

Opinion

Moving Forward: On the Limits of Motor-Based Forward Models

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The human ability to anticipate the consequences that result from action is an essential building block for cognitive, emotional, and social functioning. A dominant view is that this faculty is based on motor predictions, in which a forward model uses a copy of the motor command to predict imminent sensory action-consequences. Although this account was originally conceived to explain the processing of action-outcomes that are tightly coupled to bodily movements, it has been increasingly extrapolated to effects beyond the body. Here, we critically evaluate this generalization and argue that, although there is ample evidence for the role of predictions in the processing of environment-related action-outcomes, there is hitherto little reason to assume that these predictions result from motor-based forward models.

Humans as Anticipatory Agents

Tickling yourself is hard [1]. Although seemingly trivial at face value, this simple observation reflects a key faculty of our brain: the ability to predict the future. Specifically, the reason why self-induced tickles are underwhelming is that we can anticipate action-outcomes before they occur [2–4]. By contrast, tickles produced by others are less predictable and, thus, more salient. Such prediction effects are not restricted to tickling [5,6], and are vital for daily functioning. We live in complex sensory environments in which we are constantly bombarded with ambiguous information. By predicting input that results from our own actions, resources can be saved for the processing of externally produced input that generally has more informative value (e.g., a tap on the shoulder of a stranger requires more attention than your own hand brushing against your leg) [2,7]. The clear importance of such predictive mechanisms raises the question of how exactly our brain foresees the consequences of movement.

A dominant view is that predictions about action-outcomes are generated by forward models [7–9]. These forward models can be seen as simulations of the motor system that use a copy of the motor command, known as an **efference copy** (see [Glossary](#)), to predict the sensory consequences of the action in question (known as corollary discharge). Such forward models have been implicated in various adaptive functions ([Box 1](#)), including the aforementioned modulations of perceptual processing. For instance, the reduced ticklishness of self-produced (versus externally produced) tickles can be explained by the idea that only the former is preceded by an efference copy and, as such, can be anticipated. This anticipated input can be compared with actual sensory input, allowing self-produced input to be ‘explained away’, reducing its relative salience [2].[☆]

The forward model account has gained extensive support, and has been implicated in the prediction of a variety of action-outcomes [6,10,11]. This includes not only sensations close to the body

[☆]The exact mechanism underlying the reduced salience of self-produced effects is still a point of discussion; see [Box 2](#).

Highlights

The idea that motor predictions modulate the perceptual processing of action-outcomes in health and mental disease has been widely acknowledged.

Motor-based forward models have been implicated in the processing of a variety of action-outcomes, ranging from body-related to environment-related outcomes.

Here, we argue that the presumed involvement of motor-based forward models in the prediction of action-outcomes beyond the body is limited and hitherto unjustified.

To move forward, cognitive prediction sources have to be incorporated in research on action-outcome processing.

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Box 1. Forward Models and Their Functional Role

Motor-based forward models have been associated with a variety of adaptive functions. For example, forward models may support action control during coordinated or fast movement [8,79–82]. To execute coordinated actions (especially actions involving multiple limbs, such as clapping), the brain needs to know the position and velocity of the effectors involved. This information cannot be obtained from our senses due to the relatively long processing time of sensory feedback. These same delays also prevent sensory feedback from assisting in the execution of fast movements, such as **saccades**. Forward models solve these issues by providing predictions that can be used before feedback is received.

Forward models also have an important role in skill acquisition. When learning a new skill, such as playing the piano, there will be discrepancies between predicted and actual actions and action-outcomes. To learn from these prediction errors, the observed sensory discrepancies need to be translated into motor errors. Forward models are thought to be essential in this translation because they capture the relationship between actions and following sensory effects (a phenomenon known as distal supervised learning) [83]. Relatedly, forward models underlie our ability to mentally rehearse actions without actually performing them [8].

