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Cancelling cancellation? Sensorimotor control, agency, and prediction

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ABSTRACT

For decades, classic theories of action control and action awareness have been built around the idea that the brain predictively ‘cancels’ expected action outcomes from perception. However, recent research casts doubt over this basic premise. What do these new findings mean for classic accounts of action? Should we now ‘cancel’ old data, theories and approaches generated under this idea? In this paper, we argue ‘No’. While doubts about predictive cancellation may urge us to fundamentally rethink how predictions shape perception, the wider pyramid using these ideas to explain action control and agentic experiences can remain largely intact. Some adaptive functions assigned to predictive cancellation can be achieved through *quasi-predictive* processes, that influence perception without actively tracking the probabilistic structure of the environment. Other functions may rely upon truly predictive processes, but not require that these predictions cancel perception. Appreciating the role of these processes may help us to move forward in explaining how agents optimise their interactions with the external world, even if predictive cancellation is cancelled from theory.

1. Introduction

It was proposed decades ago that we predict the sensory consequences of our actions and subtract these from perception (Blakemore et al., 1998). The idea emerged to account for the apparent blindness that ensues when we move our eyes (Matin, 1974), but was subsequently extended to describe all aspects of sensorimotor perception. Even in simple actions, like grasping a cup, we are bombarded with many sights, touches, and sounds. Our sensorimotor system, which generates the commands to make the grasp, also generates sensory predictions that we are likely to see converging fingers, feel cutaneous stimulation on our fingertips, and hear a thud as the cup is placed back on the table. A forward model generates the sensory predictions and a comparator process assesses the input against it (Wolpert et al., 1995; Korka et al., 2022) – leading to subtraction or ‘cancellation’ of the prediction from early sensory processing and resulting in attenuated perceptual experience. The extension of saccadic ideas to other sensorimotor settings was perhaps driven by the observation that we cannot tickle ourselves (Blakemore et al., 1998), but was since supported by a range of findings across tasks and species (e.g., Audette et al., 2021; Baess et al., 2011; Bays et al., 2005, 2006; Cardoso-Leite et al., 2010; Enikolopov et al., 2018; Kilteni et al., 2019, 2020; Kilteni and Ehrsson, 2020, 2022;

Hughes et al., 2013; Knolle et al., 2013; Pinheiro et al., 2020; Schneider, 2020; Schneider et al., 2018; Shergill et al., 2003, 2005; Singla et al., 2017; Voudouris and Fiehler, 2022; Waszak et al., 2012; Weiss et al., 2011; Wolpe et al., 2016).

The idea of predictive cancellation is central to classic and contemporary thinking about sensorimotor control and action awareness. Classic accounts of control stress that cancelling expected percepts frees the limited resources of our sensory systems for processing surprising sensory events (Blakemore et al., 1998). Predictable action outcomes (e.g., touch on our fingertips as we lift the cup) are not particularly newsworthy. In contrast, unexpected events (e.g., the cup slipping out of our hands) require more processing, correction, and control. Moreover, classic comparator theories of action and awareness propose that the sensory attenuation of predictable action outcomes is central to forming our normal sense of agency (Haggard, 2017; Moore, 2016) – with failures of predictive cancellation underwriting abnormal experiences of action and control that occur in illnesses like schizophrenia.

However, while predictive cancellation has seemed foundational to successful theories of action control and awareness, research in recent years has begun to undermine the idea that predicted action outcomes really are cancelled. An emerging body of work has begun to show that – contrary to classic ideas – expected action outcomes can be perceptually

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(and neurally) enhanced (Dogge et al., 2019a, 2019b; Guo and Song, 2019; Paraskevoudi and SanMiguel, 2021; Reznik et al., 2014, 2021; Reznik and Mukamel, 2019; Thomas et al., 2022; Yon et al., 2018, 2021, 2022; see also Hudson et al., 2015, 2018). These findings accord with a general picture of perceptual prediction described by Bayesian models – which stress that it is adaptive for agents to bias their perceptual inferences towards what they expect, perhaps via increasing the gain on expected sensory channels (Bar, 2004; Yuille and Kersten, 2006; Press et al., 2020a). More readily perceiving what we expect renders our inferences more accurate in a noisy sensory world.

