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### The anterior cingulate cortex: Monitoring the outcomes of others' decisions

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# The anterior cingulate cortex: Monitoring the outcomes of others' decisions

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The ability to attribute mental states to others and understand the basis of their decisions is essential for human social interaction. A controversial theory states that this is achieved by simulating another's information processing in one's own neural circuits. The anterior cingulate cortex (ACC) is known to play an important role in the registration of discrepancies between the predicted and actual outcomes of decisions (prediction errors). When positive and negative feedback fails altogether, the failure may also signal errors in the prediction that the outcome of that decision would be informative and guide future decisions. Does the ACC signal that an outcome is unexpectedly uninformative? When an outcome directed to others is uninformative, do we understand their mental states by simulating them in the circuits of the ACC in our own brain? The aim of our study was to test for these two possibilities in the human brain with event-related fMRI. We tested whether the ACC processes errors in the prediction of informative feedback and whether the ACC is also activated when scanned subjects process the same outcomes of another's decisions. We show that each is processed by a separate subregion of the ACC.

**Keywords:** Social; Decision-making; Cingulate; fMRI; Error.

Successful interactions in highly complex social environments require that people accurately “mentalize” (C. D. Frith & Frith, 1999) (i.e., represent the intentions, desires, and beliefs of others). Previous neuroimaging work has implicated three interconnected cortical areas that are activated if human subjects process information related to the mental states of others. These comprise the paracingulate cortex (Amodio & Frith, 2006) (occupying a medial portion of the prefrontal cortex), posterior regions of the superior temporal sulcus (pSTS), and the temporal poles (TP) (C. D. Frith & Frith, 2006; U. Frith & Frith, 2003). This network is recruited by a diverse range of cognitive processes that require subjects to mentalize. For example, studies have found activation in these areas when subjects are thinking about the content of others' mental states in stories (Saxe & Kanwisher, 2003;

Saxe & Powell, 2006), when cooperating or competing with others in interactive games (Rilling et al., 2008, 2002; Singer et al., 2004), or even when attributing mental states to inanimate shapes (Castelli, Happe, Frith, & Frith, 2000). However, it has recently been shown that the ability to interact successfully with others also depends upon the integrity of additional areas that exchange information with this network (Behrens, Hunt, & Rushworth, 2009; Rilling et al., 2008).

Areas within the primate anterior cingulate cortex (ACC) might also play a role in processing socially relevant information. In animals, lesions of the ACC result in decreased levels of social interaction (Hadland, Rushworth, Gaffan, & Passingham, 2003; Rudebeck, Bannerman, & Rushworth, 2008) and decreased preference for social stimuli. (Rudebeck et al., 2008; Rudebeck, Buckley,

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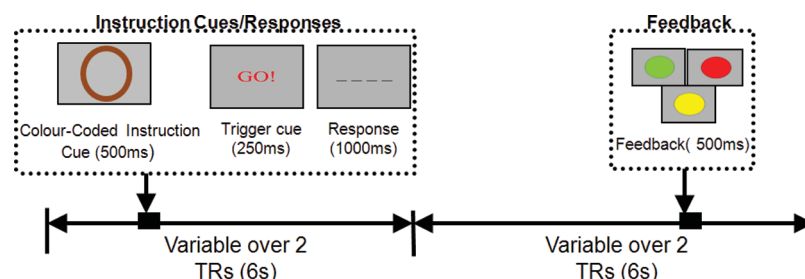
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Walton, & Rushworth, 2006). Similarly, fMRI studies in humans show ACC activity when subjects evaluate decisions in a social context (Behrens, Hunt, Woolrich, & Rushworth, 2008; Hampton, Bossaerts, & O'Doherty, 2008). The ACC is well known for its role not only in coding social information, but also in the processing of information that guides our decisions (Rushworth, Behrens, Rudebeck, & Walton, 2007; Walton & Mars, 2007). Single-unit recording studies in non-human primates have shown that neurons in the ACC are engaged by a range of variables such as reward probability, reward magnitude, and effort, which are used to optimize decision-making (Hayden & Platt, 2010; Kennerley, Dahmubed, Lara, & Wallis, 2009; Kennerley & Wallis, 2009). Interestingly, recent evidence suggests that the ACC processes these variables in the manner predicted by reinforcement learning theory (Rushworth & Behrens, 2008), in which subjects learn to minimize the discrepancies between expected and actual outcomes (Daw & Doya, 2006). Cells in the ACC have been shown to respond to errors in the prediction of positive and negative outcomes (Matsumoto, Matsumoto, Abe, & Tanaka, 2007). During trial-and-error learning, all outcomes, whether positive or negative, serve to bring subjects closer to the overarching goal of optimal decision-making. Subjects therefore attach value to the receipt of feedback per se, regardless of its valence. Thus, trial-and-error learning schedules cause subjects to generate specific predictions not only about informative outcomes (positive and negative feedback), but also more generally about whether such informative outcomes will occur at all. An important aim of our study was to investigate ACC responses to informative and uninformative outcomes when they relate to the decisions of others.