In addition to the proposed use in motor processing, forward models have also been implicated in perception, which is the central topic of this paper. In particular, by predicting the sensory consequences of action, actual self-produced effects can be attenuated or cancelled out (e.g., [2,7]; see also **Box 2**). This is adaptive because it allows for more resources to be spent on the processing of input generated by external sources, which generally hold more informative value.

(such as touch or **proprioceptive** changes), but also effects in the outside world (such as the visual changes resulting from turning on a light switch). Apart from basic perceptual processing, forward models have also been related to experiences of agency (i.e., the experience of being the causal origin of bodily movements and subsequent effects). The idea behind this proposal is that the comparison between predicted and actual states allows self-attribution of events in case of a match and external-attribution in case of a considerable mismatch [12–14]. Extending this line of reasoning, faulty forward models have been proposed to underlie disrupted self-other processing (such as a lack of experienced control) that is central to various neuropsychiatric disorders,

Box 2. Sensory Attenuation of Body-Related and Environment-Related Action-Outcomes

Sensory attenuation refers to the perceptual and neurophysiological attenuation of sensory input that can be anticipated based on one's actions. Perceptual attenuation is generally measured by means of explicit intensity ratings (such as the experienced ticklishness of touch [1,42]) or by more implicit psychophysical measures, such as the point of subjective equality (e.g., [23,24,47,84]). On a neurophysiological level, sensory attenuation is typically measured by means of event-related potentials, such as the auditory N1, the amplitude of which is diminished for self-produced (versus externally produced) effects (see [10,11] for recent reviews).

Attenuation effects have been observed for both body-related and environment-related action-outcomes. Examples of the former are self-applied tickles [1,4] and constant self-generated force [85,86], which are perceived as less intense and evoke less neural activity [2,3], compared with tactile input produced by an external source. Likewise, listening to self-produced vocalizations during speech evokes smaller auditory evoked responses compared with passively listening to the same sounds [38,87,88]. In addition, attenuation effects have also been observed for environment-related action-outcomes for which the connection with preceding actions is more arbitrary, such as visual stimuli [29,30,44,89] or tones resulting from button presses (e.g., [22–24,26,27,43]).

Although action-related attenuation effects are generally ascribed to motor-based forward models, the precise underlying mechanism remains a topic of discussion. The most common explanation is the cancellation account that is based on original descriptions by von Holst and Mittelstaedt [21]. This account proposes that motor predictions can be seen as 'photo negatives' that cancel out self-produced input. Alternatively, the pre-activation account [5,44] proposes that motor predictions result in heightened baseline activity in the sensory areas that represent expected action-outcomes. Given that this heightened baseline level is harder to distinguish from activity that is subsequently induced by actual input, self-produced effects are experienced as relatively attenuated. Finally, sharpening accounts suggest that the observed suppression of self-produced effects in fact reflects a sharpening response [90]. According to this account, activity is only increased for the minority of neurons that are tuned to the expected (self-produced) effects, while signals inconsistent with the predictions are suppressed. This results in a decrease in the net population response and, hence, in an overall attenuation effect. This account might explain why motor predictions sometimes result in facilitated rather than suppressed perceptual processing of expected effects. (For further discussion, see [55].)

Glossary

Active inference: an extension of predictive coding models that includes motor control. In particular, active inference presumes that prediction-errors regarding expected sensory states cannot only be resolved by updating one's predictions, but also by actively bringing about the expected sensory input through one's actions.

Ambiguous motion sphere: a rotating sphere with an ambiguous motion direction. The sphere comprises dots, half of which move in a leftward direction, and half of which move in a rightward direction. The sphere can be perceived as rotating in a clockwise or a counterclockwise direction depending on whether the leftward- or the rightward-moving dots are perceived to be located in the front plane (i.e., closer to the observer).

Bistable perception: a single stimulus that can result in two perceptual interpretations that tend to alternate over time.

Efference copy: a copy of the motor command that can be used as input for forward models.

Gabor patch: a visual stimulus to which the primary visual cortex is particularly responsive, comprising a sinusoidal grating.