These discrepant effects are often obtained when paradigms and analyses from the normative perception literature are used to study action: Expected action outcomes are contrasted with ‘unexpected’ outcomes that are inconsistent with learnt probabilistic structures. These empirical tasks contrast with the classic approaches demonstrating predictive ‘cancellation’ within action, which compare the perception of events in the presence or absence of action, or when events are coincident as opposed to delayed with respect to action (e.g., Bays et al., 2005; Blakemore et al., 1998; Kiltner et al., 2019). These studies attribute attenuated perception of the former to predictability, yet do not employ manipulations that isolate the consistency of events with probabilistic structures. For this reason, we here entertain the functional role of mechanisms that would influence perception during action, but not according to the probabilistic structure of sensorimotor mappings, in the generation of cancellation phenomena.

What do these shifting sands mean for classic accounts of action control and awareness that build in the assumption of predictive cancellation? In this paper, we argue that although emerging evidence casts doubt over the idea that motor predictions are ‘cancelled’ from perception, a closer inspection of action theories reveals that predictive cancellation per se is not actually central to what makes these accounts work. In many cases, the adaptive functions assigned to predictive cancellation – prioritising processing of unexpected errors, and distinguishing agents and their actions from their environments – can be achieved through *quasi-predictive* processes. These neural and cognitive mechanisms – some hard-wired by evolution – are not truly *predictive*. They influence perception without actively tracking the probabilistic structure of the environment. Nonetheless, they can support agents in controlling their actions and monitoring what they can and cannot influence. Other functions may rely upon truly predictive processes, but not require that these predictions cancel perception.

Beginning to appreciate the roles of these processes in action control and awareness allows us to see that we can retain many insights from classic theories, even if the idea of predictive cancellation ceases to be tenable. Moreover, distinguishing quasi-predictive from predictive processes will allow us to make progress in thorny debates around how perception and action truly interact.

2. Serving perception and control without predictive cancellation

While it is rarely disputed that action control requires sensorimotor prediction (e.g., Desmurget and Grafton, 2000; Kim et al., 2019; Hemed et al., 2020, 2022), the above emerging evidence suggests that the influence on perception is not necessarily attenuating. With this in mind, we consider here how quasi-predictive processes may instead attenuate experience, potentially serving a range of important functions for perception and control.

One such quasi-predictive process is that of sensorimotor gating. Namely, an extensive literature in psychology and neurophysiology shows that we have reduced processing of a multitude of inputs presented to moving effectors, regardless of whether they represent anticipated action outcomes (Chapman et al., 1987; Chapman and Beauchamp, 2006; Williams et al., 1998; see also Limanowski, 2022). Attenuated, or ‘gated’, processing of all inputs to a moving effector, regardless of their nature, is widely assumed to reflect the operation of

dissociable mechanisms from predictive ones – if effects are driven by truly predictive mechanisms they will be specific to particular predicted events (e.g., cutaneous contact on the fingertip when grasping a cup; not other events presented to similar locations or events presented to the dorsal finger surface; see Fig. 1).

Such gating mechanisms reflect reduced afference associated with efference and may operate at the spinal level (Seki and Fetz, 2012). I.e., if grasping with one’s right arm, sensory signals from the right arm are less reliably passed to the brain for analysis, resulting in a reduction of sensation on the moving effector. Empirical interrogations of sensorimotor prediction mechanisms frequently attempt to rule out gating explanations, although may not succeed due to the difficulty dissociating perception of events on moving and static effectors (see Thomas et al., 2022). Namely, even when events on static effectors produced by their moving counterparts are attenuated, perception of the gated moving events could influence responses about the static ones (Firestone and Scholl, 2016). Indeed, a recent study demonstrated that the classic attenuation effect became enhancement when stimulation was removed from the active effector (Thomas et al., 2022). Nevertheless, it is important to consider that gating can itself support a broad range of interesting and important functions.

