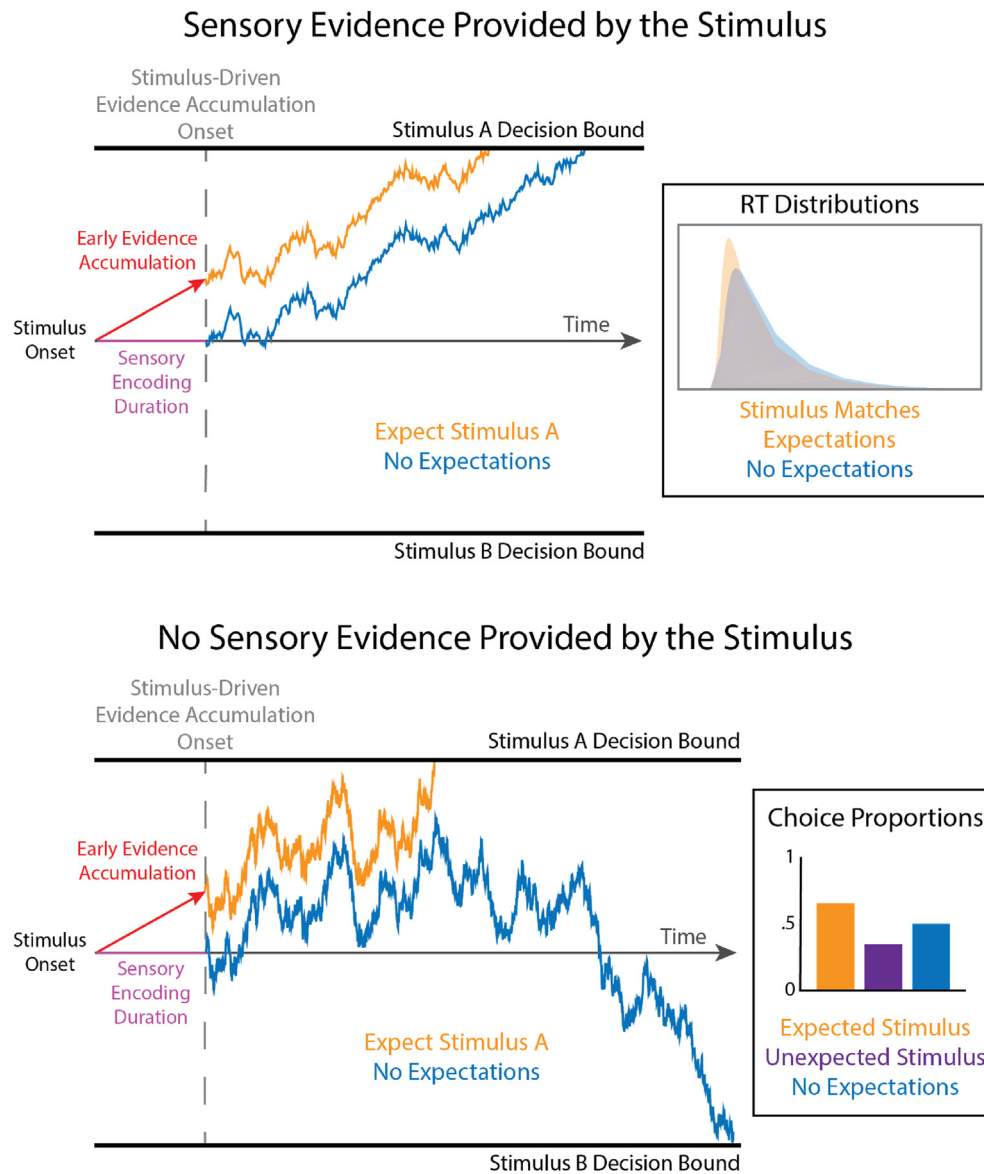


Fig. 1 – Schematic examples of how pre-activation may induce shifts in the starting point of evidence accumulation, with different consequences depending on the stimulus that is subsequently presented. When strong sensory evidence for a decision is provided by the stimulus, fulfilled expectations lead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

& Lilburn, 2020). Whether pre-activation leads to observed starting point or drift rate changes may depend on the stimulus presentation duration relative to the length of the temporal integration window. In conditions whereby the presentation duration is shorter than the integration window (e.g., as in Yon et al., 2020), pre-activated sensory representations may increase drift rates by mimicking effects of an earlier onset and prolonged presentation of the stimulus. In situations where the presentation duration exceeds the integration window the drift rate would be largely determined by the stimulus, and an earlier onset of evidence accumulation would be reflected in a starting point shift (e.g., Mulder et al., 2012). Findings of expectation-related adjustments to starting points and/or drift rates are inconsistent across studies

(Dunovan et al., 2014; Mulder et al., 2012; van Ravenzwaaij et al., 2012; Yon et al., 2020) and more systematic investigation is required to understand the situations in which each type of bias can be detected.

Three 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., 2016; Kelly et al., 2020). 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., 2020).

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 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 (Grootswagers et al., 2017; Ritchie & Carlson, 2016).