Ideomotor theory: a theory on action-selection suggesting that actions are represented in terms of their sensory consequences

Optokinetic response: reflexive movement of the eyes (as well as the head and body in some animals) in response to the full motion of one's visual field. The movement is in the same direction as the retinal motion to maintain perceptual stability.

Predictive coding: theoretical framework on perception in which the brain forms internal models about sensory input, which it continuously updates by minimizing prediction errors that result from the comparison between predicted and actual input.

Proprioceptive: the sense of one's body in space (e.g., in terms of position and velocity).

Reafferent: resulting from one's own movement.

Rivalrous gratings: the presentation of unique gratings (often in terms of their orientation) to each eye. Instead of perceiving a fused image, perception will alternate between the two possible

including obsessive-compulsive disorder [15] and schizophrenia [16,17]. Thus, forward models have a key role in a range of self-related processing that has been examined in disciplines as varied as philosophy, psychology, neuroscience, and psychiatry.

Here, we critically examine the explanatory range of forward models. In addition to a general evaluation of the role of these models in perceptual processing, we focus on the extension to the prediction of external action-outcomes. Based on recent developments in the field, we argue that the current evidence for this extrapolation is weak. We propose that more attention to different types of action-outcomes is warranted, and discuss alternative mechanisms for predicting effects beyond our body.

Predictions about the Body and Beyond

The idea that perception is influenced by motor-based predictions has a long history. Although generally attributed to Helmholtz [18], the development of this notion can be traced back to ancient times, including observations made by the likes of Aristotle [19]. Nevertheless, the forward model account did not gain traction until 1950, when two independent research groups coined the terms ‘efference copy’ and ‘corollary discharge’, which remain central to the account today [20,21]. Both groups validated the influence of motor predictions through illustrative effects in animals, such as behavior observed after surgical eye alterations. For instance, after rotating the eyes (or the entire head) by 180°, fish and flies show a curious response: they start to move in indefinite circles. This **optokinetic response** was attributed to the idea that the animals predict retinal motion that results from movement. Under normal circumstances, such predictions can be used to cancel out the influence of action on perception. However, after surgery, retinal motion will be opposite to what is expected, resulting in a prediction error. As animals pursue perceptual stability, they will start to turn to compensate for the retinal motion, which only magnifies the error and causes them to get caught in a self-reinforcing behavioral loop.

As is evident from this example, early work on motor predictions focused on action-outcomes that are narrowly tied to preceding actions. Similar prediction effects have been observed in work on sensory attenuation in humans, including the previously mentioned inability to tickle ourselves (Box 2). Aside from such body-related effects, perceptual modulation has also been observed for external action-outcomes (Boxes 2 and 3). Such outcomes are generally produced by button presses and range from abstract stimuli such as tones [22–24,26–28] and **Gabor patches** [29] to more complex visual stimuli, such as faces and houses [30]. Body-related action-outcomes have a tight and consistent coupling with preceding actions, which is either innate or overlearned during one’s lifetime. By contrast, the relationship between more external action-outcomes is relatively arbitrary and always needs to be learned. Here, we refer to these latter outcomes as environment related (a term adopted from [31]). The difference between body-related and environment-related action-outcomes is rarely acknowledged, and forward models have been similarly implicated in the prediction of both. We challenge this idea and propose that the involvement of motor-based forward models in the predictions of (especially environment-related) action-outcomes is disputable.

Convergent Evolution of Motor Predictions

Evidence for motor-based forward models has been observed across the animal kingdom [32–34]. Despite being ubiquitous, these predictive processes can express themselves in remarkably different ways. One well-studied example is the male cricket, which sings to attract and entice future mates [35]. The song of the cricket, which is generated by rubbing the forewings together, is loud (100 dB SPL) and would result in desensitization of the auditory system. To circumvent this issue, crickets use information from motor commands to inhibit the central auditory pathway in

interpretations over time (a phenomenon known as binocular rivalry).