Of note, gating mechanisms do, in fact, reflect typical probabilities within the environment. It is likely that movement of the right arm results in touch on the right arm. The important distinction to draw between these mechanisms and those described within the above Bayesian accounts is that they *reflect typical* environmental probabilities but do not *track* them. If we place an agent in a strange apparatus that alters environmental probabilities – say, causing movement of the right arm to cause touch on the left – gating mechanisms will not operate differently. Touch on the right arm would still be attenuated when the right arm moves, even though touch on the left arm is now more likely. As such, mechanisms hard-wired to reflect (but not track) environmental probabilities do not reflect the environment perfectly, even if they reflect it *on average*.

Perhaps the majority of researchers examining ‘prediction’ are interested in mechanisms that both reflect and track probabilities. These are the mechanisms that are crucial for serving adaptive synergistic relationships between perception and learning (Press et al., 2020b). If probability distributions change, the predictive mechanisms follow suit, and tracking when probabilities shift is necessary for accurately reflecting them.

Nevertheless, gating mechanisms that reflect typical probabilities without tracking can also serve many functions for action control. They will render our experiences more informative, on the whole, assuming that such mechanisms – presumably established phylogenetically – reflect probabilities that do not radically change across the generations. Despite our thought experiment above, we rarely find ourselves in a strange apparatus where moving our right arm causes touch on the left, and it is unlikely that our genetic ancestors did either. Thus, even though sensorimotor gating is non-predictive, attenuating perception in a generic way still renders us more sensitive to informative sensory signals – because moving an effector generates a variety of sensations that should, most typically, be ignored (note that these processes would be specific to action, and may act in concert with domain-general ones reactively highlighting particularly surprising events, as outlined in Press et al. (2020a)).

Attenuating all perception during the time of movement may also render our experiences more stable, for example, during saccades (Binda and Morrone, 2018). Stitching together retinal snapshots from periods where our eyes are static is likely to generate greater stability than factoring in those periods when we saccade – even if it is not specific to the predicted direction of eye motion. In this sense, gating mechanisms can provide a stabilising effect on perception even if the idea of true predictive cancellation ceases to be tenable.

