

# Prediction of external events with our motor system: towards a new framework

Ricarda I. Schubotz

Max Planck Institute for Human Cognitive and Brain Sciences, Department of Neurology, PO Box 500 355, 04303 Leipzig, Germany

**We cannot, in the proper sense, imitate or re-enact inanimate events, such as ocean waves rolling, or even non-human animate ones, such as dogs walking. However, we can anticipate the way they change and recent studies show that our motor system becomes involved while doing so. A novel framework is presented that accounts for these findings by generalizing a predictive account of the motor system from action to event perception. It is suggested that we predict events that we cannot reproduce ourselves by exploiting an audiomotor or visuomotor representation that never amounts to a real action because it lacks proprioceptive and other interoceptive information. This view inspires thinking beyond our customary conceptualization of a 'motor' system.**

## Introduction

Events involve change, and change is often brought about by living entities. The question of how we predict the actions of conspecifics has been the source of widespread scientific interest and has also inspired several recent investigations in the cognitive neurosciences [1–3]. An exciting answer to this question stems from the concept of simulation (Box 1, Figure 1). According to this view, we predict what others are doing by using our own motor system as an internal model or 'emulator'. It is suggested that motor activation triggered by action observation feeds back into perceptual processing, creating top-down expectations and constraining predictions [4].

However, this account does not explain how we are able to predict the actions of other animal species. Moreover, it cannot explain how we deal with other types of changes, namely those generated by inanimate events, caused by machines or natural forces. So how do we predict events that we cannot properly incorporate into our motor system? Recently, the principle of simulation has been proposed to account for diverse predictive phenomena in human perception and cognition [5]. What remains to be seen is how those simulations are realized in the brain, particularly those that do not seem to be nested in the domain of motor control. Even relatively simple types of object motion seem to call upon higher-order processes [6], such as internal models of gravity for the perception of falling objects [7]. However, daily experienced events

involve more complex patterns of changes and many of them, including most auditory events, are not defined merely by motion. Yet, when we attend to them, we can predict their outcomes to a reasonable extent. For instance, when observing a flying insect, we set up specific expectations about the flying pattern depending on whether the insect is a fly, bee, butterfly or beetle. And if we lie in the dark and listen to the sound of a mosquito, auditory prediction can estimate when and where it has landed.

The present article puts forward the hypothesis that predictive accounts of the sensorimotor system can be generalized from action to event perception. I propose that we use our sensorimotor system by default in a simulation mode for predictions of observable events of any kind as long as they take place within several seconds. This view will be outlined in detail over the following sections. It is based on experimental evidence that shows that the prediction of different styles of changes not only draws on the sensorimotor system but also requires an intact sensorimotor system. Perhaps most strikingly, we effectively use our sensorimotor system to simulate events that we – principally or contingently – cannot reproduce or imitate. The patterns of activation revealed by imaging studies provide the basis for this proposal concerning how our sensorimotor system qualifies to serve event prediction.

