Available online at www.sciencedirect.com

SciVerse ScienceDirect

ELSEVIER

Current Opinion in Neurobiology

Insights from the application of computational neuroimaging to social neuroscience

Simon Dunne and John P O'Doherty

A recent approach in social neuroscience has been the application of formal computational models for a particular social-cognitive process to neuroimaging data. Here we review preliminary findings from this nascent subfield, focusing on observational learning and strategic interactions. We present evidence consistent with the existence of three distinct learning systems that may contribute to social cognition: an observational-reward-learning system involved in updating expectations of future reward based on observing rewards obtained by others, an action-observational learning system involved in learning about the action tendencies of others, and a third system engaged when it is necessary to learn about the hidden mental-states or traits of another. These three systems appear to map onto distinct neuroanatomical substrates, and depend on unique computational signals.

Address
California Institute of Technology, Pasadena, CA 91125, USA

Corresponding author: O'Doherty, John P (jdoherty@caltech.edu)

Current Opinion in Neurobiology 2013, **23**:387–392

This review comes from a themed issue on **Social and emotional neuroscience**

Edited by **Ralph Adolphs** and **David Anderson**

For a complete overview see the Issue and the Editorial

Available online 18th March 2013

http://dx.doi.org/10.1016/j.conb.2013.02.007

Introduction

Since the emergence of functional neuroimaging, a considerable body of literature has implicated a set of brain regions in the processes underlying human social cognition, including the posterior superior temporal sulcus (pSTS) and adjacent temporoparietal junction (TPJ), the amygdala, temporal poles, and medial prefrontal cortex (mPFC) [1–4].

The past decade has also seen the application within cognitive and systems neuroscience of a method that has come to be known as computational or model-based neuroimaging [5]. This approach involves correlating the variables generated by a formal computational model describing a particular cognitive process against neuroimaging and behavioral data generated by participants performing a related cognitive task. This technique offers the prospect of identifying not only those brain regions that are activated during a given task, as in traditional approaches, but also provides insight into 'how' a particular cognitive operation is implemented in a given brain area in terms of the underlying computational processes.

The computational approach to neuroimaging was brought to bear initially on the domains of value-based learning and decision-making in nonsocial situations, as a means of gaining insight into the computations performed by different brain regions in learning to predict rewarding and punishing outcomes and in using those predictions to guide action selection [6–11]. Some of the key findings from this work include the determination that BOLD responses in the human striatum resemble a reward prediction error signal that can be used to incrementally update predictions of future reward [6,7,12], while activity in ventromedial prefrontal cortex (vmPFC) correlates with expectations of future reward for actions or options that are chosen on a particular trial [13,14•,15].

More recently, tentative steps have been taken to extend this approach into the social domain [16,17]. The main objective in doing so has been to gain insight into the nature of the computations being implemented in the brain during social cognition, and in particular to put computational flesh on the bones of the psychological functions previously attributed to different brain regions within the social cognition network. In this review, we highlight two main research questions that have been pursued to date: the neural computations underpinning observational learning, and the neural computations underpinning the ability to make predictions about the intentions of others.

Observational learning

In experiential learning an agent learns about the world through direct experience with stimuli in the world and/or by taking actions in that environment and reaping the consequences. In observational learning, an agent learns not through direct experience but instead by observing the stimuli and consequences experienced by another agent, as well as by observing the actions the observed agent performs in that environment. Observational learning can clearly be advantageous as it allows an individual to ascertain whether particular stimuli or actions lead to rewarding or punishing consequences without expending resources foraging or being exposed directly to potential threats.

Preliminary findings suggest that similar computational mechanisms may underpin both experiential and observational learning. More specifically, studies have reported neural correlates of reward prediction error signals in the striatum [18•,19,20•] and vmPFC [18•] while subjects learn by observing confederates receive reward feedback in probabilistic reward learning tasks. Importantly, these signals reflect the deviation of a reward from the amount expected given previous play, despite the fact that the subject merely observes the receipt of this reward by the confederate.