Saccades: fast eye movements that shift gaze from one fixation point to another.

Box 3. Intentional Binding of Environment-Related Action-Outcomes

Similar to sensory attenuation (see Box 2), intentional binding is a perceptual phenomenon that has frequently been used to assess the influence of motor-based predictions on perceptual processing (reviewed in [91]). Intentional binding refers to the perceived temporal attraction of actions and subsequent effects, compared with when these events occur in isolation. This effect disappears when action-outcomes are externally triggered, such as through transcranial magnetic stimulation (TMS) or through passive movement [28,92–94], demonstrating its reliance on intentionality. The most commonly used method to assess binding borrows from the work of Libet [95], who realized that conscious awareness of actions could be captured by means of a clock. In the standard binding paradigm, participants attend to a rotating clock hand and indicate its position at the time of action-execution or the sensory action-outcome [28]. While the temporal awareness of the action is generally shifted towards the outcome, the awareness of the outcome is generally shifted towards the preceding action. Another popular method to assess intentional binding is to directly ask participants to estimate the interval between their actions and subsequent outcomes (e.g., [93,94,96]), with reduced intervals being observed for self-produced outcomes.

In contrast to sensory attenuation, research on intentional binding has been restricted to environment-related effects. This is a consequence of the temporal separation of actions and outcomes that is inherent to the aforementioned measures. A few apparent exceptions are studies that have examined binding of somatic action-outcomes, such as the passive displacement of a finger [93,97]. Crucially, however, these somatic effects were produced in the same artificial and arbitrary way as environment-related action-outcomes (i.e., by means of button presses). As such, the overlearned, one-on-one relationship that is present for what we deem to be 'true' bodily-related effects is absent in these studies.

Intentional binding was originally attributed to similar motor-based forward models as sensory attenuation (but see [98]). However, how exactly motor-predictive mechanisms would lead to the aforementioned perceptual attraction often remains unspecified. An important exception is the preactivation account [5], which offers a specific explanation for the shift in the perceived onset time of the action-outcome. According to this account, motor-predictions lead to the preactivation of an expected sensory template. As a result of this elevated baseline, the relative amount of time needed to reach the threshold for conscious awareness is reduced for self-produced effects, as opposed to externally produced effects, for which no such preactivation can occur.

phase with wing movements and resulting chirps. A different way to take advantage of motor predictions has been observed in electric fish, such as mormyrids [33,34,36]. Electric fish generate electric fields and assess perturbations caused by objects and other animals. To distinguish between self-caused and externally caused stimulation of the electroreceptors, mormyrids use motor commands that are generated by their electric organ to predict the precise electrical field that will be sensed by their electroreceptors. As the predicted input is opposite in sign compared to self-produced input, only electric stimulation that is self-caused is cancelled out. Hence, although both crickets and mormyrids clearly use motor-based forward models, the specific expression of the predictive mechanism depends on the unique challenges the species faces [33,34].

The observation of motor-based forward models in animals, as well as the fact that similar modulations of perceptual processing are observed in humans, is often taken as support for the idea that these effects result from similar mechanisms. However, humans have unique cognitive capacities that allow them to anticipate the future in ways that transcend the predictive mechanisms in many other animals [37]. It is therefore conceivable that they have evolved alternative routes to predict action-outcomes. Indeed, there is ample evidence for such nonmotor predictions (see 'Alternative Prediction Sources'). Accordingly, the mere observation of prediction effects on the processing of action-outcomes does not necessitate the involvement of motor-based forward models. Although this reasoning holds for both body-related and environment-related outcomes, we argue that the evidence for the involvement of motor-predictions is particularly unconvincing for the latter.