## Evidence for a premotor role in event prediction

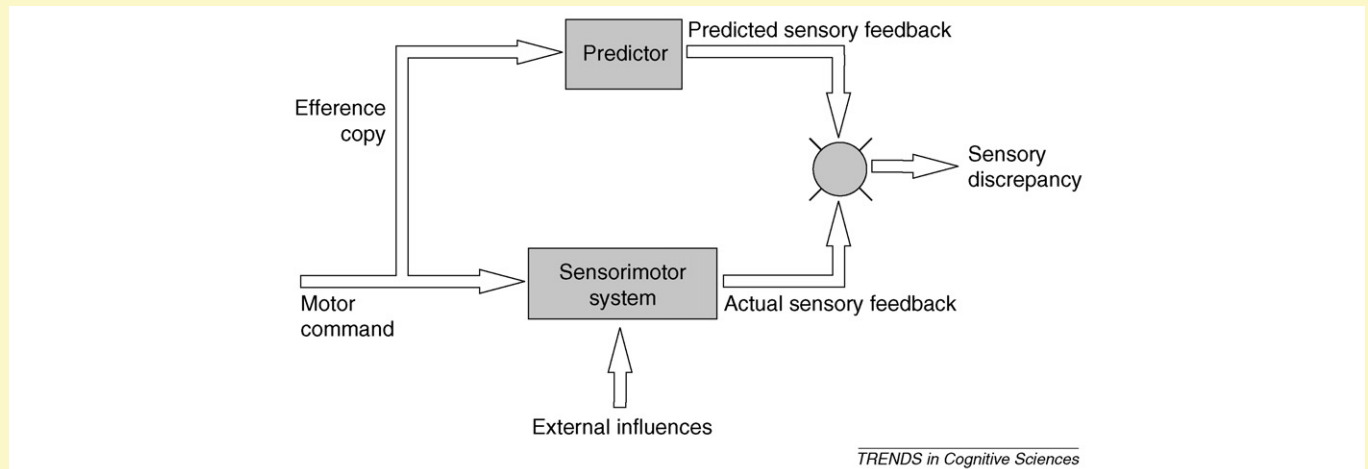
In a recent series of functional magnetic resonance imaging (fMRI) studies, we investigated the neural correlates of prediction [8] (Box 2) and showed that predictions of abstract events engage our motor system, particularly the premotor cortex and its parietal projection areas (e.g. Refs [9–14]; for a meta-analysis of related imaging findings, see Ref. [15]). Patient data [16] and repetitive transcranial magnetic stimulation data [17] rule out the possibility that motor activation in event prediction amounts simply to a task-irrelevant outflow into the motor system. Together, the findings raise the question of how the motor system might serve event prediction more generally. At first glance, there seems to be a striking difference between our prediction of other humans' behavior and our prediction of, for example, the rhythm of ocean waves, the flight of a mosquito or an unfolding sequence of abstract stimuli on a computer screen. This difference is due to our ability to reproduce (re-enact) what we see or hear in the case of humans but not in the case of ocean waves,

Corresponding author: Schubotz, R.I. (schubotz@cbs.mpg.de).  
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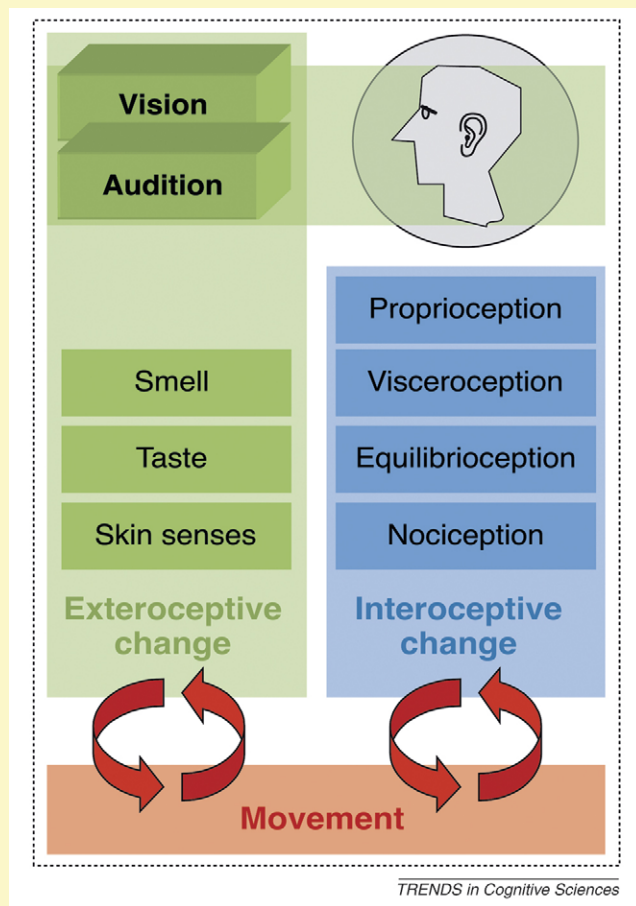
### Box 1. Predictive accounts of the motor system

Traditional models of motor control have generally emphasized the relevance of pre-programming motor commands and running them without disruptions, thus enabling only late feedback and corrections at the end of the movement. However, recent models question this assumption, emphasizing the relevance of multiple feedback loops, which rely on internal forward models (predictors) that emulate the dynamic behavior of our body and environment, thereby capturing the forward or causal relationship between our actions and their consequences [40,41] (Figure I in this box). Forward models that run 'off-line' are held to contribute to motor imagery, to estimate outcomes of

different actions and to evaluate and develop motor plans [5]. In addition, they are believed to have a role in the estimation of dynamic properties of manipulated objects [42]. Furthermore, it has been proposed that we use internal models to predict the outcomes of the actions of our conspecifics [5,40,43] (Figure II in this box). Experimental evidence corroborates the predictive function of motor activity in the observer of an action [44]. Recently, efforts have been directed at bridging the gap between computational approaches and brain research by addressing the neurocomputational underpinnings of grasping [45], sequential motor behavior [46] and imitation [43,47–49].



