Neural Pathways of Embodied Simulation

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Abstract. Simulation theories have in recent years proposed that a cognitive agent's "inner world" can at least partly be constituted by internal emulations or simulations of its sensorimotor interaction with the world, i.e. covert perception and action. This paper further integrates simulation theory with the notion of the brain as a predictive machine. In particular, it outlines the neural pathways of covert simulations, which include implicit anticipation in cerebellar and basal gangliar circuits, bodily anticipation by means of forward models in the cerebellum, and environmental anticipation in the neocortex. The paper also discusses, to some extent, possible implications of the neural pathways of covert simulation for the frame problem, and the relation between procedural and declarative knowledge in covert simulations.

1 Introduction

According to simulation (or emulation) theories [e.g. 1 ch. 9, 2-5], thinking is, quite literally, rooted in perception and action. In line with empiricist and associationist ideas, thinking is the coupling of covert actions and perceptions. What we mean by *covert action* is the ability to reactivate some of the neural processes and structures used to plan (and execute) bodily movements, but without any actual movements. Similarly, *covert perception* refers to reactivation, in the absence of external stimulation to the sense organs, of some of the neural structures and mechanisms that process sensory input. Thus, simulation processes are off-line processes which can operate in the absence of sensory input and also without causing any movements (see Figure 1).
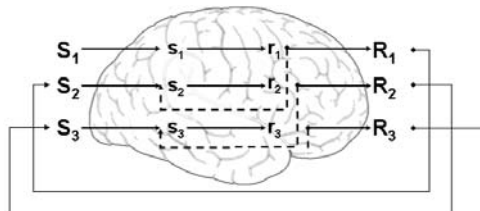

Fig. 1. Covert simulation. Instead of eliciting a new action, covert action r_1 generates a covert perception, s_2, which then generates a new covert action r_2 and so on. (Adapted from [3])

Coupling covert actions and perceptions into covert or off-line simulations allows organisms to form, roughly speaking, an internal world. Several advantages come from having such an internal world, one being the ability to try out behavioral options in total safety; "letting our hypotheses die in our stead" to borrow a phrase from Popper [cf. 6]. These *Popperian creatures*, as Dennett calls them, are the opposite to the stupid "who lights the match to peer into the fuel tank, who saws off the limb he is sitting on, who locks his keys in his car and then spends the next hour wondering how on earth to get his family out of the car." [7]. Although not the main topic of the paper, it is worth pointing out that endowing agents with this kind of internal models might lead to something akin to the frame problem [7]. The frame problem was originally posed as a problem for traditional AI, but philosophers have applied it more generally and it may also be a problem that should be addressed by simulation theories, or any other theory, which aim to explain Popperian internal worlds [8]. Haselager and van Rappard [9] interpreted the general frame problem as follows:

> Psychologically speaking, people have an amazing ability to quickly see the relevant consequences of certain changes in a situation. They understand what is going on and are able to draw the right conclusions quickly … The problem is how to model this ability computationally. What are the computational mechanisms that enable people to make common-sense inferences? Especially, how can a computational model be prevented from fruitlessly engaging in time-consuming, irrelevant inferences? A rather straightforward suggestion is that seeing the relevant consequences of an event is made possible by an understanding of the situation. … Yet, human beings posses an enormous amount of information. The real difficulty underlying the frame problem is how the relevant pieces of knowledge are found and how they influence one's understanding of the situation. [9]

Covert simulations may be part of the process of understanding a situation by producing simulations of the possible future states that can be reached from the current [cf. 10, 11]. However, there must be mechanisms that constrain simulations to the relevant aspects of the situation if covert simulations are to be part of the complex task of understanding a situation.

Dennett [7] argued that a problem with many theories, for example associationist theories, was that they did not specify any real (physical) mechanisms to solve the frame problem [cf. 8, 9]:

> Hume explained this in terms of habits of expectation, in effect. But how do the habits work? Hume had a hand-waving answer - associationism - to the effect that certain transition paths between ideas grew more likely-to-be-followed as they became well worn, but since it was not Hume's job, surely, to explain in more detail the mechanics of these links, problems about how such paths could be put to good use - and not just turned into an impenetrable maze of untraversable alternatives - were not discovered. [7]

Simulation theories have argued to extend associationist ideas by paying close attention to how brains work [3], which may provide answers to how the covert simulations are organized and constrained. Looking at the neural mechanisms that produce

covert simulations, it seems that evolution have resulted in a rather general solution - anticipation. We argue in this paper that covert simulations to a large extent reuse the neural circuitry for so called procedural and declarative predictions [12, 13]. Downing [12] pointed out the possible compatibility of his work and simulation theories and also suggested that simulation theories need to explain the relationship between lower- and higher-level representations in covert simulations.

The paper further incorporates the notions of procedural prediction and declarative prediction, although somewhat redefined, with simulation theories, reviews other sources of evidence for its incorporation including neurophysiological mechanisms, and addresses the relationship between lower- and higher-level representations.