Evaluating Evidence for Motor Prediction Effects beyond the Body

There are two main issues that can be identified when evaluating existing support for the involvement of forward models in the processing of environment-related action-outcomes: (i) the used experimental designs; and (ii) the robustness of results. With regard to the first issue, most

empirical studies use a design that cannot exclude the contribution of alternative (nonmotor) factors. In particular, motor-based influences on perception are generally examined by comparing a condition in which participants execute actions with a condition in which participants merely observe sensory input. This comparison builds on the idea that forward models can only generate action-outcome predictions for voluntary actions that are accompanied by an efference copy, whereas no such predictions are present in the absence of action. However, as has been reviewed in detail elsewhere [6,11], these conditions differ in more ways than the presence of motor-based predictions about upcoming effects. For instance, self-produced and externally produced effects differ in temporal predictability (i.e., the predictability of the moment in time at which effects occur) and the attention that is allocated to them.

One way to control for these factors is by directly comparing how predicted versus unpredicted or mispredicted effects of actions are processed. Given that these conditions only differ in the match between predicted and actual action-outcomes, predictive action-mechanisms are isolated from the aforementioned confounding influences. In addition, this comparison allows one to assess the extent to which the prediction effects are specific to the precise identity of the upcoming action-outcome. Such specificity is necessary for effects to be attributed to motor-based forward models, because precise predictions about upcoming effects are required for their involvement in motor-control. For body-related action-outcomes, such prediction-specificity has been observed. For instance, in the auditory domain, the neurophysiological attenuation of one's own voice diminishes when its playback has an altered pitch [38–40], as well as when the sound one utters differs from one's general median production (i.e., the predicted utterance) of that sound [41]. Similarly, when participants tickle themselves by means of a robotic arm, reported ticklishness increases when spatial perturbations are introduced [42].

However, evidence for specific motor-prediction effects on the perception of environment-related outcomes is less convincing. Some studies have observed evidence in line with motor-based forward models. For instance, reduced neurophysiological attenuation was observed for tones the identity of which could be predicted compared with tones the identity of which was unpredictable [43] or did not match with action-outcome expectations [22]. Likewise, reduced sensitivity was observed for visual stimuli, such as letters [44] and Gabor patches [29], when the identity of these stimuli was congruent (versus incongruent) with previously learned action-effect associations. However, some of these effects have not been replicated in recent replications studies [45]. In addition, other studies have failed to obtain (clear) evidence for attenuation of predicted compared with unpredicted [46] or mispredicted tones [47], and sometimes even for the difference between self-produced and externally produced effects [48]. Similarly, work on other perceptual phenomena, such as intentional binding (Box 3), has also failed to show an influence of specific motor predictions. To be more precise, comparable binding was perceived for all outcomes following actions, regardless of whether their specific identity was predictable [46,49,50]. These studies therefore cast doubt on the influence of motor predictions on the perceptual processing of environment-related action-outcomes.

This issue was further assessed by recent work capitalizing on **bistable perception** [51]. This perceptual phenomenon occurs when the brain is exposed to a single stimulus that can yield two conflicting perceptual interpretations [52,53]. Considering that conflict of different stimulus identities is at the heart of bistable perception, the authors hypothesized that it could be more susceptible to modulation by motor-based forward models than sensory attenuation or intentional binding. Participants executed an action that initiated a bistable stimulus, of which one possible interpretation matched previously learned action-outcome expectations. The observed results were mixed and depended on the type of bistable stimulus that was used. In particular,

while motor predictions biased the perception of an **ambiguous motion sphere**, no such effect was observed for **rivalrous gratings**. Combined with previous work, these results suggest that the support for the extension of forward models to the prediction of effects beyond the body is hitherto not substantial. This is evidenced by both confounds in typically used experimental designs, as well as mixed evidence resulting from studies that try to control for these confounds.