**Figure I.** Prediction in motor control. A forward model (predictor) predicts the sensory consequences of a movement based on the motor command. When a movement is self-produced, its sensory consequences can be accurately predicted and this prediction can be used to attenuate the sensory effects of the movement. Adapted, with permission, from Ref. [50].



**Figure II.** Sensory consequences of performed and observed actions. The sensory consequences of an action amount to two sorts of reafferent feedback: interoceptive change (generated within the body) and exteroceptive change (generated outside the body). Nociception stands for pain from organs, joints and bones. Proprioception refers to the sense of relative position of the body parts, viscerosception to the sense of the inner organs and equilibrioception to the sense of balance. Skin senses stands for touch, vibration, pressure, cutaneous pain and temperature. Information from vision, audition and, less frequently, smell and cutaneous temperature is principally available to an observer of the action as well.

mosquitoes or abstract stimulus sequences. However, this logic might be misleading. In the following section, I argue that the difference between the prediction of reproducible events and the prediction of irreproducible events is smaller than it seems and that, even when this difference is taken into account, it does not impede the usage of the motor system to support prediction of events that are not actions.

### How much re-enactment is required for simulation?

The ability to reproduce what we see or hear has an influence on the sensorimotor system, as demonstrated in studies that compare action experts and novices [18–21]. The accuracy of prediction is a function of how closely an observed action and one's own ability to produce this action are related [22,23]. In terms of internal models, one might say that, in the case of movements we can reproduce, we use our motor memories to run a simulation of the observed movement (Box 1, Figure II). Here, all our interoceptive and exteroceptive experiences can be exploited. In accordance with this, it has been shown that lacking a sense of touch and proprioception affects action prediction [24].

Although this modulatory influence of our ability to reproduce the observed movement on the sensorimotor system is fascinating, it is important to keep in mind that it only modulates – it does not determine – the involvement of this system in particular situations. Namely, the studies mentioned here show that the sensorimotor system responds in a qualitatively similar way for movements that can and cannot be performed, with differences being purely quantitative and reflected mostly in stronger activity for actions that can be performed. Therefore, 'proper' producibility and imitability does not seem to be a prerequisite either for our ability to predict events or for the concurrent activation in the motor system. However, as pointed out in the last section, fMRI data indicate that not even principal producibility is required. In contrast to proper producible actions, which we can actually perform, principally producible actions denote those for which we have the required body but not the required experience for performance. For example, consider an enthusiastic fan listening to Glenn Gould play Bach's Goldberg Variations repeatedly. Although his predictive abilities will reach ceiling during this pleasurable training, his performance will remain poor. Being a piano novice, the Glenn Gould fan cannot rely on a mental simulation of Glenn Gould's finger movements because he has no memories of pitch- and amplitude-defined acoustic effects of his finger movements. How else can he simulate the melody he is listening to? I will now present the idea that prediction of events is based on a fraction of action representation and then elaborate two aspects in detail.

### Predicting events we cannot reproduce

When we listen to a melody repeatedly, the lateral premotor cortex establishes sensorimotor representations (it can be suggested that this process is implemented by unsupervised learning [25]), using the input provided by the parietal and temporal association cortex (Figure 1a). (See Ref. [26] for sensorimotor integration and transformation in premotor–parietal loops.) The 'motor'

part of the sensorimotor representation does not amount to a movement that, when executed, leads to the sensory part. Rather, the sensorimotor representations are the audiomotor portion of such a movement, whereas proprioceptive-motor and all other sensorimotor representations that belong to a movement are missing. To understand that the motor part of the listener's representation itself does not depend on or require a proprioceptive representation, consider deafferented patients who have lost cutaneous touch and proprioception from their bodies but who can still, heavily relying on visual and/or auditory control, build up motor representations and move their deafferented limbs. Sound by sound, the lateral premotor cortex establishes an internal model of the melody, which can, in many ways, be termed a forward model, equivalent to those described in the context of motor control. This forward model can, after learning (Figure 1b), be used for melody prediction in a simulation mode in the same sense that forward models are used in motor imagery. (Please note that event prediction is not motor imagery; I will elaborate on this later.)