The paper is structured as follows. Section 2 provides a brief overview of simulation theories and introduces three notions of anticipation: implicit, bodily, and environmental anticipation. Section 3 is about implicit anticipation in simulations. The section first presents some empirical evidence for the presence of implicit predictions and then describes how implicit predictions might be implemented by the cerebellum and basal ganglia and their role in off-line simulations. Section 4 briefly reviews bodily anticipations in simulations and presents the view of the cerebellum as a forward model. Section 5 focuses on environmental predictions and relates this view to the ideo-motor view of cognition, as well as provides some empirical support for environmental predictions. Furthermore, it presents the view that environmental predictions based on efference copies at various levels of the neocortex plays a crucial role in simulated behavior. The paper ends with a discussion in Section 6.

2   Simulation Theories: What Are the Components?

Simulation or emulation theories explain many aspects of cognition ranging from perception to conceptualization. These theories share, although to various extent, the idea that cognition must be explained in terms of covert perceptions and actions, as defined above [14]. There are differences though. Some simulation theories argue that covert simulations are to be considered as reactivated perceptions and actions [3], inputs and outputs of emulators [5], or perceptual symbols [15]. Although these might be seen as merely minor semantical differences, they can, for example, imply different views on the extent to which simulations require additional theoretical and neural mechanisms beyond the sensorimotor systems. Related to this is whether simulations require the reactivation of the neural substrate closest to the sensory input and motor output terminals [cf. e.g. 11]. However, a more pragmatic perspective consistent with the empirical evidence is that covert simulations exist at many different levels of the sensorimotor hierarchy. There are also different views on the representational nature of covert simulations. Our view of simulation theory, suggests that covert simulations should not be equated with cognitivist notions of representation and internal models in cognitive science and AI. If covert simulations are to be seen as representations with epistemic functions, they cannot only be observer defined correspondences between aspects of the model and aspects of the world [16]. Rather, the covert simulations function as representations because they reactivate the neural activity present during embodied interaction. Covert simulations are representations in the Piagetian sense:

[R]e-presentations in Piaget's sense are repetitions or reconstructions of items that were distinguished in previous experience. As Maturana explained … such representations are possible also in the autopoietic model [[e.g. 17]]. Maturana spoke there of re-living an experience, and from my perspective this coincides with the concept of representation as Vorstellung, without which there could be no reflection. From that angle, then, it becomes clear that, in the autopoietic organism also, "expectations" are nothing but re-presentations of experiences that are now projected into the direction of the not-yet-experienced. [18]

Covert simulations may result in these kinds of reactivated experiences, but they can also be present without resulting in conscious experiences. The paper makes no further attempt to explain what states or processes are likely to be conscious ones.

The starting point of our explanation of covert simulations is Hesslow's [3] "simulation hypothesis", which postulates the following elements of covert simulations:

(1) Simulation of actions: we can activate motor structures of the brain in a way that resembles activity during a normal action but does not cause any overt movement. (2) Simulation of perception: imagining perceiving something is essentially the same as actually perceiving it, only the perceptual activity is generated by the brain itself rather than by external stimuli. (3) Anticipation: there exist associative mechanisms that enable both behavioral and perceptual activity to elicit perceptual activity in the sensory areas of the brain. [3]

The next section describes the empirical evidence for the existence of simulations of perception and action, or covert perceptions and actions as they are termed here. Section 2.2 outlines the second aspect of simulations, anticipation, and distinguishes three different forms of anticipation, which are then elaborated in the remainder of the paper.

2.1   Reactivation

A wide range of psychological and neuroscientific studies have shown that cognition to a considerable extent involves the reactivation of the neural processes active during perception and action in humans [for a detailed review see e.g. 19]. Reactivations might also be present in other animals as well. An indicative, but not conclusive, observation is the running movements and yapping of sleeping dogs, which suggests that something like a mental simulation might be present [20].

Reactivation has for a long time been a hypothesis in memory research, dating back to William James, which specifically states that sensory and motor brain regions that are active during encoding are also reactivated during retrieval of memories [21-24]. One of the first neuroscientists to adopt this reactivation hypothesis was Damasio [25] who explained procedural and declarative memory as "time-locked multiregional retroactivation". According to Damasio [25],

perceptual experience depends on neural activity in multiple regions activated simultaneously … during free recall or recall generated by perception in a recognition task, the multiple region activity necessary for experience occurs near the sensory portals and motor output sites of the system rather than at the end of an integrative processing cascade removed from inputs and outputs. [25]

Both behavioral and, recent neuroimaging experiments have provided further support for the reactivation hypothesis in memory tasks [26]. One of the most spectacular behavioral demonstrations of the importance of the overlap of encoding and retrieval context comes from Godden and Baddeley's [1975, cited in 27] memory context experiment with divers. Using a free recall methodology, Gooden and Baddeley had divers learn lists of words either on land or submerged, and to recall the words either in the same context as during encoding or in the other context. When encoding and retrieval context matched memory performance was enhanced compared to non-matching contexts. These results indicating an interdependence of encoding and retrieval are consistent with the hypothesis that similar neural mechanisms are being used.

