

Social learning in the medial prefrontal cortex

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The functions of the medial prefrontal cortex (mPFC) and particularly the Anterior Cingulate Cortex (ACC) are some of the most controversial and extensively investigated topics in cognitive neuroscience. Over the last three decades there has been considerable debate, and multiple theoretical accounts of the contribution of the mPFC to cognition, based largely on studies examining the sulcus of the ACC (ACCs) and adjacent dorsal regions [1]. Much of this evidence converges on the notion that the ACCs signals information in a manner consistent with the principles of Reinforcement Learning Theory (RLT). That is, it computes predictions about the value of a behaviour, and when outcomes are discrepant from expectations, the ACC codes the magnitude of the difference – a prediction error (PE). Such PEs drive learning and optimise future decision-making.

In contrast to the ACCs, there has been a notable absence of theoretical or empirical examination of the adjacent portion of the ACC lying in the gyrus (ACCg; area 24a/b[2]). What limited evidence there is points to this region playing a vital role in social cognition[3]. Recent theoretical accounts have posited that the computational properties of the ACCg may also conform to the principles of RLT [3,4]. However, rather than coding expectations and PEs about one's own decisions, neurons in this region code such information for *other people's* decisions. Such computational and functional properties would place the ACCg as a core region that guides 'social' learning (i.e. learning about the behaviour of others). But, such theoretical accounts come with an important caveat: only one previous study had recorded extensively from cells in the ACCg and this study did not examine PE coding[5].

Hill and colleagues' (2016)[6] new study is the first to provide evidence that neurons in the ACCg signal PEs when monitoring others' outcomes. They implanted electrodes in 10 *human* patients about to undergo surgery for epilepsy. Subjects performed a RLT based task, in which they had to learn to choose which of two stimuli had a higher probability of a positive outcome (obtaining a reward or avoiding a loss). On some trials they learnt from the outcomes of their decisions (Self), but on other trials they were able to observe the decisions and outcomes of two other players (Observed). Hill and colleagues

aimed to record from the orbitofrontal cortex (OFC), amygdala and a portion of the cingulate cortex at the border of regions often referred to - and also by the Hill and colleagues - as dorsal and rostral ACC. However, closer inspection shows that in some subjects, electrodes recorded from cells in the ACCg, and in some from the ACCs (**Fig.1**). Although the original aim of the study was not to distinguish these regions, broadly speaking, they found that activity in ACCg neurons correlated with both the expected outcome and actual outcome of trials - the key elements of RLT - but only when monitoring the behaviour of another person. Such a finding would point to the ACCg signalling PEs when monitoring others' behaviour. Interestingly, such a profile was not present in neurons in the Amygdala, OFC or ACCs. The ACCg therefore has functional properties when interacting with others that are distinct from other regions, and such a profile of response fits with claims that it signals information key to social learning.

The role of mPFC sub-regions in social cognition are under considerable debate. However, understanding how different regions contribute fundamentally relies on accurate anatomical localisation[7]. Regions within the mPFC - all often labelled as ACC - in fact refer to a number of different zones (**Fig.1**) that each have distinct cytoarchitecture and connectivity [2,3,8]. By demonstrating the relative specialisation of the ACCg, Hill and colleagues results closely align with two important claims about the mPFC. First, it is often argued that anatomy and function change along both rostro-caudal and dorsal-ventral axes in the mPFC[2,8,9] and second, it has been claimed that the specific connections of this region make it ideally placed to process information that guides social learning [3,8]. The ACCg may therefore have the anatomical fingerprint supporting a role in signalling information that allows people to learn about the consequences of others' actions. Functional evidence also supports such a claim. Lesions to the ACC impair social behaviour, but spare other cognitive processes [3], and both neurophysiology and neuroimaging studies suggest this region preferentially codes outcomes obtained by others but not one's own [4, 5]. Taken together, these results would suggest that a large proportion of neurons in the ACCg signal information in an allocentric frame of reference, signalling the consequences of actions of - or for - others, rather than egocentrically about the outcomes of one's own actions or decisions.

Notably, this may be in sharp contrast with signals that have been recorded in more dorsal regions of the mPFC (ACCs, 8m, 9m)[7], as well as in parts of the amygdala and orbitofrontal cortex [6], areas that are often strongly implicated in social cognition[7]. In these regions a large proportion of neurons signal information and PEs, in solely egocentric, or in both egocentric and allocentric reference frames. This would suggest that the contribution of other mPFC sub-regions may be to integrate self and other information in order to update our own behaviour. As such signals in other mPFC sub-regions are distinguishable from those in the ACCg by not operating in a similar allocentric reference frame of [3,5]. This finding may therefore be vital for understanding disorders of social cognition, and how regions that typically operate in different reference frames may not show such a profile in disorders of social cognition. Indeed, there is evidence emerging that allocentric PE deficits in the ACCg are linked to social cognition problems in individuals on the autistic spectrum[10].

By highlighting allocentric coding in the ACCg, but the absence of such a coding scheme in other areas, Hill and colleagues highlights that using the analogy of “reference frames” can be fruitful for understanding social cognition. Whilst “reference frames” have typically been used to characterise functions within sensory motor systems (e.g hand-centred or eye-centred), such an approach can be used to dissect the relative contributions of areas of the brain for social cognition[5]. Although not necessarily the original aim of Hill and colleagues, their research directly links to growing evidence of a specialisation for processing social information in the ACCg. Their unique sample has therefore provided a timely and clear demonstration of the role that key allocentrically framed computations have in guiding typical social learning and cognition. Moreover they link with other work in primates and neuroimaging research in humans which point to the relatively unique nature of social signals in the ACCg, and the role that allocentric PE deficits may have in disorders of social cognition.

Figure legend

Fig.1. Location of the Amygdala and subdivisions of the medial wall. Hill et al. recorded from the Amygdala (Amy, yellow), anterior cingulate gyrus (ACG, orange), the OFC (light green) and in a small number of patients in the ACCs (dark blue). Neurons in the ACG were differentiated from others in signalling an observational learning specific prediction error. This region is a distinct anatomical location from others in the midcingulate sulcus (MCCs, black), ACCs as well as other regions in the dorsal (areas 8, light blue; and 9, darkgreen) medial prefrontal cortex and frontal pole (area 10, red). These regions have both distinct cytoarchitecture and connectivity [see 8], leading to the unique roles these region may have in social cognition, with the ACCg have a particularly important role in social learning. The masks displayed are thresholded clusters taken from the resting-state connectivity based parcellation by Neubert et al., (2015) [8], except for the ACCg (unthresholded cluster).

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