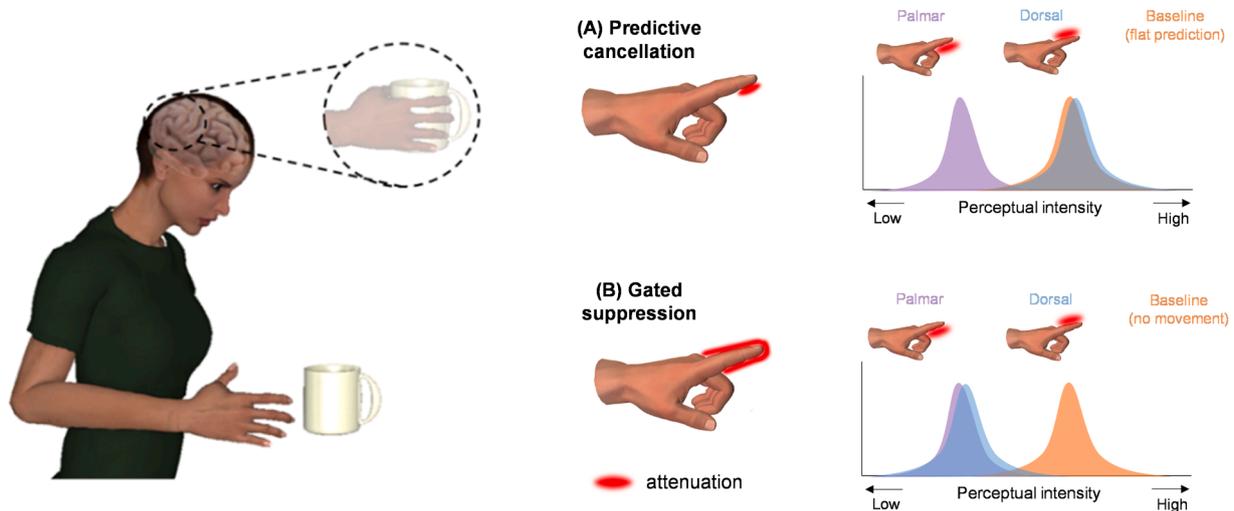


Fig. 1. The difference between predictive cancellation and gated suppression. When reaching to grasp a cup we predict contact sensation on the palmar (fingertip) surface of our fingers, as they touch the hand. (A) A predictive cancellation mechanism would specifically attenuate perception of contact events on this surface – shown for an example index finger, with similar logic applying to all fingers. (B) A generalised gating mechanism would attenuate perception of all events (also vibrations and shocks) on all finger surfaces – e.g., the dorsal as well as palmar surface. Quasi-predictive gating processes can play important roles in agency and awareness.

3. Inferring agency without predictive cancellation

Other action functions traditionally associated with predictive cancellation are those allowing us to determine our agency over the world. Classic accounts suggest a tight connection between motor prediction and feelings of agency – such that we judge ourselves to be in control of our actions and their consequences when there is a close match between predicted and actual outcomes. The complement of this idea is that salient mismatches between prediction and outcome lead to attenuated feelings of control.

For this reason, some accounts suggest that predictive cancellation of self-produced sensations is central to constructing accurate feelings of agency. This functional logic is perhaps clearest in how these models describe pathological experiences of agency, which are seen as demonstrations of what our experiences would be like if predictive attenuation failed. For example, some psychotic patients develop delusions of control – the sense that their actions are not their own but instead controlled by an alien force. Classic theories suppose that these unusual experiences arise because of a failure to attenuate predicted self-generated sensations – leading to unusually salient experiences of one’s own actions that require a delusional explanation. Such ideas have drawn support from studies showing that perceptual attenuation effects are reduced or absent in patients with delusions, or in those prone to delusional thoughts (Blakemore et al., 2000; Shergill et al., 2005; Teufel et al., 2010).

However, as discussed above, emerging evidence suggests that motor predictions may not cancel perception of expected sensory outcomes. How can we reconcile the empirical evidence with the central ideas behind these classic theories? In fact, on closer inspection, the key ingredients of classic accounts of agency do not strongly depend on the idea of predictive cancellation at all.

First, feelings of agency and control can depend upon motor prediction processes – even if these processes do not change perception in a characteristic way. There is certainly strong evidence that feelings of control crucially depend on predictively tracking the fine-grained correspondence between actions and outcomes (Perez and Dickinson, 2020; Yon et al., 2020; Schwarz et al., 2022; Hemed et al., 2020), but such processes could underwrite the sense of agency even if predictions do not act to cancel perception. By the same token, unusual experiences of action could arise due to disruptions in our ability to predict action outcomes – and there is evidence for these kinds of generic distortions of

action prediction in illnesses like schizophrenia – that cannot be explained via a specific disruption of an attenuation mechanism (Synofzik et al., 2010).

Second, much of the explanatory work assigned to *predictive cancellation* in models of agency (and its disturbance) could also be achieved by the gating mechanisms described above. For example, Corlett et al. (2019) argue that certain pathological experiences seen in psychosis may arise because of imbalances in the weight afforded to information from the internal and external world. Such imbalances could arise due to failures of predictive attenuation but could also arise due to atypicalities in more generic gating mechanisms – as failures of generic gating would also make the world seem unusually salient while we act.

4. Resolving debates about how prediction works

In this piece, we have considered how accounts of action could incorporate recent evidence weakening the classic idea of predictive cancellation. However, it is worth noting that not all researchers agree that the evidence base for predictive cancellation is weakened – with some continuing to marshal evidence in support of it (Audette et al., 2021; Fuehrer et al., 2022; Kilteni and Ehrsson, 2022; Schneider, 2020). Beginning to appreciate the inter-twined and nuanced mechanisms that may be at play can perhaps move these debates forward.