Recent neuroimaging experiments of memory have provided further support for the reactivation hypothesis and the assumption that the behavioral effects are due to the activation of the sensory and motor areas used to process the percept or associated action [cf. 21]. Using Positron Emission Tomography (PET), Nyberg et al. [24] found that remembering visual words that had been presented together with sounds at the encoding stage activated some of the auditory brain regions that were active during encoding. Moreover, this effect was present even when the subjects did not have to explicitly remember the sound, but only determine whether the word was part of the original list. This effect also transfers to other types of information, such as spatial location [Persson & Nyberg, 2000, cited in 24], and vivid visual information [23]. Furthermore, Nyberg et al. [22] found that both overt enactment and imaginary enactment of the to be remembered action phrase are accompanied by encoding-retrieval overlaps. However, it should be noted that the studies also show that encoding and retrieval are associated with different activity patterns [22]. However, they do show that sensory and motor regions participate in some cognitive processes that do not involve perception and action [cf. 22].

The reactivation hypothesis generally supports the reactivation of both perceptual and motor areas used during the encoding of the memory. Covert perceptions and covert actions are thus special cases of this general principle of memory and brain function. The two following sections focus on studies that emphasize the perceptual or motor aspect of the reactivation.

Covert Actions. Many experimental results suggest that, to some degree, the same neural substrate is used for action and covert action. Although reactivation of motor actions has been observed in other cognitive tasks such as language understanding, the most encompassing reactivation occurs in explicit or implicit motor imagery [cf. 28] leading some to suggest that covert actions are in fact actions, with the exception that no overt movement occurs [e.g. 29]. Motor imagery is usually defined as the recreation of an experience of actually performing an action, for example, the person should feel as if he or she was actually walking [30]. Motor imagery experiments have shown that mentally simulating an action is similar to overt action in the following aspects: execution time including the reproduction of Fitt's law and isochrony [5, 31-33], physiological effects [34, 35], PET, fMRI, and TMS [for reviews see 4, 36, 37].

In the case of motor imagery, the reactivation of actions is quite independent of the current input stimuli, i.e., independent in the sense that the reactivation is not caused by it. Covert motor activity has however also been found to be automatically elicited by various kinds of external sensory stimuli. The discovery of mirror neurons in the

macaque monkey [38, 39] and the possible existence of mirror systems in humans [40, 41] clearly illustrate this ability. Mirror neurons and canonical neurons have been found in the rostral region of the inferior premotor cortex (area F5) of the monkey brain which contains neurons that are known to discharge during goal directed hand movements, such as grasping, holding, tearing, or manipulating [42]. The special property of mirror neurons is that they are also activated by observation of the same goal-directed hand (and mouth) action being performed by someone else [38, 39].

The empirical evidence suggests that the brain has the ability to reactivate the brain areas responsible for action by means of internal or external stimuli. It also shows that it is possible to do this without causing overt actions. If the covert actions are sufficiently similar to the patterns normally producing movements and actions, the covert actions could internally drive activations in the sensory cortex to resemble the activation that would have occurred if the action had been executed.

Covert Perceptions. There is much empirical evidence, both behavioral and neuroscientific, that suggest that reactivation of covert perceptions is common in human cognition [43-45], but there are also animal learning studies that could suggest that even rats are able to reactivate a perception based on earlier cues [46]. Several studies have indicated that imagination evokes similar experiences to actual object interaction [e.g. 47], and are almost indistinguishable from the real perception [Perky, 1910 cited in 43, 48]. The seminal study by Shepard and Metzler [47], had subjects determine whether two three-dimensional forms had the same shape or not. The results showed that reaction times increased linearly with the angular difference, indicating that the imagined rotations were performed at a constant rate, as if a physical object were rotated [cf. 43]. Furthermore, they found reaction times not to be longer for depth rotations than for rotations in the picture plane. These two findings suggest that imagined rotations in some aspects correspond to actual physical rotations of objects [43]. Moreover, the subjects reported that they solved the task by mentally forming and rotating three-dimensional forms to "see" if they were the same, which might also be taken as support for the involvement of perceptual processes in mental imagery. There have also been findings that suggest a considerable overlap between the mechanisms of spatial attention and spatial working memory [49]. Furthermore, Lauwereyns et al. [50] found that their finding generalizes to non-spatial visual dimensions, such as color and shape.

A recurring issue in neuroscience is to what extent the sensorimotor loop and the off-line simulation overlap. As discussed above, some findings based on behavioral, physiological, brain imaging and single neuron recordings suggest that the overlap is almost complete, except for the overt execution. Other studies have observed small differences in some of the structures, such as a small shift in the rostral direction in the basal ganglia and dorsal premotor cortex for imagined as compared to real actions [51, 52]. The differential activation could perhaps be useful for thinking about an action, while performing another.