Although the outcomes obtained by another individual represent a valuable source of information for an observer, the mere choice of action made by an observee may also influence the vicarious acquisition of instrumental responses. These observed actions may be relevant because they are often motivated by similar preferences for outcome states and may therefore represent an additional source of information regarding the optimality of available actions [18•], or, relatedly, because reward may be directly contingent on successful mimicry of the actions of another agent with differing preferences over those states [20•]. Action prediction error signals, representing deviations by an observed confederate from the actions expected of them by the subject, may be used to update the subject's own behavior in computational models of learning, and have been reported in dorsolateral prefrontal cortex (dlPFC) [18•,20•], dorsomedial prefrontal cortex (dmPFC) [20•], and bilateral inferior parietal lobule [20•]; a collection of areas that exhibit significant interconnectivity (see [21,22]) The involvement of dlPFC in such learning is consistent with evidence from electrophysiological and neuroimaging studies that this area is involved in the representation of task-relevant contingencies and goals [23] and the manipulation of task-relevant information in working memory [24,25]. Given that posterior parietal cortex has also previously been implicated in attention [26–28], one possibility is that this region contributes to learning through the allocation of attention engendered by surprising or unexpected actions, compatible with some computational accounts in which attention is suggested to modulate learning [29].

Strategic learning

The studies mentioned thus far have examined how information acquired about the experiences and actions of other individuals can be incorporated into representations used to guide one's own behavior. However, as social animals we are often engaged in situations where we need to interact with other individuals in order to attain our goals, whether it is by co-operating or by competing with them. In order to succeed in such situations it is often necessary to be able to understand their intentions, and to use this knowledge to guide action selection. At the core of this capacity is the psychological construct known as mentalizing, in which representations are formed about the hidden mental states and intentions of another.

Such mentalizing processes can vary in their complexity. Behrens *et al.* [10] examined a situation in which, in contrast to the studies of Burke *et al.* [18], and Suzuki *et al.* [20•], information from a confederate regarding the optimal action to take varied in its reliability, because the confederate's interests sometimes lay in [29] deceiving the subject. In order to perform well in this type of task, it is prudent to maintain an estimate of the confederate's fidelity, to be used to modulate the influence of their advice. Neural activity corresponding to an update signal for such an estimate was found in anterior mPFC, as well as in a region of temporoparietal junction.

Hampton *et al.* [16] studied a paradigm (Figure 1a) in which two human subjects played in a variant of the competitive economic game matching pennies. In this coordination game, players choose between two actions on each round, with one player winning if the two chosen actions are the same, and the other if they are different. Such a game takes on interesting dynamics with repeated play, as players typically vie to predict their opponent's next choice of action while masking their own intentions, providing the potential for the engagement of complex mentalizing processes. To capture the learning processes underlying action selection in this context, Hampton *et al.* [16] modified an algorithm called 'fictive play', drawn from the game theoretic literature [30–32]. An agent using a fictive play algorithm iteratively updates the probability that their opponent will choose a particular action based on previous choices of action. There is some evidence that, when engaged in competitive economic games against computer opponents, nonhuman primates may be capable of incorporating fictitious play into their action selection, as well as more simple strategies such as Win-Stay Lose-Switch and simple reinforcement learning [33–35], However, using even fictitious play ignores the danger that ones opponent is likely to be similarly adept in tracking ones own behavior. Hampton *et al.* [16] therefore extended the fictive learning algorithm to incorporate the effect an opponent's predictions of ones own actions has on their action selection, endowing the agent with a 'secondorder' mental state representation [3,36]. Hampton *et al.* [16] found that activity in vmPFC encoding the expected value of chosen actions incorporated this second-order knowledge, while activity in pSTS and anterior dorsomedial frontal cortex correlated with a learning signal that could be used to update the second-order component of this representation (Figure 1b).

The types of learning and inference described above involve first-order and second-order strategic reasoning, but in principle one could engage in increasing orders of iterative reasoning: thinking about you thinking about me thinking you and so on. Ideally, an agent should tailor the