It has been suggested that understanding others' decision-making may be achieved through simulation: the engagement of neural processes that one uses for one's own decision-making for the purposes of

making inferences about the same decisions in others (Gallese & Goldman, 1998). Interestingly, a large body of research has shown that understanding the actions of others may rely on a process of embodied simulation (Gallese, 2007; Reithler, van Mier, Peters, & Goebel, 2007; Schubotz, 2007; Schubotz & von Cramon, 2009). However, very few experiments have investigated whether we understand others' decision-making by simulating their information processing in the circuits we use to process our own decision-making. If understanding the basis of others' decisions occurs through simulation, this raises the possibility that the same areas of the ACC may be used to process errors in one's own or another's prediction of receiving informative feedback. The purpose of our study was to test this hypothesis. We scanned subjects while they learned the arbitrary relationships between a set of visual instruction cues and a range of responses through trial and error (see Figure 1), and while they observed a third-person similarly learning a different set of associations. There were three forms of outcome: A green dot was presented to indicate a correct response, a red dot for an incorrect response, and—critically in our experiment—a yellow dot to denote the absence of an informative outcome. This ambiguous outcome unexpectedly failed to reinforce the chosen response either positively or negatively. It therefore signaled an error in the prediction that the informative feedback would be delivered. The first-person (the scanned subject) was also able to monitor the performance of a third-person training partner (a confederate) and a non-agent computer (control) in real time, while they also learned a different set of associations in exactly the same circumstances. Our design enabled us to time-lock activity specifically to outcome events, and therefore test the hypotheses that (1) the ACC responds to uninformative outcomes, and (2) the same areas of the ACC respond to uninformative outcomes directed not only to the first-person, but also to the third-person.



**Figure 1.** Conditional motor learning trial structure and event-timings. Each trial consisted of an arbitrary instruction cue (an arbitrary shape, instructing a response), a trigger cue (cueing a response), a response cue (identifying the response made), and outcomes (either correct, incorrect, or ambiguous (uninformative)). The uninformative outcomes were fixed to occur on one-third of trials. The instruction cue and response period were separated from the feedback period by a variable delay. As a result, activity time-locked to the outcome stimuli was temporally uncorrelated with any other trial elements.

METHODS

Subjects

Subjects were 12, healthy (eight female, mean age 21 years), right-handed, undergraduate volunteers from Royal Holloway, University of London. All subjects gave written, informed consent. The study was approved by the Royal Holloway, University of London, Psychology Department ethics committee, and the study conformed to regulations set out in the CUBIC MRI Rules of Operations ([www.pc.rhul.ac.uk/sites/cubic/](http://www.pc.rhul.ac.uk/sites/cubic/)).










Apparatus

Subjects lay supine in an MRI scanner with the fingers of the right hand positioned on a four-button, MRI-compatible response box. Stimuli were projected onto a screen behind the subject and viewed via a mirror positioned above the subject's face. Presentation software (NeurobehavioralSystems, Inc., USA; <http://www.neurobs.com/>) was used for experimental control (stimulus presentation and response acquisition). A custom-built, parallel port interface connected to the Presentation PC received transistor-transistor logic (TTL) pulse inputs from the response keypad. It also received TTL pulses from the MRI scanner at the onset of each volume acquisition, allowing events in the experiment to become precisely synchronized with the onset of each scan. The timings of all events in the experiment were sampled precisely, continuously, and simultaneously (independently of Presentation software) at a frequency of 1 kHz, using an A/D 1401 unit (Cambridge Electronic Design, UK; <http://www.ced.co.uk>). Spike2 software was used to

create a temporal record of these events. Event timings were prepared for subsequent general linear model (GLM) analysis of fMRI data (see below).

Experimental design

We used a  $2 \times 3$  factorial design (see Figure 2) to examine the role of the ACC in processing outcomes which fail to reinforce a choice, either positively or negatively and also test whether the ACC processes the same outcomes of another's decisions. The first factor manipulated was Feedback, which could be either informative (a correct outcome) or uninformative (an ambiguous outcome). Correct outcomes were highly informative and thus did not signal an error in the prediction of the receipt of informative outcomes. Conversely, ambiguous outcomes conveyed no information about whether the response made was correct or not and thus signaled an error in the subjects' prediction of receiving useful information. Thus, we were able to examine activity occurring after an outcome event that signaled a prediction error for the receipt of informative feedback. It should be noted that correct outcomes are not uniformly informative during the experiment; that is, the first correct outcome for a stimulus is highly informative, with each subsequent correct outcome for that stimulus being less informative. However, each correct outcome is itself still always informative, regardless of the extent to which it provides new information. As informative outcomes (both correct and incorrect) occurred on the majority of trials, subjects would have predicted that the outcome of each trial would be informative. Thus, while the informative nature of correct outcomes was not stable over trials, each individual correct outcome always signalled that a prediction of receiving an informative

		Uninformative	Informative
First-person			
Third-person			
Computer			

**Figure 2.** Experimental design. A  $2 \times 3$  factorial design was employed. One factor manipulated Agency, i.e., which agent should respond on each trial. The instruction cues were color-coded, such that the first-person responded to the brown cues, the third-person to the purple cues, and the computer to black cues. The scanned subject was therefore able to determine which agent was responding to each trial and to which agent the outcome belonged. The second factor was Feedback. An outcome of a decision could be either informative (green, correct outcomes) or uninformative (yellow; ambiguous outcomes). To test the hypothesis that the ACC would respond when the first-person's prediction of informative feedback was erroneous, we looked for interactions between Feedback and Agency (first-person  $\times$  computer). To test the simulation hypothesis, that the same area of the ACC would respond to the third-person's neutral outcomes, we looked for interactions between Feedback (informative vs. uninformative) and Agency (third-person vs. computer). To determine whether an effect was exclusive to the third-person, we exclusively masked out the effects of Feedback (informative vs. uninformative) in the first-person.

outcome was correct. Ambiguous outcomes therefore always signalled that a prediction of an informative outcome was erroneous.