2.2 Anticipation

So far we have reviewed evidence concerning the existence of covert perceptions and actions and the extent to which they are similar to actual perceptions and actions. The next step is to address the mechanisms which enable the coupling of covert actions

and perceptions into extended covert simulations (cf. Figure 1). Based on Downing's [13] distinction between declarative and procedural prediction, we suggest that three forms of predictive processes are used to establish covert simulations, implicit, bodily, and environmental anticipations[1]. *Implicit anticipation*: Action selection mechanisms can be seen as anticipations, but of an implicit [53] or procedural [13] kind. This kind of prediction, formed by evolution or learning, allows an animal to act as if it has access to some future goal state, but without the need to produce a (sensory) state that correspond to that goal. In other words, implicit predictions generate actions, which mean that the only information about the external state is in the way that the animal coordinates its behavior with it. *Bodily anticipation*: Many models suggest that it is necessary to produce predictions of the (sensory) state of the body [54-56], because of the inherent time delays in the sensorimotor system. That means, since it is often not possible to successfully plan all motor commands in advance based on the current state and the time delays would prevent error correction during motion, predictions of the future states of the body have to be provided to update the motor planning process. *Environmental anticipation*: The ability to generate a prediction of a future perceptual state that is associated with a particular response in a given situation could be advantageous. For example, if this would lead an animal to reactivate the "image" of a predator, it could also automatically execute the associated action programs and might escape the predator (Hesslow, unpublished manuscript, cf. also [13]). Covert perceptions could initiate action selection mechanisms in similar ways as actual perceptions because of their similarity in terms of neural activity.

3   Implicit Anticipation

Although actions are situated in the sense that they are highly influenced by a particular bodily and environmental situation, prediction and the internal construction of simulated interactions are crucial aspects for the behaving animal. In AI one alternative has been to conceive of the internally constructed plans as prescriptions for actions [57]. An alternative view, the one favored here, is that internally constructed plans are but one of the causal influences (internal or external) on the resulting behavior and that the influence on actual behavior is less direct [cf. 58, 59]. Marques and Holland [60] extensively discussed the necessary and sufficient criteria for an embodied agent capable of planning by means of simulations or, in their terms, functional imagination. The neural mechanisms of implicit anticipation described in this section may also contribute to the understanding of such an agent by providing some hints about the neural mechanisms for goal-seeking behavior (i.e., approaching a goal without explicitly representing it) and action selection. These mechanisms also ensure that simulations are effective, i.e., only relevant simulation paths are considered, rather than simulating every possible action in a situation. However, this would also be the case for creatures not endowed with simulation abilities, since it is only possible to perform a few actions out of an almost infinite pool of possible actions simultaneously [cf. 61]. Thus, our hypothesis is that the non-simulating brain's solution to the action selection problem is reused by the simulating brain. These mechanisms do

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[1] The terms prediction and anticipation are used synonymously.

not only speed up simulations by constraining them to a few simulation paths by means of implicit predictions, but also allow them to be directed towards future goals, without explicitly representing the goal.

3.1   Implicit Predictions in Humans and Animals

The establishment of stimulus-response (S-R) associations has been a major theory of animal learning. In the context of this paper, S-R associations can be seen as simple forms of implicit predictions. For example, eyeblink conditioning can be explained in terms of (implicitly anticipatory) S-R associations. A neutral conditioned stimulus (CS), e.g. a tone, is followed by an unconditioned stimulus (US), e.g. a puff of air, which elicits a conditioned response (CR), a blink [62, 63]. After training, the neutral stimulus directly elicits the conditioned response in anticipation of the unconditioned stimulus. The neural substrate of eyeblink conditioning is discussed further in the next section. Cisek and Kalaska [64] provided evidence for predictively activated (but not executed) motor representations in the dorsal premotor cortex of monkeys. More importantly, they also found that the predictive and performance related activity was strikingly similar. Thus, it implements a predictive relationship between the stimuli and the about to-be-activated action. A similar finding is that the perception of objects automatically activates motor representations of the action normally performed when using the object [65].

3.2   Neural Substrate of Implicit Predictions

Although many factors, processed in different parts of the brain, affect behavioral choices [66], basal-ganglia–cortex loops (including amygdala influence) [67] and cortico–cerebellar loops [68] are commonly considered crucial for action selection. These action selection mechanisms are in some respects anticipatory in nature since the agent's actions are directed towards a future situation. However, as described next, there are no explicit predictions involved in the anticipatory behaviors learnt by these action selection mechanisms [cf. 2, 13, 69].

Cerebellum. It has been suggested that the cerebellum learns sensory-motor contingencies through supervised learning [13, 70]. The cerebellum receives input from several different subcortical and cortical areas through mossy fibers to granular cells where the granular cell's axon forms parallel fibers (PF). Each PF synapses onto the dendrites of many Purkinje cells (PC) (~100000:1), whose firing ultimately inhibit a motor response via cells deep in the cerebellum. Each PC receives input from one climbing fiber (CF) (1:1) which gives feedback from afferents located nearby the muscles via the inferior olive [71, 72]. The supervised learning is dependent on the timing of the error feedback, which is explained in the form of eligibility traces that enables long term depression of PF-PC synapses that was active around 100-250msec prior to climbing fire activation [13, 73-75]. In other words, the error feedback from the muscles, affects the signals that was active some time ago, often around the time when those actions that caused the error signals were activated. Some studies have also found that motor imagery activates the spinal cord and muscle spindles [76]. In these cases, it might be possible to covertly generate (simulate) the error signals that the cerebellum needs for learning the correct actions [cf. 71]. Increased activity of the

cerebellum in motor imagery [e.g. 4] and the ability of motor imagery to improve later performance [e.g. 35] is in line with this hypothesis.