The simulation starts with the supplementary motor area (SMA) sending a signal to the lateral premotor cortex, the so-called corollary discharge or efference copy (see Ref. [27] for evidence that this signal stems upstream from primary motor cortex). This signal is a copy from the efference that travels from SMA to the primary motor cortex but, because simulation runs off-line, this efference is suppressed before reaching its target area. Note that I avoid the term 'motor command' because it is simply a signal that emanates from the SMA to another motor area but is blind with respect to any content. The corollary discharge or efference copy leads to an updating of the emulator: it triggers the next entry in the forward model of the melody and therewith elicits a perceptual expectation (a mock reafferent feedback), just as in motor imagery [5]. As in motor control, prediction consists of an attenuation of perceptions that are expected [27]; here, however, expectation does not result from body movement but from an externally generated perception that is simulated. When melody prediction is run in parallel to melody perception, then the real tone from the melody is perceived concurrently with, or slightly delayed to, this expectation and compared with the expected tone. Depending on the learning stage, a mismatch – if there is one – is perceived either as a prediction error (when the system gives more weight to the perceived tone) or as exafferent information – that is, as true change in the world (when the system gives more weight to the expected tone). Event prediction resulting from these computations is error-prone because it is realized in a noisy system and environment. Computationally, it might be best described as a Bayesian strategy, optimizing expectation by weighted combinations of priors and sensory likelihoods [28].

In contrast to someone who plays a piece of music (e.g. Glenn Gould), the observer's motor system simulates the piece of music based only on partial sensory information, namely audition. Glenn Gould relies on a specific – and unique – motor repertoire, meaning that he has specific memory traces of all kinds of real interoceptive and exteroceptive feedback from playing that piece of music. Thus,

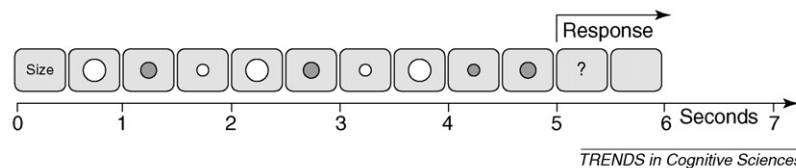
## Box 2. Investigating serial prediction in the brain

We developed the serial prediction task (SPT) to investigate the neural correlates of prediction in humans [8,15]. This task requires subjects to attend to a sequence of abstract visual or auditory stimuli, which is repeated within the trial (Figure I in this box). Using this experimental paradigm, a series of fMRI studies showed robust activations of the motor system, particularly premotor and corresponding parietal areas (for an overview, see Refs [8,15]). The findings from the lateral premotor cortex yielded the following characteristics of prediction correlates. The activation of the lateral premotor cortex was found:

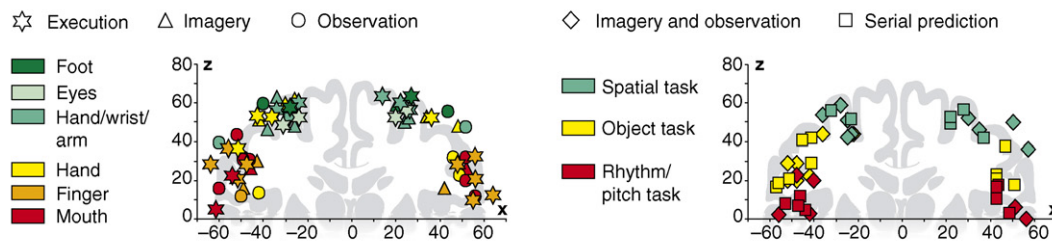
- (i) to depend solely on the subject's attempt to extract and predict a sequential pattern from the stimulus train and not on the presence or the detectability of a sequential pattern;
- (ii) to be anatomically distributed according to the to-be-predicted stimulus properties;
- (iii) to be flexible with respect to the employed stimulus material;

- (iv) to show, independently of the effect of the attended stimulus property, a modality preference but no specialization (inferior ventral and superior ventral premotor cortex are preferentially activated by auditory and visual stimuli, respectively);
- (v) to reflect a task-relevant process in serial prediction, as indicated by studies on the effects of real or virtual premotor lesions.