The second factor manipulated was the Agency of the respondent. On each trial, either the subject inside the scanner responded (first-person), a confederate outside the scanner responded (third-person), or a computer responded. Therefore, the outcome of each trial corresponded only to the decisions made by one of these agents. Potential attentional confounds were controlled for in two ways. First, to ensure that subjects were monitoring the outcomes of all agents' decisions, subjects were informed that, after the experiment, they would have to verbally report the associations that were correctly made by each agent and also the number of trials that were missed by each agent. Thus, subjects were required to attend to all elements of every trial. Second, since attention is directed externally when monitoring another's decisions and internally when monitoring one's own decisions, a control condition was needed in which attention to the same contingencies was directed externally to a non-human rather than a human agent. Both the third-person's and the computer's outcomes required attention to be directed externally; however, only the third-persons' outcomes corresponded to another biological agent's decisions.

Subjects were familiarized with all aspects of the task, by being pre-trained together with their partner (a confederate) in front of a computer screen one day prior to a scanning session. Immediately prior to the scanning session, subjects observed their partner seated in the control room in front of a computer screen, with a response box. They were informed that their partner would perform trials in the same manner as during the training session outside the scanner. They themselves were able to see all the trial elements displayed to their partner, on a screen inside the scanner.

We looked for interactions between Feedback and different levels of Agency to examine whether the same region within the ACC responded to the ambiguous outcomes of each agent's decisions. We looked for an interaction between Feedback (informative vs. uninformative) and two levels of Agency (first-person vs. computer) masked exclusively by the interaction between Feedback and external Agency (third-person vs. computer) to identify regions which showed an effect exclusive to the first-person. To find effects exclusive to the third-person, we looked for an interaction between Feedback (informative vs. uninformative) and two levels of external Agency (third-person vs. computer) masked exclusively by the interaction between Feedback and Agency (first-person vs. computer). By using interactions between first-person and computer and third-person and computer, masked by interactions between the

other conditions, we were able to examine the specific effects of third-person uninformative and computer uninformative feedback. It is important to note that we did not include the negative outcomes in our contrasts. There is a large body of evidence implicating the ACC in signaling whenever an action is erroneous (Amiez, Joseph, & Procyk, 2005; Frank, Woroch, & Curran, 2005; Holroyd et al., 2004). Thus, activity would be expected in the ACC on all the negative trials in this experiment, as they constituted an error (Bush, Luu, & Posner, 2000; Carter et al., 1998). We therefore did not include negative outcomes in order to avoid their potentially confounding effects.

## Trial structure

In this experiment, subjects made decisions within a conditional motor learning framework. This paradigm has been used extensively to investigate decision-making processes and their neural basis in both humans and non-human primates (Wise & Murray, 2000). In a typical conditional motor learning experiment, subjects are required to learn associations between instructions and actions through trial and error. Importantly, there is no information inherent within the cues that can be used to guide decisions. In this experiment, each trial (see Figure 1) consisted of an instruction cue (a colored shape, 500 ms), indicating that a response should be prepared; a trigger cue (four horizontal lines, 200 ms), indicating that a response should be made on one of the four buttons on the keypad; a response cue (an asterisk appearing above one of the horizontal lines, 1000 ms), indicating which button had been pressed; and delayed outcomes (correct, incorrect or ambiguous, 500 ms). For the feedback, a green dot indicated a correct response, a red dot indicated an incorrect response, and, crucially in this experiment, a yellow dot was ambiguous as to whether the response was correct or incorrect. The ambiguous outcomes were fixed to occur on one-third (20) of each agents' trials. To indicate which agent should respond on each trial, the instruction cues were color-coded, such that the scanned subject responded to brown cues, the partner responded to purple cues, and the computer responded to black cues. Trials were pseudo-randomly ordered (i.e., the same random order used for each subject) and were only valid if subjects responded less than 1000 ms after trigger cue onset.

## Training

During the training session, each subject was paired with another (a confederate). Subjects sat in pairs, in front of a computer screen and performed conditional



motor learning trials, using separate response keypads. Subjects were required to learn associations, by trial and error, between a set of six instruction shapes and four responses (indicated by pressing one of the four buttons with the four fingers of the right hand). Subjects were also required to monitor the instructions, responses, and outcomes of the training partner and of a computer. Each of these agents also learned different sets of paired associations between six instruction cues and four responses. This training phase enabled subjects to familiarize themselves with conditional motor learning trials and also to understand the decision-making processes of their partners.