Eyeblink conditioning is also thought to be mediated by the cerebellum. In the case of eyeblink conditioning, the CS is presented via mossy fibers and the US via CFs [62]. During training, the PF-PC synapses are altered such that the PC response is decreased around the time of the tone (CS), which causes a disinhibition of the interpositus nucleus and the downstream motor pathways leading to a blink (CR) that coincides with the airpuff (US) [62].

The general conclusion is that the cerebellum can implement S-R relations; as soon as a particular sensory context is present, the cerebellum computes the correct signal to the motor system. The cerebellum could be part of extended simulation loops by helping to establish the S-R links (cf. Figure 1), i.e., to select the actions represented in the neocortex [cf. 77]. In that case, the cerebellum only implements an implicit model of the world, which means that the only criterion for being a model is that it generates correct actions. Other models suggest that the cerebellum functions as a forward model capable to generate predicted (sensory) states (discussed in Section 4).

Basal Ganglia. The basal ganglia have been suggested to play a major role in action selection [78]. For example, Humphries, Stewart and Gurney [79] suggested that "the BG are a critical neural substrate in the vertebrate action selection system, resolving conflict between multiple neural command centers trying to access the final common motor pathway" (p. 12921). The way the basal ganglia implements implicit predictions requires a longer explanation than is possible here [for full descriptions see 12, 13, 78], but in essence the input station of the basal ganglia, the striatum, learns to detect important (cortical) contexts which it maps to actions, represented in the cortex and the brain stem. The learning of a context-action pair is then guided by the emotional response that the action results in. As in the cerebellum, eligibility traces makes sure that contexts active roughly 100msec before an emotional response are the ones strengthened. Furthermore, earlier and earlier contexts can be made to predict the emotional response [13]. The prediction of emotional states allows the basal ganglia to learn context-action pairs that anticipate emotional states.

Several models argue that the basal ganglia together with associated cerebral and cerebellar structures are involved in off-line simulations [61, 80]. For example, Doya [80] suggested that a network consisting of the basal ganglia, parietal cortex and frontal cortex as well as the cerebellum could implement off-line simulations used for planning. However, in Doya's model, the cerebellum does not generate implicit predictions but provides predictions of the new (sensory) state (discussed in Section 4). A role more consistent with the view of the cerebellum as generating implicit predictions is that it contributes to covert simulations by fine-tuning the covert actions selected by the basal ganglia [81]. For example, Sears, Logue and Steinmetz [82] argued, in the context of eyeblink conditioning, that an efference copy of the CR may project to motor cortex, which serves to fine-tune movements and integrate simple responses with more complex movement sequences. A possible function of the basal ganglia (together with the cerebellum) in off-line simulations could be to direct and constrain the course of simulations by selecting some actions over others, but at the same time also prevent them from causing overt movements [2, 83]. In other words, just as the basal ganglia support action selection through reinforcement

learning they also might be able to select the action content of our thoughts [61]. The neuron populations in prefrontal, premotor and motor cortex activated by the basal ganglia can then serve as the input to cortical mechanisms, which predict the sensory consequences of that action (cf. Section 5).

In summary, the resulting sensori-motor associations formed by the cerebellum and basal ganglia may during simulations anticipatorily activate the various parts of the motor system, resulting in covert actions (some of which might be experienced as motor images [30]) or actions [cf. 2, 81]. A central aspect of the learning mechanisms is the eligibility trace, which ensures that the associative learning occurs on synapses that were active roughly 100-250msec prior to a teaching signal [13, 73, 74]. This is could in some cases be an example of co-evolution between the nervous system and body [cf. 84], since the neurochemical processes that allow for the modification of synapses are closely tied to the feedback delays of the sensorimotor system.

4   Bodily Anticipation

For most people it is very difficult to tickle one self. However, it might be possible if you use a feather or better yet if someone else tries to tickle you (using a feather). A possible explanation is that since we have had lots more practice with and can with some certainty know what actions we are about to perform we can predict the proprioceptive signals. Blakemore and colleagues [85-87] argued that the neural mechanisms that produce this phenomenon are based on efference copies feed to the cerebellum. The cerebellum both predicts the sensory consequences of that action and compares it with the resulting sensory feedback from touch sensors, which if there is no discrepancy attenuates the activity in somatosensory cortex. This is usually described as that the cerebellum implements a model of the world, a so called forward model [e.g. 68, 80]. This means that the cerebellum implements a prediction of the state of the body or the sensory afference from the proprioceptive (and proximal sense) organs based on efference copies [e.g. 68][2].