When subsuming our findings and embedding them in a meta-analysis of imaging studies that also reported activations in the lateral premotor cortex, we found a telling pattern that describes how prediction tasks use the motor system [8,15] (Figure II in this box). The Habitual Pragmatic Event Map (HAPEM) (formerly Habitual Pragmatic Body Map) suggests that prediction-related activity is structured according to different motor effectors. In a direct comparison of premotor correlates of rhythm, object and spatial serial prediction tasks with mouth, hand and arm imagery tasks, the HAPEM account was substantiated [13].



**Figure I.** Example of a serial prediction task (SPT). Sequential structure is provided by one stimulus property (e.g. size, not color), to which the subjects must attend to fulfill their task. Subjects are asked to work out how the sequence will evolve. At the end of a trial, subjects must indicate in a forced-choice mode whether the sequential order of the to-be-attended stimulus property was correct until the end of presentation or whether it was violated. Equally demanding tasks that provide the same amount of physical information without requiring the identification and prediction of a sequential structure serve as control conditions. For instance, in a serial match-to-sample task, subjects are asked to decide whether the last stimulus in a sequence equals the first one; because the length of the sequences varies from trial to trial, subjects must always compare the first stimulus in a trial with each of the following stimuli within the same trial (e.g. Ref. [10]).



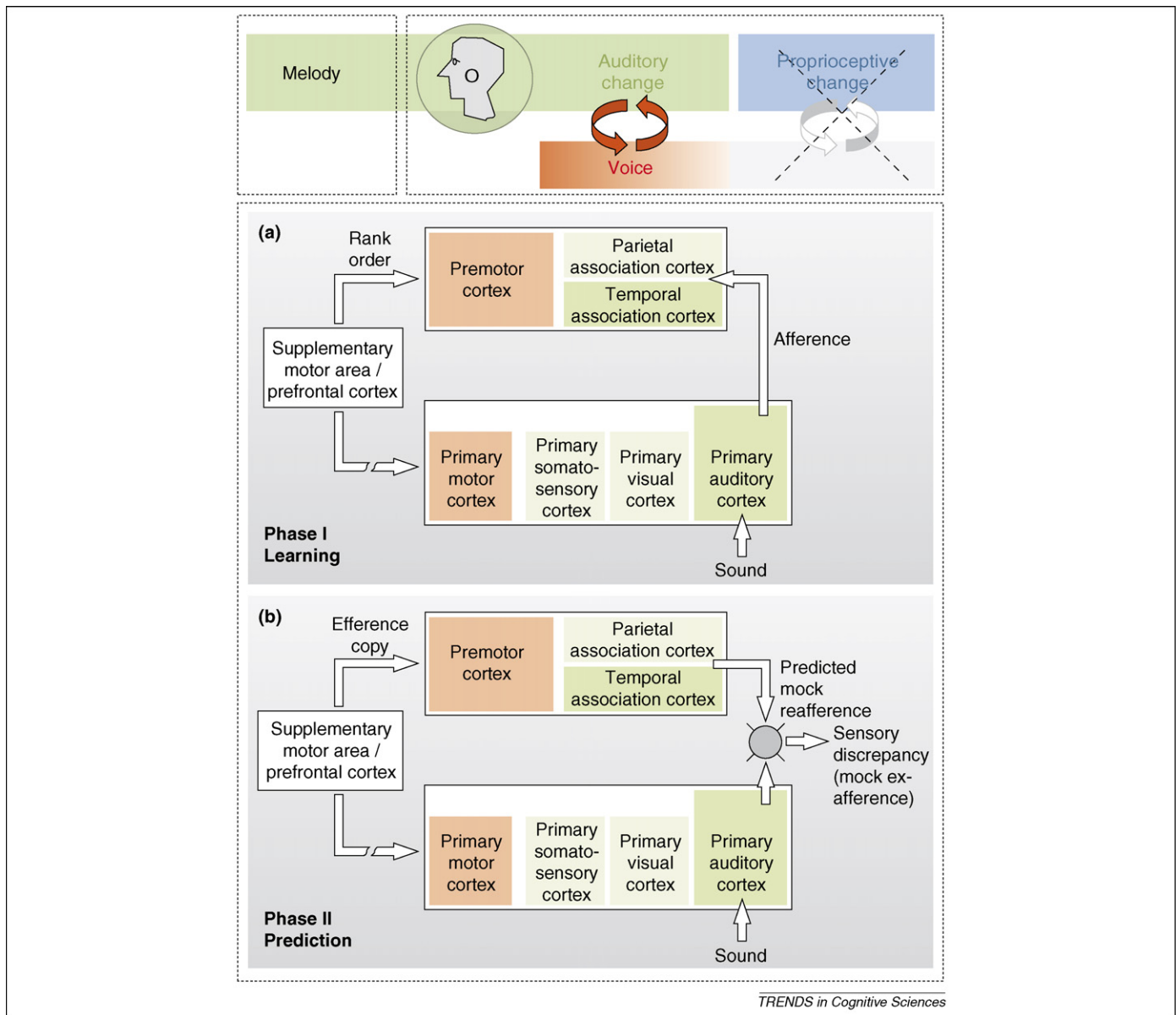
**Figure II.** Meta-analysis on motor and cognitive activations in the lateral premotor cortex. The Habitual Pragmatic Event Map (HAPEM) framework proposes that prediction-related activity is structured in the lateral premotor cortex according to different motor effectors [8]. Adapted, with permission, from Ref. [15].