## Scanning

In the scanning session, each of the agents continued to perform conditional motor learning trials, and each learned new sets of associations between eight shapes and one of four button presses. These were separated into two learning sets in which each agent was presented with one of four instructions cues (the second set was introduced halfway through the scanning session, at which point none of the first set of instruction cues were presented again). The use of learning sets was introduced, following the behavioral pilot, so that behavioral performance resulted in the number of presentations of each outcome type being comparable across subjects. Each instruction cue was presented five times. Before subjects entered the scanner, they observed their training partner seated in the scanner control room in front of a monitor with a response box, ready to perform the task in the same manner as during the training sessions. During the experimental task, the instruction cues, responses, and outcomes of each agent were relayed in real time to the subject inside the scanner. Thus, subjects were able to monitor all elements of the decision-making trials being performed by the third-person and the computer, as in the training session. However, in order to maintain experimental control, both the responses by the third-person and the computer were actually computer generated. The simulated behavior of both the computer and the third-person—that is, the choices made and reaction times of responses—was based on the behavior of subjects in a separate pilot experiment. Thus, during scanning, the behavior exhibited by the third-person and the computer was the same as that of human subjects. During the debriefing, subjects were asked a set of standardized questions relating to their belief that the responses they observed were of their partner outside the scanner. Subjects would have been excluded if they had not maintained the belief that a training

partner was responding in the control room and if they had guessed that the training partner was a confederate. The responses of all subjects during this interview indicated that they had all clearly maintained the belief that their partner was performing the task with them from inside the control room.

## Experimental timings

An important feature of the study was the ability to time-lock activity specifically to the outcome events. A variable delay was introduced between the response cues and the outcomes, such that BOLD activity was sampled without the contaminating effects of other trial elements, as in previous studies (Balsters & Ramnani, 2008; Ramnani & Miall, 2003, 2004). Event timings were as shown in Figure 1. Events in each trial took place across four scan repetition times (TRs) (0–12 s, TR = 3 s). To optimally sample evoked hemodynamic responses (EHRs) time-locked to our stimulus events, we introduced a uniformly distributed random interval (0–6 s) between the scan onset and the onset of the instruction and outcome stimuli. Hence EHRs time-locked to outcome stimuli were sampled at a finer resolution than one TR (3 s). The instruction cues, trigger cues, and motor responses all occurred within the first two TRs (0–6 s), and outcome presentation was varied over the third and fourth TR (6–12 s).

## Image acquisition

For each subject, 785 T2\* weighted echoplanar (EPI) images were acquired with a 3 Tesla Siemens Trio Magnetic Resonance Imaging scanner (Royal Holloway University of London). The field of view covered the whole brain (36 slices; field of view = 192 × 192 mm; voxel size = 3 × 3 × 3 mm; image matrix = 64 × 64 mm TR = 3 s; TE = 32 ms; flip angle = 90°). Prior to the functional scans, high-resolution, T1-weighted structural images were acquired at a resolution of 1 × 1 × 1 mm, using an MPAGE sequence.

## Image analysis

All preprocessing and statistical analyses were conducted in SPM5 ([www.fil.ion.ucl.ac.uk/spm](http://www.fil.ion.ucl.ac.uk/spm)) and Matlab (Mathworks, Version 2007a; <http://www.mathworks.co.uk>). Scans were spatially realigned to first image of the EPI sequence, and normalized to the ICBM template, using both linear affine transformation and nonlinear transformation.

The functional images were then spatially smoothed, using a Gaussian kernel of 8 mm, in order to conform to the Gaussian assumption of GLM analysis (Friston et al., 1995).

## Statistical analysis

### *First level*

Previous research has shown that the BOLD response does not conform to a canonical time course across the whole cortex, including the ACC (Handwerker, Ollinger, & D'Esposito, 2004; R. Henson & Rugg, 2001; R. N. A. Henson, Price, Rugg, Turner, & Friston, 2002; Lau, Rogers, & Passingham, 2006). As in previous studies, (Balsters & Ramnani, 2008; Lau et al., 2006; Ramnani & Miall, 2003, 2004), our aim was to flexibly model the hemodynamic responses time-locked to events without making stringent assumptions about the form and time course of the BOLD response. We achieved this by convolving our event-onset delta functions with a Fourier basis set of five harmonic functions (two sine, two cosine, and one Hanning window, 32 s). Activity time-locked to instruction cues, imperative trigger cues, and motor responses were modeled as a single compound event type since we did not need to distinguish between these. Our model therefore contained regressors that explained the following event types: instruction cues (collapsed across agents), correct outcome (x 3, one for each agent), incorrect outcome (x 3, one for each agent), ambiguous outcome (x 3, one for each agent), and missed trials (x 3, one for each agent).

Since each of these was convolved with 5 Fourier components, there were 65 event-related regressors in the GLM. Six head motion parameters (three translations and three rotations), estimated during realignment, were incorporated as confounding regressors. Prior to data acquisition, the degree of rank deficiency of this design was assessed by examining the correlations among all regressors, and it was found to be very low.

### *Second level*

The second-level analysis strategy followed that used by Balsters and Ramnani (2008). SPM{t} contrast images from the first-level analyses, one corresponding to each basis function, for each condition, for each subject, were incorporated into a second-level, random-effects ANOVA. F-contrasts were applied at the second level to look for interactions between Conflict and Agency. The resulting SPM{F} maps

identified voxels in which a linear combination of the five basis functions resulted in estimated responses that were significantly different across conditions at the group level. Results were corrected for multiple comparisons by small volume correction for the volume of the ACC (see "Localization" below).