Motor control experiments have also suggested that forward models are necessary because the motor system needs to act on predictive knowledge of future states to, for example, compensate for feedback delays [e.g. 54, 56]. Many models argue that the forward models are found in the cerebellum, and that the forward models can be run off-line to generate covert simulations [e.g. 5, 71]. For example, if motor activity (generated by a cerebellar S-R association, cf. Section 3.2) does not lead to overt action, an efference copy might still be sent to the cerebellum to generate a sensory prediction. These kinds of covert simulations are likely to be closely tied to details of the execution and proximal consequences of bodily movement. Hence, the sensory predictions are related to proprioceptive signals and the proximal senses of touch (and perhaps taste) [88].

Bodily anticipation as we have chosen to call it is also declarative prediction in that it generates states that correlate to external states, i.e., external to the central nervous system, but at the same time the information is about events internal or at surface of the body.

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[2] However, whether or not the cerebellum implements a forward model that predicts future sensory states is a matter of discussion [88].

5   Environmental Anticipation

Environmental anticipation differs from bodily anticipation both in its function and neural substrate. The function of environmental anticipation is to generate predictions of future sensory states relating to objects and situations in the world external to the animal's body. Environmental predictions are similar to declarative predictions in that they associate two neural states which each correlate to some environmental state. For example, if a particular perception is associated with the "image" of a predator then the animal might have a better chance of escaping its predator. This type of sensory-sensory associations is certainly present in many mental simulations [3]. Some simulation theories emphasize, as we do in this section, that motor patterns are often crucial in eliciting the sensory activity that is normally associated with the execution of the corresponding action [cf. 2, 3]. This type of environmental prediction might be crucial for implementing longer and more specific or goal directed covert simulations.

5.1   Environmental Predictions in Humans and Animals

The prediction of (sensory) effects was already a central tenet of William James's Ideo-Motor Principle (IMP), i.e., the idea that every action is preceded by a prediction of its effect.

> An anticipatory image, then, of the sensorial consequences of a movement, plus (on certain occasions) the fiat that these consequences shall become actual, is the only psychic state which introspection lets us discern as the forerunner of voluntary acts. [James, 1890/1981, p. 1112, quoted in 89]

The action-effect association is bi-directional [90], implying that it is both a prediction of the effects and a determinant of the behavior [89]. However, in this section the focus is on the prediction of sensory effects, rather than the action selection aspect. The predictive action-effect association has been demonstrated in several animal learning experiments. For example, Colwill and Rescorla [as described in 89] showed that rats do not only learn S-R relationships, but their behavior is determined by the response reinforcer association by devaluation of one of two previously learned response-reinforcement associations.

> Rats were first separately reinforced with food pellets after performing R1 and with a sucrose solution after R2. Once instrumental training had occurred, one of the two reinforcers (outcomes/effects) was devalued by associating it with a mild nausea. Finally, the rats were given the choice between the two responses, but with all outcomes omitted. In this test-phase rats showed a clear suppression of performing the response the outcome of which had been devalued. Obviously, the rats had not only associated the two responses with a situation wherein these were reinforced (S-R1 and S-R2), but they had also learned which response leads to which outcome (R1-food pellets, R2-sucrose solution). [89]

That means, the rats' behavior is guided by the effect associated with the response. Response-effect predictions have been found in several experiments with humans as well [reviewed in detail in 91]. Furthermore, some of these experiments suggest that

the effects are in the form of covert perceptions as suggested by simulation theories [Kiesel & Hoffmann, 2004; Kunde, 2003 in 91].

Furthermore, the experiments performed by Libet could be taken to demonstrate that the initiation of a movement reaches our awareness 50-80msec before the movement has actually started [56], which lends further support to the existence of predictive action-effect associations. Since the movement has not begun, the awareness cannot be generated by proprioceptive or sensory feedback but must be generated by other means, i.e., a prediction/simulation. The similarity of perceptions and covert perceptions, discussed earlier, indirectly also suggests the existence of predictive mechanisms for sensory activity.

5.2   Neural Substrate of Environmental Predictions

The ability to predict sensory states that correspond to various external states is the final functional aspect of simulation to be addressed. The sensory predictions close the simulation loop such that agent-environment interactions can be rehearsed internally in various cognitive processes. They might provide the means to generate chained simulations at various levels of abstraction. However, we shall not discuss the process of abstraction per se here. There are at least three different neural circuits that could implement environmental predictions, the neocortex, thalamo-cortical loops and the hippocampus [13]. The focus here is on the neocortex, but as described in the last subsection there is a common mechanism for environmental predictions.