the activation of Glenn Gould's motor system, should he listen to a record of his own performance, would feed back into the processing of all interoceptive and exteroceptive systems activated during performance (Figure II in Box 1). By contrast, in the Glenn Gould fan (a piano novice), listening activates fractions of his vocal and articulatory system only, which feeds back into auditory perceptual processing, thereby creating expectations in the auditory domain only.

For the prediction of inanimate events, I suggest exactly the same processes. However, what remains to be clarified is which part of the motor system simulates an inanimate event. This is not a trivial question for the Glenn Gould example either because the account so far suggests that a manual performance is simulated with the vocal and articulatory system in the observer. Still, this discrepancy is more obvious for inanimate events: to what sensorimotor representation can a rolling ocean wave be a mock refference (i.e. the imagined sensory feedback to an off-line simulation)?

## Suggestions on the cerebral implementation of event prediction

A possible answer to this question is provided by the Habitual Pragmatic Event Map (HAPEM; formerly Habitual Pragmatic Body Map) framework [15], which is based on imaging findings (Box 2). The HAPEM framework holds that, by default, the prediction of an event that is structured with regard to a property  $P$  engages the area of the lateral premotor cortex that is best adapted to specify its motor output in terms of property  $P$ . Let us consider ocean waves rolling iteratively on the shore. Their regularities are mainly determined by rhythmical properties. Predicting the time of the next wave arriving on the shore would call upon the vocal and articulatory system because rhythmic information is at the heart of vocal and articulatory production. However, most events are structured by more than one property. Therefore, not only the paces of the waves but also their height (i.e. rhythmic and spatial properties) have to be considered for predicting the next wave. Accordingly, prediction will involve both premotor