Pre-activation as measured using MEG/EEG has so far been reported exclusively in experiments where the expected stimuli were attended and task-relevant, had predictable onset times, and had specific features that were predictable (such as orientation or location, e.g., Kok et al., 2017; Blom et al., 2020; Aitken et al., 2020; but see the fMRI study by Ekman et al., 2017). If pre-activation is enabled via attention-based mechanisms that act on stimulus-selective visual neurons, then our account would also predict that the corresponding electrophysiological effects would be diminished or abolished when attention is directed away from the critical stimuli (e.g., as done by Larsson & Smith, 2012) or when specific stimulus image properties cannot be predicted in advance (e.g., as in Bang & Rahnev, 2017). Experiments that manipulate the focus of attention and the feature-specificity of participants' expectations may better characterise how pre-activated representations are generated in the visual system.

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 (de Lange et al., 2013; Donner et al., 2009; Kelly et al., 2020). 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). Stimulus expectations should also be experimentally dissociated from effects of recent stimulation history, such as stimulus repetition or adaptation effects (e.g., Kohn, 2007; Patterson et al., 2013). Stimulation history effects are often present in designs whereby expectations are entrained based on the frequency of stimulus presentation (discussed in Feuerriegel et al., 2020).

Effects of pre-activation may also be conceptually related to imagery-induced perceptual biases as reported in binocular rivalry tasks. Across several experiments run by Pearson et al. (2008) participants were biased toward perceiving those stimuli that were imagined during a preceding interval. These effects of imagery appeared similar to effects of presenting a weak, low-contrast stimulus prior to the binocular rivalry stimuli, however this link remains speculative. Effects of imagery persisted over multiple-second intervals in their experiments, and also across an intervening letter discrimination task. It is unclear whether such long-lasting biases would arise from pre-activation associated with stimulus expectations. It is plausible that both expectation- and imagery-related representations in visual cortex are enacted via the same mechanism, which affects the response gain of stimulus-selective neurons (Pearson, 2019). Interestingly, both expectation and imagery appear to produce higher-level representations before low-level ones, showing an opposite time-course to stimulus-driven visual processing (Kok et al., 2017; Blom et al., 2020; Dijkstra et al., 2018). However, given that expectations and imagery are each associated with a different phenomenology, more work is needed to characterise the similarities and differences between the extended networks associated with each effect (discussed in Pearson, 2019).

Here, we note that our proposed model is designed to account for the hypothesised consequences of a specific phenomenon (pre-activated neural representations of expected sensory events) within discrete choice perceptual decision tasks, whereby a single decision-relevant stimulus is presented to an observer. Accordingly, this model should not be viewed as a general framework that encapsulates the diverse range of expectation-related effects that have been reported in the literature. For example, cue stimuli have been found to bias perceptual reports in binocular rivalry tasks toward the expected percept for simple stimuli such as oriented gratings (Denison et al., 2011). However, reports were biased away from

the expected percept in statistical learning tasks with more complex face, object and scene stimuli (Denison et al., 2016). Similarly, when objects were presented in a visual scene (such as a cup in a kitchen) the detection of this object was impaired in a change detection task when the object could be expected to be present within that scene (Spaak et al., 2020). In addition, the expectedness of a stimulus identity also appears to modulate the perceived brightness of a subsequently-presented stimulus, with either reductions or increases in perceived brightness depending on the stimulus presentation latency following the expected or surprising event (Yon & Press, 2017). More generally, sensory stimuli appear to be reported as less intense when that stimulus was expected, compared to when it was surprising (reviewed in Press et al., 2020). These effects have largely been reported in different stimulation contexts than those of typical discrete choice decision tasks that are modelled using the DDM. They also describe effects on different measures (such as subjective stimulus intensity) that are not captured by the DDM, except when additional assumptions are made that link a measure of interest to the decision-making process. We caution that our model does not account for this broader range of expectation effects, and it is not designed to do so.

2. Why we do not typically 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. This idea is congruent with the findings of Pereira et al. (2020) who reported that near-threshold tactile stimuli were only perceived after a fixed amount of decision evidence had been accumulated.

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., Fig. 1, left panel). When the expected sensory input fails to arrive, pre-activation 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 (Fig. 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, 2020).

Here we note that there is an important distinction between alterations in conscious perception and biases in choice proportions as measured in psychophysical experiments. In some tasks whereby participants must choose between two or more discrete choice options, one could plausibly observe biased choice proportions that partly reflect 'best guesses' in favour of the expected or more probable stimulus, rather than assertions that the participant had subjectively perceived that stimulus. Therefore, measures of biased choice proportions may represent an upper bound on the frequency with which an observer's conscious perception was biased by their expectations. Additional measurements of subjective awareness or decision confidence may be useful in these situations. However the relationships between these measures and conscious perception are not straightforward (discussed in Peters & Lau, 2015).

3. 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., Gold & Stocker, 2017; Summerfield & de Lange, 2014). More concretely specifying how we can bias our own perceptual decisions may also inform wider philosophical debates regarding qualitative and quantitative differences between perception and hallucination (discussed in Dorsch, 2016; Corlett et al., 2019).

Credit author statement

Daniel Feuerriegel: Conceptualization, Methodology, Visualization, Writing- Original Draft Preparation. Tessel Blom: Conceptualization, Writing- Original Draft Preparation. Hinze Hogendoorn: Conceptualization, Writing- Original Draft Preparation.

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