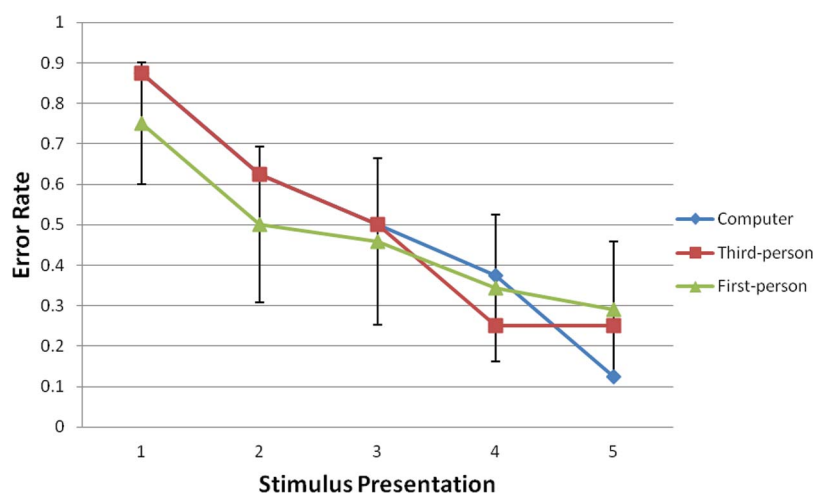
## Anatomical localization

A maximum probability mask of the ACC was constructed from the subjects scanned in this study. To create the mask, we used the anatomical boundary of the posterior midcingulate cortex according to the cytoarchitecture of Vogt and colleagues (Palomero-Gallagher, Mohlberg, Zilles, & Vogt, 2008; Vogt, Nimchinsky, Vogt, & Hof, 1995). The masks covered any region of the ACC anterior of a line vertical to the anterior commissure. To create the masks, the T1-weighted structural images were first normalized to the MNI template. A binary mask was then created of the ACC in MRICRON and thresholded by including only voxels which were present in the masks of all subjects. Corrections for multiple comparisons by our masking approach ensured that activation in all 12 subjects would lie within the anatomical area defined as the ACC in each of the 12 subjects. To mitigate type I errors, a Bonferroni correction was applied to the threshold ( $p < .05$ ) that took into account the number of resels in within this region. By this approach, it was plausible that spatial pattern of activation may be atypical, as voxels would only be considered as statistically significant if they fell within the ACC of all subjects.

## RESULTS

### Behavioral results

To identify whether subjects were learning the conditional associations between arbitrary instruction cues and motor responses, we examined the effect of instruction cue repetition on error rate (four cues in each of two sets; eight different cues for each agent; each cue presented five times). Mauchly's test of sphericity revealed that the data did not violate the assumption of sphericity,  $W(9) = 0.303$ ,  $p = .267$ . A repeated-measures ANOVA showed a significant main effect,  $F(2.9, 32.3) = 37.92$ ,  $p < .001$  (see Figure 3), of error rate over time. Following the scanning session, subjects were interviewed to determine whether they had learned which associations had been correctly made by the third-person and the computer and whether they had maintained the belief that their



**Figure 3.** Behavioral results. Graph shows the mean error rate of all subjects (first-person) and also the simulated error rate of the computer and the third-person (identical across all subjects). Error bars depict the standard error of the mean (SEM) of all scanned subjects. A repeated-measures ANOVA showed an effect of instruction cue repetition (four shapes  $\times$  five repetitions) on error rate (the percentage of correct responses),  $F(2.9, 32.3) = 37.92$ ,  $p < .001$ , for the first-person behavioral results. Subjects were also able to report the associations correctly made by the third-person and the computer. Thus, the scanned subjects were learning the arbitrary relationships between instruction cues and motor response and also understanding the learning of the other agents.

training partner (a confederate) was a real subject, responding accordingly, inside the scanner control room. All subjects were able to report the associations made by the other agents and maintained belief in the deception. Thus, subjects were learning their own associations and understanding the associations being learned by the other agents.