Formation and Neural Encoding of Motor-Based Forward Models

The weak support for the influence of motor-based forward-models on the perceptual processing of environment-related effects might not be so surprising when more carefully considering the time course underlying the formation of these models. The most detailed information regarding the updating of forward models and their underlying neural networks comes from animal research. One particularly well-mapped circuit is the motor-auditory circuit that is involved in auditory suppression in mice [54,99]. Similar to humans, mice suppress body-related action-outcomes, such as vocalizations. In addition, recent research suggests that mice can also learn to suppress environment-related action-outcomes for which no existing associations exists. In two studies, mice were exposed to associations between tone bursts and either lever presses [56] or treadmill running [57]. Movement-related suppression was observed in the auditory cortex that was specific for the learned **reafferent** frequency. This effect could partially be ascribed to increased activity of inhibitory interneurons that are known to receive input from the M2, demonstrating the involvement of a motor-auditory network [57]. Most importantly, however, the updating process was gradual. While one hour of learning was insufficient to produce specific suppression of the reafferent frequency, this effect became increasingly more apparent after extensive practice over the course of several days [57].

It is likely that a similar Hebbian learning mechanism can account for attenuation of body-related action-outcomes in humans. By contrast, the slow modulation of neural networks does not match with the fast attenuation of environment-related action-outcomes in our species, which is often observed after only minimal learning. Indeed, the acquisition phases of most human experiments do not surpass the one hour of learning that was insufficient to yield any prediction-effects in mice [11]. Considering that the timescale on which formation of neural connections takes place is likely to be comparable for mice and humans, the fast modulations in our species suggests the involvement of an additional predictive mechanism. In other words, perceptual processing of self-produced action-outcomes appears to rely on at least two distinct mechanisms: one relatively slow, motor-based mechanism as described by forward models, and a more direct (nonmotor) mechanism.

Alternative Prediction Mechanisms

The anticipation of sensory input can take place independently of the motor system and can result from various sources [58,59]. An example of such a nonmotor prediction effect is the neurophysiological attenuation of tones the pitch of which can be predicted from a preceding tone sequence, as opposed to tones that are unpredictable from the preceding tone set [60]. Over the past few years, there has been an increasing interest in the influence of such nonmotor predictions on motor-perception interactions. For example, research on instruction effects has shown that instructions about stimulus-response or response-stimulus mappings can elicit automatic response tendencies without any practice [61,62]. Although these studies do not directly examine expectation effects, their findings are relevant for the present discussion because they suggest that action-outcome relations can be activated without the presence of any motor-act and, hence, without the involvement of a motor-based forward model. The fact that these instruction effects are observed without any practice is particularly interesting in light of the generally short duration of studies on environment-related action-outcomes. That is, processes similar to

the ones that underlie instruction effects might explain how predictions about action-outcomes can be formed in the absence of extensive learning.

In recent work [63], the influence of instructed task sets on the perceptual processing of action-outcomes was examined. In this experiment, participants initiated the movement of a bistable rotating sphere. In the absence of any learning, participants tended to perceive the sphere as rotating in the same direction as their action. This motion bias was abolished after participants learned (both through instructions and short exposure) that sphere motion would be opposite to the preceding action. By contrast, compatible learning did not add anything to the already existing bias. In other words, both the task setting, as well as the existing bias, affected the perceived percepts. It remains to be seen whether instructions in the absence of any practice would lead to similar expectation effects (see Outstanding Questions). While indirect, these joint findings provide evidence for the idea that more general prediction mechanisms could be involved in expectations of environment-related action-outcomes (see also [64]).

The idea that action-outcome anticipation might result from more general mechanisms concurs with other related theoretical accounts, such as **predictive coding** and **ideomotor theory**. These accounts are similar to forward models in that they propose a key role for action-outcome anticipation in perception and/or action-control. Unlike forward models, however, the predictions in these accounts do not rely on efference copies.

Predictive coding accounts were originally formulated to explain action-unrelated prediction effects in perception [65,66]. According to these accounts, the brain constructs an internal model of the world, which is used to generate hypotheses about upcoming sensory input.