Neocortex. Possible routes for predictions of sensory or perceptual consequences are located throughout the neocortex. The hierarchical structure of the motor and sensory cortices and the reciprocal connections between them at various levels [3, 92, 93] suggest the possibility of the cortex implementing both predictions from motor to sensory activity and the reverse. Cotterill [2] argued that the premotor areas send information back to the sensory cortex by way of axon collaterals. He further noted that "there are three such efference copy routes…One goes directly, another passes through the anterior cingulate, and the third goes via the thalamic ILN" (p. 22). Efference copy routes might indeed be a ubiquitous property throughout the sensorimotor hierarchy [Hesslow, personal communication cf. 92]. Gomez et al. [94] have, based on their own experiments with the contingent negative variation and other corroborating studies, suggested that there exists an attentional-anticipatory system that "include[s] not only the frequently described prefrontal, SMA, and primary motor cortices, but posterior parietal cortex, cingular cortex, and pulvinar thalamic nuclei too. The neural substrate of the perceptual domain is not so well-described, but, of course, the participation of primary sensory areas has been hypothesized" (p.67). Gomez et al.'s studies do not, however, show decisively how the preparatory activity of the sensory cortex is elicited, i.e., directly via the sensory cues or indirectly by preparatory activity of the motor related cortices. The study by Kastner et al. [95] showed influence from frontal and parietal areas on extrastriate cortex during covert attention shifts, suggesting the possibility of motor areas modulating the activity of sensory areas in an anticipatory manner.

The existence of predictive loops in the neocortex is also supported by research on the mirror neuron system. Canonical neurons are neurons whose response properties are somewhat more specific to particular visual (interaction) properties of objects (action affordances) rather than the action-object conjunction typical of mirror neurons

(India Morrison, personal communication). Iacoboni [as described in 88] postulated that the mirror neuron related areas can implement predictions of the consequences of actions. This would involve projections from area F5 of the ventral premotor cortex, through area PF, and to STS, essentially "converting the motor plan back into a predicted visual representation (a sensory outcome of the action)". However, it should also be pointed out that Miall [88] argued similar transformations might be implemented by pathways incorporating the cerebellum. In line with the distinction between bodily and environmental anticipation, Miall pointed out that mirror neuron related activity reflects more general aspects of actions, whereas forward models in motor control would be more detailed, suggesting that prediction of sensory effects might take place at several different levels of abstraction. It should also be noted that although the emphasis has been on the generation of sensory activity by motor activity, several associations form between perceptual stimuli, which do not include a motor aspect [3]. In other words, covert perceptions may elicit other covert perceptions.

Another type of covert simulations implicating the neocortex are the as-if loops of Damasio [96, 97]. He argued that feelings can occur in the absence of their normal bodily causes, by short circuiting the body loop. Instead, the feelings are simulated in loops involving the prefrontal cortex and the somatosensory cortex. One advantage according to Damasio [96], is that the connection between the prefrontal cortex and the somatosensory cortex, especially the insula, are very short, which means that the signaling can occur in hundreds of milliseconds as opposed to the body loop that takes up to 1 second to complete due to the long, often unmyelinated, axons. In effect, the as-if feelings can be seen as predictions of "bodily feelings".

Declarative Prediction Networks and Simulation. Downing [13] suggested a common model for how the kinds of declarative predictions are learnt in cortical, thalamo-cortical, and hippocampal circuits, which he called the general declarative predictive network (GDPN). Although his focus was the association of consequent sensory states, the neurophysiology behind this type of association might also explain the predictive association between a motor representation and its sensory consequence (at some or several levels of the sensorimotor hierarchy, cf. [92]). The declarative prediction networks that Downing postulates provide an unsupervised learning scheme. This would work in the neocortex as described briefly in the following text. The neocortex is organized horizontally into layers, and vertically into groups of cells linked synaptically across the horizontal layers called cortical columns or microcolumns [98]. As described by Swanson [99], the neocortex consists of the same number of layers throughout, six layers in both humans and rats while phylogenetically older parts of the cerebral cortex, such as the hippocampus only have 3 layers. In humans, as in rats, the first (outer) layer of the neocortex consists mainly of wiring and has relatively few cell bodies, layer 2 and 3 typically contain small pyramidal neurons which project to other cortical regions in the same and different hemispheres respectively. Layer 4 consists mainly of granule cells which form local circuits, while layers 5 and 6 contain larger pyramidal neurons typically projecting to the brainstem, thalamus, and spinal cord, as well as to the motor system broadly defined. The precise makeup of these layers in terms of the density of cell bodies in each layer varies considerably in different regions of cortex. Even though their function is not agreed upon, it has been suggested that they are essentially predictive elements [13, 100]. In brief, Hawkins [100] explained it as follows:

Imagine you are a column of cells, and input form a lower region causes one of your layer 4 cells to fire. You are happy, and your layer 4 cell causes cells in layers 2 and 3, then 5 and the 6 also to fire. The entire column becomes active when driven from below. Your cells in layers 2, 3, and 4 each have thousands of synapses in layer 1. If some of these synapses are active when your layer 2, 4, and 5 cells fire, the synapses are strengthened. If this occurs often enough, these layer 1 synapses become strong enough to make the cells in layers 2, 3 and 5 fire even when a layer 4 cell hasn't fired[cf. [101]] - meaning parts of the column can become active without receiving input from a lower region of the cortex. [100]

Given that a large number of the connections onto a column come from other parts of the cortex, it is not to unlikely that some of the predictive associations are made between the motor areas of the cortex and sensory areas of the cortex via the different routes suggested above. Furthermore, as noted above it is possible that these associations form at different levels of the sensorimotor hierarchy. It is possible that the general declarative prediction network in the hippocampus is able to learn even more complex and abstracted sensory-motor and motor-sensory associations.