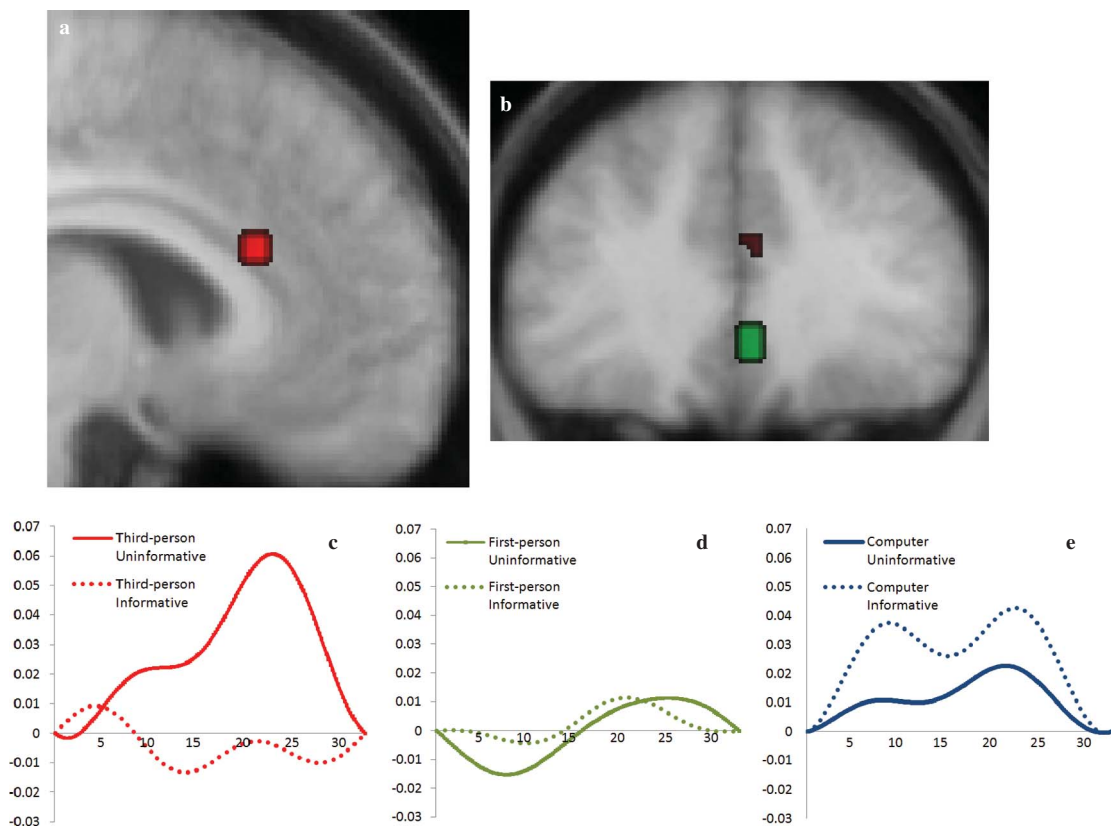
## fMRI results

Using a  $2 \times 3$  factorial design, we tested two hypotheses. Firstly, that the ACC would respond to the uninformative outcomes of the first-persons' decisions, and secondly that the same areas of the ACC would respond to the uninformative outcomes of the third-persons' decisions. Our experimental design allowed us to examine activity time-locked specifically to the outcome events of the three agents. To test the first hypothesis, we looked for an interaction between Feedback (informative vs. uninformative) and two levels of Agency (first-person vs. computer). We found activity occurring below the genu of the corpus callosum, in the subgenual region of the ACC—Brodmann's area (BA) 25. To ensure that this effect was specific to the first-person outcomes, we exclusively masked out voxels which showed an interaction effect between Feedback (informative vs. uninformative) and the other two levels of Agency (third-person vs. computer). The effect was still present in the cluster shown in Figure 4b. Therefore, a region within

the ACC showed an effect of Feedback specific to the outcomes of the first-persons' decisions.

To test the hypothesis that the same region in the ACC would also respond to the ambiguous outcomes of the third-person decisions, we needed to control for any potential attentional confounds that may occur when subjects were attending externally to the third-person outcomes and internally to the first-person outcomes. Testing for differences between the first-person and third-person outcomes would therefore not be appropriate. Instead we looked for an interaction between Feedback and two levels of Agency (third-person vs. computer). This contrast enabled us to remove the confounding effects of externally directed attention, ensuring that activity time-locked to the outcomes of the third-persons' decisions was specific to monitoring the outcomes of another biological agent's decisions. An interaction between Feedback and external Agency (third-person vs. computer) was identified in a different region within the ACC (see Figure 4a; BA 24a/b) (Vogt et al., 1995). In addition, to ensure that this effect was exclusive to the third-persons' decisions, we exclusively masked out the interaction between Feedback and the other two levels of Agency (first-person vs. computer). The interaction effect was still present. Examination of the peristimulus time histogram (PSTH) plots identified increased activation exclusive to the uninformative outcomes of the third-persons' decisions (Figure 4c–e). This cluster did not show a main effect of Agency or a main effect of Feedback ( $p > .01$ ). The hemodynamic response in the





**Figure 4.** Interaction between Feedback (informative vs. uninformative) and Agency (third-person  $\times$  computer). (a) Activity shown in the ACC in red on a sagittal plane (6, 27, 21;  $Z = 4.8$ ,  $p < .001$ , small volume correction—svc). (b) Same activation shown in red on a coronal plane, additional activation indicated in the subgenual cingulate (in green), showing an interaction between Feedback (informative vs. uninformative) and Agency (first-person  $\times$  computer; 6, 30, -6;  $Z = 3.24$ ,  $p < .001$ , svc). Effects are identified in the two interactions in different regions of the ACC. (c–e) Peristimulus time plot of the peak voxel (6, 27, 21), showing an interaction between Feedback (informative vs. uninformative) and Agency (third-person vs. computer). The plot shows the linear combination of basis functions for each condition for all subjects. The bold lines show the hemodynamic activity time-locked to the ambiguous outcomes of the third-person decisions, and the thin lines show the activity time-locked to the correct outcomes for (c) third-person, (d) first-person, and (e) computer.

ACC depicted in Figure 4c shows a rise time that is slower than the canonical HRF, and peaks relatively late. Although uncommon, this is not unknown, particularly for responses in the ACC (Lau et al., 2006). Previous studies have also identified BOLD responses that peak later than the canonical HRF (Handwerker et al., 2004; R. N. A. Henson et al., 2002).

## DISCUSSION

Simulation theory (ST) suggests that individuals understand decision-making in others by simulating the same processes in their own neural systems (Gallese & Goldman, 1998). We tested the simulation hypothesis that when outcomes fail to provide informative feedback, the same part of the ACC would be activated whether in relation to one's own decisions, or decisions made by others. When uninformative

outcomes were directed to scanned subjects, the subgenual portion of the ACC (BA 25) was activated. However, when scanned subjects monitored the same outcomes that were directed to others, activity was observed in the ACC again, but in a different, more dorsal location (BA 24). Thus, our results broadly support the view that the ACC is engaged by stimuli that signal that outcomes are uninformative, whether they are directed to oneself or to another. However, these areas of the ACC are different, so our result is inconsistent with the strict interpretation of simulation theory.