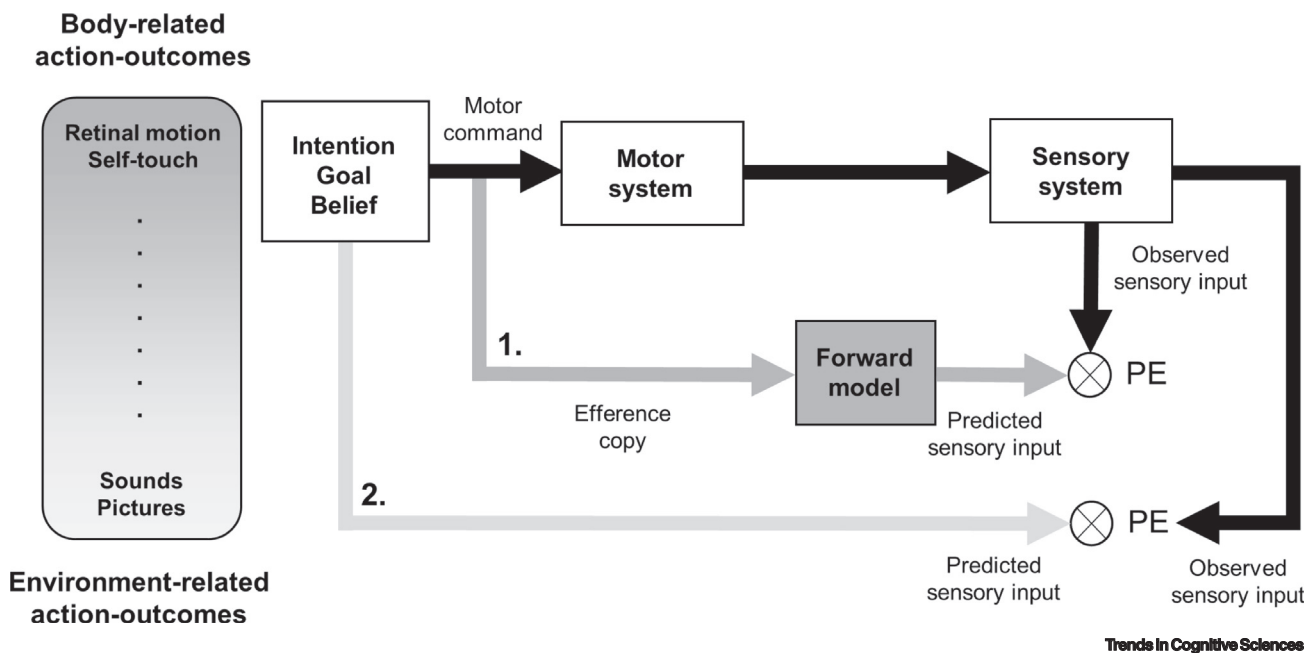


Figure 1. Hybrid Prediction Model. In this hybrid model, the predictive mechanisms driving the effects of action-outcome anticipation on perception depend on the type of action-outcome that is involved. In particular, in the case of body-related (or overlearned) action-outcomes, the involvement of a motor-based forward model (1), shown in dark gray, is plausible. However, when there is no innate or overlearned relationship between actions and sensory events, the prediction of action-outcomes is more likely to rely on general prediction mechanisms. This alternative pathway, shown in light gray (2), involves the prediction of sensory input based on cognitive sources, such as intentions, goals, and beliefs. For both prediction routes, the predicted sensory input is compared with the observed sensory input, resulting in a potential prediction error (PE).

What we eventually perceive is thought to be the result of a prediction-error minimization process, in which the internal model is adapted until its predicted input matches actual input as closely as possible. Recently, these accounts have been extended to action-control. In particular, it has been proposed that prediction errors can be minimized not only by updating one's predictions, but also by producing expected sensory states through action (known as **active inference** [67,100]). As such, in contrast to forward model accounts, there is no separate mechanism for perception and action, because both rely on sensory expectations. The absence of a distinct mechanism for action-effect anticipation also means that there is no need for efference copies [68]. Instead, all predictions result from the same general predictive mechanism.