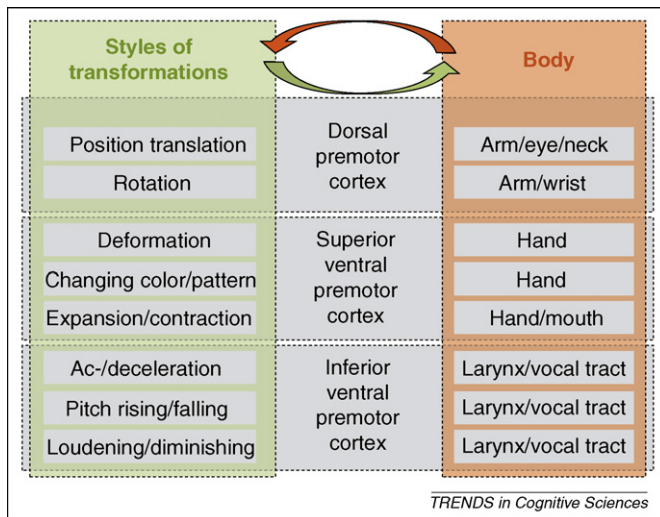


**Figure 1.** Learning to predict events. For observed events and actions that observers cannot perform, they fail to have an action memory, but they can still establish a sensorimotor representation that serves as a forward model. When listening to a melody, auditory information provides the learning basis. **(a)** First, the stimulus (e.g. sound of a melody) is used to train a forward model by unsupervised learning. The acoustic afference is coupled to vocal and articulatory representations; these audiovisual representations are one piece in the mosaic of sensorimotor representations that underlie a real (vocal) action. That is, proprioceptive effects of the voice and further sensorimotor couplings that would be required for the full-blown sensorimotor representation of a vocal action are not established. (Pre-)Supplementary motor area (SMA), under prefrontal influences, can provide the rank order of the sounds that make up the melody [29], whereas loops connecting the lateral premotor cortex to the parietal and/or temporal cortex serve sensorimotor learning and storage. **(b)** After learning, the forward model can be used to predict the perceived event (e.g. a melody) as mock reafferent feedback. When the predicted sound and the perceived sound are compared, a mismatch is taken to reflect a prediction error in early learning stages but taken to reflect a change in the world in advanced learning stages (mock ex-afference, i.e. an imagined feedback from change attributed to an external generator).

loops for vocal and articulatory action and those for actions that are most strongly defined by spatial properties (i.e. reaching and pointing). As with different effectors during action, the (pre-)SMA is presumably relevant for the coordination and integration of these predictive models working in parallel [29].

Returning to the question of which part of the motor system is used to simulate an observed inanimate event, the property (or set of properties) *P* ruling the structure of an event (as mentioned above) determines which part of the premotor cortex becomes involved. Accordingly, a spatially defined event (e.g. a rotation) will be simulated using the premotor–parietal loop for reaching because an

arm-action plan amounts to the expectation of a sequence of mostly spatially defined perceptions. The same mapping logic holds for other pairings as well, connecting object-defined events to the grasping circuit and pitch or rhythm-defined events to the vocal and articulatory circuit. Note that we do not have to presuppose an articulatory action corresponding to the rhythm of a wave, nor a reaching or pointing action corresponding to its height. Rather, it is assumed here that a subset of sensorimotor neurons in the areas controlling such actions is exploited in a rudimentary simulation mode. This simulation suffices to predict some of the relevant dynamics of the observed event, but it cannot serve as an exhaustive event description.



**Figure 2.** Styles of transformations. The lateral premotor cortex is modulated both by the style of transformation that an external object or a body part undergoes (left) and by the body part undergoing that change (right). Experimental evidence is presented in Box 2.

### Internal models of events: a neuroanatomical classification

Conceptually, it would be useful to have a terminology that describes the role of the premotor cortex in the simulation of action and in the simulation of events in a unifying framework. This should be possible because forward models for events are not categorically different from forward models for actions. Forward models for events are just a fraction of forward models for actions, a fraction that misses the full-blown interoceptive and exteroceptive description of action models. A term is needed that avoids the reference to action, which seems inadequate for most events, and one that can be applied to both the environment and the body. As a possible solution, I propose that the premotor cortex houses sensorimotor forward models that are neuroanatomically ordered according to the styles of transformations they describe. One style of transformation (see Ref. [30] for this concept in event perception) is that of rotation, which can be applied to many objects in our environment and parts of our bodies (e.g. wrist, arm). A list of possible styles of transformations is illustrated in Figure 2. I suggest that, by using one or several of these styles of transformations, one can generate a sensorimotor description (in the described rudimentary sense) of most of the events we are able to predict and most of the movements we are able to perform.

### Implications on motor imagery, action perception and the human sensorimotor system

Motor imagery cannot account for event prediction. Although, in mental rotation, it might be appropriate to assume that motor areas 'are active in producing motor commands of the sort that would lead to the overt counterpart of the imagined event' ([5], p. 387), this formula is misleading when generalized to event prediction. It implies that we possess a complete representation of all expected sensory consequences of an action that amount to the observed event, which in most cases is impossible. Prediction of events is often in the service of action – for

instance, when we want to catch a falling object. However, a post-hoc fallacy would be to conclude that all kinds of prediction aim at (or are reminiscent of) a concrete action. The view that prediction is not *per se* in the service of action has been substantiated by the observation that the estimation of parameters of object motion is strongly modulated by real or imagined motor interaction [7]. In line with this, we found that the default mapping described in the HAPEM framework is systematically modulated by the acquisition of sensorimotor associations [12].