Interestingly, BA 24 and 25 have anatomical connectivity profiles that highlight their membership of distinct anatomical systems. These areas are interconnected with each other (Barbas, Ghashghaei, Dombrowski, & Rempel-Clower, 1999; Pandya, Vanhosen, & Mesulam, 1981; Vogt & Pandya, 1987), the inferior temporal cortex (Petrides & Pandya, 2007; Vogt & Pandya, 1987), the amygdala (Amaral

& Price, 1984; Porrino, Crane, & Goldman-Rakic, 1981), the hippocampal formation (Vogt & Pandya, 1987), the striatum (Yeterian & Pandya, 1991), and parts of the orbitofrontal cortex (Pandya et al., 1981). These areas are commonly considered as parts of a system that allow decisions to be biased by outcomes such as rewards (Doya, 2008). However, in monkeys, BA 24 has strong additional connections with homologous areas activated during mentalizing in humans (see introduction). These include medial parts of the superior frontal gyrus (Barbas et al., 1999; Pandya et al., 1981; Vogt & Pandya, 1987), i.e., paracingulate cortex (BA 9), the TPs (Barbas et al., 1999; Seltzer & Pandya, 1989), and the pSTS (Pandya et al., 1981; Seltzer & Pandya, 1989; Vogt & Pandya, 1987). In contrast, we are not aware of any significant connections between BA 25 and either the TP or the pSTS (although there are connections with parts of BA 9 distinct from those connected with BA 24). Previous work supports the idea that there are anatomically segregated areas of the ACC that support distinct functional operations. A recent study combined a DTI connectivity-based parcellation of the ACC with a meta-analysis of functional studies (Beckmann, Johansen-Berg, & Rushworth, 2009), and reported the correspondence between anatomically and functionally distinct areas. However, studies which have investigated the processing of others' decisions were not specifically considered in this analysis. Hence, representing the erroneous predictions of informative feedback of another may require the exchange of information between BA 24 and circuits which appear to process others' mental states.

It is notable that in this study increased activity was found in the ACC when a prediction about the outcome of a third-person's decision was erroneous. This profile of increased activity when a prediction is erroneous does not conform to the strict interpretation of prediction error signals in reinforcement learning theory. This theory states that unexpected outcomes should depress the response of neurons that code for prediction errors (Schultz & Dickinson, 2000). However, it has been recently shown that there are neurons in the ACC that increase their activity when an outcome is unexpected. Indeed, the firing of some neurons in the ACC increases parametrically with the magnitude of a prediction error, regardless of the valence of the prediction or the outcome (Hayden, Heilbronner, Pearson, & Platt, 2011). Thus, prediction errors may be coded for in the ACC in an unsigned manner, with unexpected outcomes always eliciting an increased response, as was found here.

Our findings are consistent with those of Behrens et al. (2008), who showed that this region is activated

when subjects compute the volatility of another's advice, and with those of Hampton et al. (2008), who reported activations in a similar location when subjects computed the effect of their own decisions on the decisions made by another. However, an important limitation of these studies is that the effects might not have been specific to information processing about a biological agent. They did not employ control conditions in which the same manipulations were applied in relation to a non-biological agent. In contrast to their studies, we used a computer control condition that allowed us to control for any potentially confounding effects that could result from subjects directing their attention internally (to their own outcomes) and externally (to others' outcomes). Although previous studies investigating social cognition have used computer control conditions (Ramnani & Miall, 2004; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003), none of these previous studies have time-locked to the outcomes of a first-person's, third-person's, and computer's responses.

Previous studies have reported evidence supporting ST by different approaches. These have shown that observation of painful experience in others activates the "pain matrix" (Hooker, Verosky, Germine, Knight, & D'Esposito, 2008; Jackson, Meltzoff, & Decety, 2005; Singer et al., 2004). Additionally, stimuli that evoke disgust responses, and that signal disgust in others, both activate the anterior insula (Jabbi, Bastiaansen, & Keysers, 2008). Similarly, it has been suggested that understanding the goals and intentions of others' actions is achieved through embodied simulation in the mirror neuron system (Gallese, Keysers, & Rizzolatti, 2004; Rizzolatti & Craighero, 2004). For example, observing others' goal-directed actions activates areas of the premotor cortex and posterior parietal cortex that are engaged when one performs the same actions (Iacoboni et al., 2005; Kilner, Neal, Weiskopf, Friston, & Frith, 2009). However, there is evidence to suggest that a strong form of ST may not be sufficient to account for all mentalizing processes. Ramnani and Miall (2004) reported set activity in the cortical motor system at the time that instructions for later actions were presented to the first-person (scanned subject). Comparable instructions intended for a third-person were observed by scanned subjects and also evoked activity in the cortical motor system, but in a subset of motor areas distinct from those related to first-person instructions. The authors argued that a strong version of simulation theory could not be supported by the results because identical areas were not activated, but a weaker version of the theory was consistent with the results because the motor system

was engaged in both first- and third-person conditions. Our results parallel these, because, although anatomically and functionally similar circuits in the ACC were activated by both first- and third-person conditions, these areas were not identical. Both studies support the view that first- and third-person conditions require processing in similar rather than identical circuits, where third-person circuits may additionally access information from the pSTS and paracingulate cortex that is not available to first-person circuits.