It is possible that sensorimotor researchers sometimes have in mind processes closer to a gating mechanism when describing prediction, which may be at the heart of some disagreements. Specifically, it is frequently proposed that action predictions can only be formed on the basis of ‘natural’, rather than ‘arbitrary’ learnt mappings (Kilteni and Ehrsson, 2022). However, for those interested in the interactions between perception and learning, and predictive accounts of perception (typically defined), no learnt mappings are arbitrary. Once a contingency is established between two events, they provide meaningful probabilistic information about the other. Representing these constantly fluctuating probability distributions is considered the central function of predictive mechanisms in the wider perception literature (de Lange et al., 2018; Press et al., 2020a, 2020b; Summerfield and de Lange, 2014; Summerfield and Egner, 2009). If one is instead concerned with effects surrounding ‘natural’ mappings – thus concerning only particular body-related outcomes – mechanisms could plausibly come in the flavour of phylogenetically-determined gating mechanisms.

Such mechanisms may be ‘predictive’ in the sense that phylogenetic evolution creates mechanisms that reflect the probabilities of our ancestral environment (Allen and Friston, 2018) but are not predictive in the sense that the term is typically used by psychologists and neuroscientists – to refer to mechanisms within the mind and brain that encode and track probabilistic patterns. For this latter kind of prediction mechanism, influences on perception are mediated similarly regardless of whether they are direct body outcomes (fingers moving) or indirect effects on the world (car slowing as we squeeze the brake pedal). Clarifying the empirical picture will require us to be clear about whether we are interested in studying mechanisms that predictively track probability distributions, or simply coincide with them on average.

5. Distinguishing effects and mechanisms

As well as some theories specifically incorporating the idea of predictive cancellation, cancellation has been built into the *study of action* more widely. That is, researchers examine the level of sensory attenuation as a proxy for the level of prediction, and by extension, level of agency (Bays et al., 2006; Haggard, 2017; Kilteni and Ehrsson, 2022; Moore, 2016; Weiss et al., 2011). If perception or sensory processing is reduced, it is assumed that predictive mechanisms operate or that one feels in control of the sensory events. Conversely, if probabilistic information from action is found to enhance, rather than cancel, perception, it has been claimed that the underlying mechanisms cannot actually be predictive (Kilteni and Ehrsson, 2022). Such reasoning points to the necessity of distinguishing effects from mechanisms (Press et al., 2022), considering that there are many ways that action could lead to attenuated perception even if the underlying processes are not predictive (Press and Cook, 2015). If we are to determine the true effects generated by particular mechanisms, we must not interchange effects and mechanisms. Future research can avoid this kind of problem when studying sensorimotor *prediction* by always experimentally manipulating the features that define these mechanisms – i.e., under typical characterization of prediction, the probability distributions mapping actions to outcomes.

So where does this leave us? What should we do with studies that have used levels of sensory attenuation as a proxy for levels of prediction? The data patterns are still, of course, informative, but we must draw firm lines between effects and mechanisms if we wish to be able to alter mechanistic accounts in light of new evidence (Press et al., 2022).

6. Conclusion

Challenging longheld assumptions means reinterpreting existing data, which sometimes leads to the house of theoretical cards tumbling to the floor. However, theories linking action, perception and awareness often form such complex edifices, that it can be difficult to determine which cards are particularly load-bearing. Here we hope to have persuaded the reader that while doubts about predictive cancellation may urge us to fundamentally rethink how predictions shape perception, the wider pyramid using these ideas to explain action control and agentic experiences can remain largely intact. In particular, appreciating the role of quasi-predictive processes may help us to move forward in explaining how agents optimise their interactions with the external world, even if predictive cancellation is ultimately cancelled from theory.

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