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Learning to Perceive and Perceiving to Learn

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We thank Corlett for his thought-provoking response [1] to our recent article [2]. Corlett shares our concerns about inconsistencies in theories of perceptual prediction and highlights some reminiscent debates in learning theory. He also proposes why the perceptual prediction mechanisms may operate differently in the domain of action relative to other sensory cognition. Here, we highlight how we share the conviction that dialogue across disciplines will inform both models of perception and learning, but clarify that important distinctions between the explananda mean the theoretical puzzles are not reducible to each other. We also question whether action prediction mechanisms do indeed operate differently.

Corlett considers how animals establish the relationships between events in their environment (cues and outcomes; model uncertainty), outlining debates over whether we should learn more from cues that strongly predict particular outcomes or cues where the ensuing outcomes are uncertain. We agree these debates are important for issues addressed in our article [2], concerning how we establish which events are 'out there' at the moment (sensory uncertainty). However, there are some important differences between the ways in which we resolve model and sensory uncertainty, and relatedly, between the particular debates in question. In the literature Corlett considers, this key puzzle concerns which cues animals attend to in order to build their predictive model of the environment. This differs from our focus on how perception of events changes when they are *predicted (outcomes)* rather than *predictive (cues)*, and it is worth noting that differences in attention cannot explain all effects of prediction on perception [2]. While learning may therefore have been long implicated in some form in perception, consideration of attention towards cues is only one component of the perceptual puzzle.

Perhaps most importantly, it is valuable to clarify that the opposing processes we propose are realised within hundreds of milliseconds during the presentation of single events, whereas the switch between sampling of predictive and uncertain cues highlighted by Corlett operates across many 'trials' – as the animal refines its estimates of causal relationships [3]. To recap, we propose that perception of expected events is initially upweighted, due to combination of the prior and likelihood to determine the posterior (Bayesian accounts). This process will typically generate veridical representations of our environment rapidly, though this will of course be 'veridicality on average' – as noted by Corlett, percepts may be erroneous when typical regularities are disrupted (e.g., illusions). However, if the posterior deviates sufficiently from the prior to generate surprise responses identified in the learning literature (relatively high KLD), the sensory gain is subsequently increased – in the order of hundreds of milliseconds after the event in question is presented [4,5]. Corlett considers that our proposed temporal order places the processing of surprise too late to be adaptive. We agree this would be a concern for delays in the order of trials – like proposed above in the learning literature between predictive and uncertain cues [3] – but less so delays in the order of milliseconds as we propose for perception. Such a delay may be necessary to allow us to achieve adaptive advantages associated with the use of expectations to generate both broadly veridical and informative percepts.

Corlett also suggests that a predictive cancellation mechanism that pre-emptively suppresses the predicted consequences of action is key for determining whether we were the cause of events in the world, and that uncertainty-based inferences are not especially required during action. We challenge both of these points. While we agree that the 'error' between expected and actual action outcomes is a vital cue for computing agency, determining agency does not require action predictions to shape the percept in distinct (cancelling) ways. In fact, much recent work – including from our lab – suggests that they shape perception similarly to other types of prediction [1, e.g., 6]. It is important to note that our claims relate solely to sensory *prediction* mechanisms during action, and that sensory suppression generated when we move our eyes or limbs may reflect a non-specific suppression of all sensory input to a moving body part (Box 1; While suppression mechanisms may not therefore be predictive, a disruption in them could still lead to the relative upweighting of external sensory evidence when forming perceptual inferences [7]). We believe that the perceptual prediction paradox is still present when predictions are made during action, as it is crucial for us to generate robust representations of our actions rapidly in the face of sensory noise (veridicality) and remain sensitive to unexpected outcomes that occur as we move (informativeness).

In conclusion, we believe that dialogue between different disciplines in perception and learning sheds complementary light on how animals like us deal with an uncertain environment. These debates reinvigorate older questions about how we continuously forge models of the world around us via our perceptual experiences, and raise new questions about how we use these to guide perception of what is here right now.

Box 1. Generalised sensory suppression or predictive cancellation?

Certain mechanisms attenuate perception during action, but do not differentially influence expected and unexpected events – and are therefore dissociable from prediction mechanisms [2]. For example, when we move we suppress *all* tactile input to a moving effector, perhaps due to spinal gating mechanisms [8]. This mechanism may explain some dissociations between influences of action on ‘body-related’ and ‘environment-related’ action outcomes [9]. Relatedly, ‘active inference’ predictive coding models propose that action initiation requires reduced processing across all sensory channels that could report on the present state of the to-be-moved effector [10], and if conceptualising action production as an additional task, classic working memory models would hypothesise reduced sensory processing when events are presented in combination with action [11]. Studies cited in support of cancellation frequently compare processing of predictable events presented during action against events when passive – or where the action and sensory events overlap less due to temporal misalignment – and generalised suppression likely therefore contributes to effects. We hypothesise that *predictive* 'cancelling' influences of action on perception [e.g., 12] will be determined by processes that operate after stimulus presentation rather than any that subtract information from the input, but make no claims about generalised suppression mechanisms.

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