6   Discussion

In the introduction we argued that covert simulations might provide some answers to the human brain's solution to the general frame problem. One part of the answer lies in the way covert simulations are constructed to only focus on the relevant consequences of an action and are able to influence overt behavior in time. The neurochemical properties of the eligibility trace that closely matches the embodiment of the organism, or more specifically, time delays of the sensorimotor system ensure that the feedback signals that provide valuable information about the usefulness of an action is likely to be associated with the action that lead to the environmental state which the feedback is about. Furthermore, the learnt implicit predictions make the covert simulations effective by constraining the number of simulation paths that could otherwise be explored. At a higher level of abstraction, the general declarative prediction networks are biased toward only creating predictions that have been supported by environmental evidence to emerge. Covert simulations may then provide the kind of intrinsic representations thought to be necessary to be able to represent the world without describing everything about it [cf. 9]. The ability to focus on relevant consequences is, even though only briefly discussed in this paper, also crucially dependent on the existence of special brain circuitry for affect and emotion and their close relationship to action selection mechanisms and off-line simulations [e.g. 102] constitute mechanisms for connecting additional meaning to sensorimotor associations. The view of covert simulations as implicit, bodily, and environmental anticipations is to some extent already implemented in computational models [11, 103, 104], which is where the actual frame problems arise [9]. For example, Möller and Schenck [11] showed how covert simulations could support the understanding of space and shape in object recognition. However, it might be argued that these models are still too simple for frame problems to be an issue as it is often thought to be a problem of common sense reasoning in humans [cf. 9]. Future work aiming to

achieve more advanced forms of planning [cf. 60] may need to consider the implications of the frame problem in more depth and especially to what extent the neural mechanisms proposed in this paper are able to resolve the problems.

An important property of the neocortex that has largely been ignored in the paper, but may prove important to covert simulations is its hierarchical organization. Information flows up and down within the sensory and the motor hierarchies and not just between them, as emphasized above, which can explain several aspects of off-line simulations. This can perhaps provide useful insights about how covert simulations are established at different levels of abstraction [100]. Furthermore, it can explain why brain damage closer in the lower parts of the hierarchy, such as primary motor and sensory areas sometimes (although not always) leaves the capacity for mental imagery intact [44]. Farah [44] argued that can be explained by the hierarchical structure of the neocortex and considering mental imagery mainly as a top-down process.

> Assume the damaged parts are among those shared by imagery and perception, not purely perceptual afferents, and consider the impact of interrupting processing at this stage: When the flow of processing is bottom-up or afferent, as in perception, the impact will be large because the majority of visual representations cannot be accessed. In contrast, when the flow of processing is top down or efferent, as in imagery, the impact will be smaller because just a minority of the representations normally activated in imagery is unavailable. [44]

Similarly, but in the context of motor imagery, Jeannerod [4] speculated that lesions higher-up in the motor hierarchy, including the supplementary motor area (SMA) and premotor cortex, would cause more impairment to the imagery process. This is consistent with brain imaging experiments of motor imagery which do not always find activations of the primary motor cortex [105].

A final question to be addressed is the one posed by Downing [12]. He argued, on neuroscientific grounds, that declarative knowledge could not be created from procedural knowledge and asked how this distinction could be explained by simulation theories. Our answer is that the two types of knowledge complement each other in covert simulations via multiple neural simulation pathways. As discussed earlier, a typical example of a task that involves off-line simulations is motor imagery (MI). MI involves both procedural and declarative properties, according to both neural and psychological definitions. Procedurally, MI is associated with unconscious effects, such as increased respiratory and heart rates with increased imagined effort, and has been shown to activate the cerebellum, basal ganglia and primary motor cortex. Declaratively, MI is more or less defined as the conscious feeling of performing an action, and it involves higher motor areas, and perhaps also sensory areas [5]. This is not surprising as many real agent-environment interactions would involve both procedural and declarative elements. For example, Downing [12] argued that although each word or phrase of a song is stored in the cortex, the extraction of a particular word or phrase is "mediated by the preceding cortical context (declarative) and basal gangliar wiring (procedural)" (p. 97). In other words, you access the declarative structures, the words and phrases, by performing a skill, in this case singing. In accordance with simulation theories, the extraction can be made either by singing or by rehearsing it internally without producing any actual sounds. It would seem that simulation theories that aim to explain conceptualization based on the reactivation of sensorimotor structures [15, 106], would not have to cross the gap between the procedural and declarative

either. Simulations are in those theories thought to enact the concept, which could then consist of both declarative knowledge and procedural or skill-based knowledge.

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