Furthermore, event prediction differs considerably from action prediction, even if both exploit the same sensorimotor system. First, full-blown action memories, including all kinds of exteroception and interoception, can be exploited only for prediction of observed action. However, the effect of motor expertise in expert–novice studies should not lead us to conclude that only events we can perform can be predicted or that prediction inevitably teaches us to perform (although, according to theories of motor control, performance inevitably teaches us to predict; see Ref. [31] for the difference between motor prediction and motor control). Second, only actions instantiate goals (and intentions), which can be hidden [32]. Accordingly, during prediction of observed action, goals often have to be inferred rather than interpolated from visible or auditory cues. In other words, prediction of observed actions calls not only for the prediction of change, as other events do, but also for the prediction of a goal that the action is aimed at. The lateral premotor cortex is probably engaged in the prediction of change, whereas BA 44/45 of the inferior frontal gyrus is engaged in the prediction of goals [33]. Finally, this article has outlined the potential contribution of the lateral premotor cortex to event prediction, but how this region interacts with other network components to subservise event prediction, particularly with the cerebellum and (pre-)SMA, needs to be detailed. I have briefly addressed the role of (pre-)SMA in event prediction, which might be principally the same as in action planning: driving and orchestrating the simulation process on the lateral premotor piano, so to speak [34]. However, I have not discussed in great depth the role of the cerebellum, although it provides a model of mapping between sensorimotor representations by multiple paired inverse and forward models, just as premotor areas [35]. Additionally, comparable to premotor areas, it contributes not only to motor control but also to higher cognitive functions [36]. Nevertheless, substantial differences exist between these areas. So what is the essential difference between cortical and cerebellar mapping and why have I focused on the lateral premotor cortex? One straightforward answer was proposed by Doya [25], who differentiated the cerebellar and cerebral cortex based not on the goals but on the methods of their computation, suggesting that the cerebellar cortex underlies supervised learning and the cerebral cortex underlies unsupervised learning. The lateral premotor cortex is, therefore, involved in comparably slow but flexible forward models, whereas the cerebellar cortex is involved in fast and accurate but comparably rigid pairs of forward and inverse models. Event prediction might call upon premotor unsupervised learning because this algo-

### Box 3. Questions for future research

- What are the limits of our abilities to predict events, and (how) are they related to the limitations of our motor abilities?
- What are the brain correlates of predicting natural but inanimate events? Prediction of inanimate events has been extensively investigated on the basis of highly abstract stimulus material to control for undesirable influences of naïve physics or context cue-heuristics [8,15]. Now it would be interesting to understand how these factors interact.
- In motor learning, demands on cognitive control drop while performance reaches a level of automaticity. It is suggested that the cerebellum acts as a short-cut circuit or a look-up table for sensorimotor mappings, originally developed by the more time-consuming cortico-cortical processing [25]. Does learning and hence prediction of external events ever reach automaticity and, if so, does the cerebellar cortex contribute to the storage of event short cuts, as is supposed for motor control?

ithm is based on the statistical properties of the input signals. By contrast, and possibly less adequately in the case of event prediction, cerebellar supervised learning modules might work as short-cut circuits or look-up tables for mappings that were first developed by time-consuming unsupervised learning modules.

### Concluding remarks

Currently, there is much discussion about how cognition might be rooted in 'motor'- and 'body'-related functions (e.g. embodiment and re-enactment; e.g. Refs [37–39]). The current paper has outlined the idea that a predictive account of the motor system can be generalized from action to events and has described how simulation of events can be realized in our sensorimotor system. According to this view, prediction of events is achieved by the aid of sensorimotor-driven forward models. Note that this is not to claim that event prediction is a motor function. It is partially realized by a brain network that has so far been named 'motor system', but it could turn out that 'prediction system' is a more appropriate label.

I have emphasized that event prediction might benefit from the capacity of the sensorimotor system to represent sensorimotor information in sequential order. Another benefit (not elaborated on here but which might turn out to be important) involves integration of all categories of interoception and exteroception by the motor system. I stated that motor activations that are triggered by event prediction generate visual and/or auditory expectations only; however, future research should investigate whether proprioceptive expectations or imageries are also generated via spreading or collateral activation, which might enhance event prediction. Furthermore, the present paper has addressed the issue of internal models of external events but has not mentioned other strategies to cope with external events, such as naïve physics or context cue-heuristics [7]. These approaches are likely to be complementary rather than mutually exclusive and a challenge for future research will be to bring them together (Box 3).

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