A similar argument is put forward by ideomotor theory, which proposes that perceiving action-outcomes and action-planning are equivalent on a functional level [69–71]. Specifically, this theory proposes that repeated exposure to actions and subsequent sensory effects results in a bidirectional relationship between these events, expressed by a common code. As a result, activating the representation of an action-effect automatically triggers the action. Although this theory has mainly been used to examine the effects of perception on action, the account does not preclude the influence of action on perception. Indeed, the ideomotor account has been used to explain a phenomenon that is similar to sensory attenuation, known as action-induced blindness. In a typical paradigm, participants are asked to prepare one of two actions. Subsequently, they are exposed to a masked stimulus just before overtly executing this action. Both detection [72] and identification [73,74] of the stimulus are impaired if it shares a common code with the prepared action. For instance, participants are worse at correctly identifying a left-pointing arrow compared with a right-pointing arrow, when preparing to press a left key. The idea behind this effect is that preparing the action occupies the 'left' code, leaving it temporarily unavailable (or blind) for perception. Intriguingly this effect is not only observed for overlearned or hardwired action-effect relationships, but also for more arbitrary learned effects [75]. This suggests that ideomotor theory applies to both body-related and environment-related effects (although see [31]).

Both ideomotor theory and predictive coding frameworks are able to explain effects of action-outcome prediction on perception while circumventing the issues that result from the reliance on efference copies. This raises the question whether forward models are involved in the prediction of action-outcomes at all, because body-related action-outcomes might also be predicted based on more general, in-the-moment prediction mechanisms. Although this possibility cannot yet be ruled out, other scenarios can also be imagined. For instance, the contribution of forward models and more general prediction mechanisms might vary as a function of action-outcome type. In particular, while motor-based models are (more) likely to be involved in predictions of body-related and highly overlearned outcomes, these models might contribute less to predictions about environment-related events that are not tightly linked to actions (Figure 1). This dichotomy does not need to be strict. In some circumstances, the models might interact, such as when the timing of the upcoming action-outcome is important and cognitive models could benefit from using motor-based predictions as input. Whether a more general predictive account (as proposed by ideomotor theory and predictive coding) is more parsimonious than such a hybrid account remains to be seen (see also [68]).

Concluding Remarks

We have reviewed the role of motor-based forward models in the processing of action-outcomes. While evidence for these models is ubiquitous across species, we argue that the extrapolation of these effects to environment-related action-outcomes is hitherto unjustified. The observation of prediction effects does not in itself necessitate the involvement of motor predictions, and many studies fail to disentangle different sources of predictions. The relatively few studies that have

Outstanding Questions

Can cognitive expectations about action-outcome associations (e.g., expectations based on instructions) lead to similar perceptual modulation (e.g., sensory attenuation) as predictions relying on innate or overlearned associations?

What are the different characteristics of body-related and environment-related predictions, in terms of, for instance, their resistance to evidence-based updating (i.e., flexibility) or the relative importance of temporal predictability (e.g., 'when' an effect might occur might be less important for environment-related effects that are not as closely linked to the preceding action).

Are predictions about body-related and environment-related action-outcomes equally disrupted in disorders that are commonly associated with aberrant predictive mechanisms (such as schizophrenia)?

attempted to isolate motor-predictions have yielded mixed evidence. In addition, prediction effects on the perception of environment-related action-outcomes are often observed after minimal learning in humans, which does not match the relatively slow modulation of neural pathways underlying novel action-perception interactions that have been observed in animals. We therefore propose that predictions regarding effects beyond the body rely on different nonmotor mechanisms, such as proposed by ideomotor theory and predictive coding. The notion that we can use cognitive processes to anticipate the consequences of our actions is hardly controversial. Indeed, this presumption is central to classic models of goal-directed behavior [76–78]. In these models, actions are driven by an attempt to reduce the discrepancy between current and desired states. Here, we have attempted to reignite and expand these ideas by emphasizing the importance of cognitive prediction processes, not only for directing action, but also for the sensory processing of action-outcomes themselves.

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