Pathways of embodied simulation

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Introduction

Recently, so called simulation (or emulation) theories [e.g. 1 ch. 9, 2-5] have discovered and embraced, to a greater or lesser degree, the old empiricist and associationist idea that thinking is covert action and perception. In brief, *covert action* refers to the brain's ability to reactivate several of the neural processes and structures used to produce an overt action, but without any overt movements. Consequently, *covert perception* means reactivating several of the neural processes that create percepts without any external stimulation to the sense organs. Furthermore, chained covert actions and perceptions can be used to plan ahead, and as pointed out by [6], for example, this type of planning is biologically plausible since it reuses existing behavior generating structures [cf. 7].

Inspired by existing models of embodied simulation [2, 3, 6, 8], we identify the necessary components for the realization of extended and adaptive simulated chains of behavior, and identify possible biological mechanisms of embodied simulation, which include at least two types of prediction [9], to inform modeling approaches. The details of our own robotic experiments are omitted here, due to spatial restrictions, and left for the full paper.

Embodied simulation taken apart

Efforts have been made to model simulation theory using various types of computational models [e.g. 10, 11]. Although these models certainly provide important insights, they are often limited in that they only deal with a single aspect of simulation. We have to distinguish different pathways in which embodied simulations come about. By decomposing what the brain does when constructing embodied simulations in this way we hope to show the breadth of the simulation phenomena and what aspects need to be implemented in a full account of embodied simulation. The following discussion is divided into four parts based on a rough distinction between covert perception and covert action but also the predictive elements that elicit them: (1) Procedural prediction and action selection (2) Covert actions generate efference copy based predictions, (3) Covert perceptions elicited through declarative prediction, (4) Covert perceptions initiate action-selection.

Procedural prediction and action selection

For planning and thinking to be adaptive they typically need to be constrained to one or a few simulation paths. This is precisely the action-selection problem of any behaving animal [12]. Although many factors processed in different parts of the brain affect behavioral choices [7], basal-ganglia-cortex loops (including amygdala influence) [13] and cerebellum are crucial for well-functioning interaction. The basal ganglia can have a similar function guiding the direction of simulations by selecting some actions over others, but at the same time also preventing them from causing overt movements [2, 8]. Just as the basal ganglia supports action selection it can select the action content of our thoughts [12]. The neuron populations in prefrontal, premotor and motor cortex that are activated through the basal ganglia can then serve as the input to cortical mechanisms, which predict the sensory consequences of that action. Another aspect of basal ganglia mediated action selection is the influence of dopamine neurons which can be viewed as implementing predictions of future rewards [9, 14]. Re-using the mechanisms for action selection constrains simulations to those alternative action paths relevant for the simulated sensory situation. In some simulations, action selection might also involve the cerebellum, which is known to be able to implement procedural predictions in the form of S-R associations [9]. Brain imaging studies on motor imagery and problem solving do show cerebellar and basal ganglia activity [for references to individual experiments cf. 4].

According to Downing [9], cerebellum and basal ganglia implement procedural predictions, which means that the predictions are based on brain states that are only weakly correlated with events in the world, such that they will not give rise to conscious thoughts about these events. Thus, their opposite, declarative prediction, is conscious while procedural thoughts are not. However, imagining doing something also involves the conscious feelings of performing an action. This might not be due to the covert action output though but rather the afferent proprioceptive information [cf. discussion in 5] that is reactivated as a consequence of covert actions.

Covert actions generate efference copy based predictions

Simulation theory argues that the basic input to cognitive processing is intended but not executed actions. Intended, planned or executed actions are thought to be internally associated with their effects [e.g. 15, 16]. In mental simulations, covert actions [cf. 17] generate efference copies, which eventually result in predictions of the consequences of the actions [2]. Cotterill [2] distinguished three efference copy routes from the premotor cortex back to the sensory cortex: “One goes directly, another passes through the anterior cingulate, and the third goes via thalamic ILN” [2]. Efference copy routes might be a ubiquitous property throughout the sensorimotor hierarchy [Hesslow, personal communication cf. 18]. Related evidence of predicted effects comes from studies of animal learning, in particular reward devaluation, where goal-directed behavior is caused by associations between responses and their effects [19-21]. For example, Hoffmann [21] cited the study of Colwill and Rescorla (1985), which showed that devaluating one of the rewards of two previously learned response-reinforcement associations lead to a subsequent decrease in the associated response indicating that the rats’ behavior in this case was guided by the effect associated with a particular response.

Covert perceptions elicited through declarative prediction

The ability of animals to predict the effects of actions in a context was already addressed in a previous section, but the kinds of effects can vary. The predicted effect may be reward signals, proprioceptive signals, or exteroceptive signals [cf. 14, 19, 21]. There is much empirical work that suggests that reactivation of covert conscious perceptions is common in human cognition [17], but there are also animal learning studies that suggest that even rats are able to reactivate a perception based on earlier cues [20]. A further result that supports the prediction of perceptual and proprioceptive effects is the finding that the initiation of a movement reaches our awareness 50-80msec before the movement has actually started [16]. 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 simulation/prediction.

Among others, Downing [9] suggested that predictions of sensory contexts can occur through cortical columns, thalamocortical loops and the hippocampus. Similarly, Cotterill [2] suggested that the hippocampus is able to capture associations between motor and sensory areas of the brain.

There is also evidence that the predicted sensory effects can be generated by the body itself. It has been suggested that motor imagery activates the spinal cord and some of the organs of proprioception, muscle spindles [22].

Covert perceptions initiate action-selection

To guide behavior internal models need to be fairly accurate. There is ample evidence that covert perceptions are very similar to the perception they replace [17]. Indeed, they might be sufficiently similar to those sensory contexts that normally stimulates the action selection mechanisms of the basal ganglia and cerebellum [cf. 9] such that they initiate action selection. Several studies have indicated that imagination evokes similar experiences to actual object interaction [e.g 23] and are almost indistinguishable from the real perception [Perky, 1910 cited in 24, 25]. Furthermore, neuropsychological and neuroimaging studies have shown that visual mental imagery activates many of the areas thought to be responsible for visual perception [17].

Final remarks

This abstract has briefly outlined different pathways of embodied simulations and empirical results supporting these. It has also pointed to the existence of both declarative and procedural prediction in embodied simulations. Procedural predictions are common in the action-selection part of simulations, while declarative prediction is ubiquitous in reactivations of covert perceptions. The remainder of the full paper will detail robotic experiments using neurocomputational models of simulation theory and relate these models to neurophysiological evidence.

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