In summary, we have shown that ACC is activated by the outcomes of decisions that signal errors in the prediction of informative feedback. Within the ACC, there are distinct functional zones which are specialized to process the outcomes of one's own and other's decisions. A specific gyral portion of the ACC, dorsal and just posterior to the genu of the corpus callosum, plays a specific role in processing the mental states of others. Future work might test this hypothesis more directly by recording from neurons in homologous areas of the ACC in non-human primates.

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## REFERENCES

- Amaral, D. G., & Price, J. L. (1984). Amygdalo-cortical projections in the monkey (*Macaca fascicularis*). *Journal of Comparative Neurology*, 230(4), 465–496.
- Amiez, C., Joseph, J. P., & Procyk, E. (2005). Anterior cingulate error-related activity is modulated by predicted reward. *European Journal of Neuroscience*, 21(12), 3447–3452. doi: 10.1111/j.1460-9568.2005.04170.x
- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition [Review]. *Nature Reviews Neuroscience*, 7(4), 268–277. doi: 10.1038/nrn1884
- Balsters, J. H., & Ramnani, N. (2008). Symbolic representations of action in the human cerebellum. *NeuroImage*, 43(2), 388–398. doi: 10.1016/j.neuroimage.2008.07.010
- Barbas, H., Ghashghaei, H., Dombrowski, S. M., & Rempel-Clower, N. L. (1999). Medial prefrontal cortices are unified by common connections with superior temporal cortices and distinguished by input from memory-related areas in the rhesus monkey [Review]. *Journal of Comparative Neurology*, 410(3), 343–367.
- Beckmann, M., Johansen-Berg, H., & Rushworth, M. F. S. (2009). Connectivity-based parcellation of human cingulate cortex and its relation to functional specialization [Review]. *Journal of Neuroscience*, 29(4), 1175–1190. doi: 10.1523/jneurosci.3328-08.2009
- Behrens, T. E. J., Hunt, L. T., & Rushworth, M. F. S. (2009). The computation of social behavior [Review]. *Science*, 324(5931), 1160–1164. doi: 10.1126/science.1169694
- Behrens, T. E. J., Hunt, L. T., Woolrich, M. W., & Rushworth, M. F. S. (2008). Associative learning of social value. *Nature*, 456(7219), 245–U245. doi: 10.1038/nature07538
- Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex [Review]. *Trends in Cognitive Sciences*, 4(6), 215–222.
- Carter, C. S., Braver, T. S., Barch, D. M., Botvinick, M. M., Noll, D., & Cohen, J. D. (1998). Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science*, 280(5364), 747–749.
- Castelli, F., Happe, F., Frith, U., & Frith, C. (2000). Movement and mind: A functional imaging study of perception and interpretation of complex intentional movement patterns. *NeuroImage*, 12(3), 314–325. doi: 10.1006/nimg.2000.0612
- Daw, N. D., & Doya, K. (2006). The computational neurobiology of learning and reward [Review]. *Current Opinion in Neurobiology*, 16(2), 199–204. doi: 10.1016/j.conb.2006.03.006
- Doya, K. (2008). Modulators of decision making [Review]. *Nature Neuroscience*, 11(4), 410–416. doi: 10.1038/nn2077
- Frank, M. J., Woroch, B. S., & Curran, T. (2005). Error-related negativity predicts reinforcement learning and conflict biases. *Neuron*, 47(4), 495–501. doi: 10.1016/j.neuron.2005.06.020
- Friston, K. J., Holmes, A. P., Poline, J. B., Grasby, P. J., Williams, S. C. R., Frackowiak, R. S. J., et al. (1995). Analysis of fmri time-series revisited. *NeuroImage*, 2(1), 45–53.
- Frith, C. D., & Frith, U. (1999). Cognitive psychology – interacting minds – a biological basis [Review]. *Science*, 286(5445), 1692–1695.
- Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing [Review]. *Neuron*, 50(4), 531–534. doi: 10.1016/j.neuron.2006.05.001
- Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing [Review]. *Philosophical Transactions of the Royal Society. B, Biological Sciences*, 358(1431), 459–473. doi: 10.1098/rstb.2002.1218
- Gallese, V. (2007). Before and below 'theory of mind': Embodied simulation and the neural correlates of social cognition. *Philosophical Transactions of the Royal Society. B, Biological Sciences*, 362(1480), 659–669. doi: 10.1098/rstb.2006.2002
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading [Editorial]. *Trends in Cognitive Sciences*, 2(12), 493–501.
- Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, 8(9), 396–403. doi: 10.1016/j.tics.2004.07.002
- Hadland, K. A., Rushworth, M. F. S., Gaffan, D., & Passingham, R. E. (2003). The effect of cingulate lesions on social behaviour and emotion. *Neuropsychologia*, 41(8), 919–931. doi: 10.1016/s0028-3932(02)00325-1
- Hampton, A. N., Bossaerts, P., & O'Doherty, J. P. (2008). Neural correlates of mentalizing-related computations during strategic interactions in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 105(18), 6741–6746. doi: 10.1073/pnas.0711099105
- Handwerker, D. A., Ollinger, J. M., & D'Esposito, M. (2004). Variation of BOLD hemodynamic responses across subjects and brain regions and their effects on

- statistical analyses. *NeuroImage*, 21(4), 1639–1651. doi: 10.1016/j.neuroimage.2003.11.029
- Hayden, B. Y., Heilbronner, S. R., Pearson, J. M., & Platt, M. L. (2011). Surprise signals in anterior cingulate cortex: Neuronal encoding of unsigned reward prediction errors driving adjustment in behavior. *Journal of Neuroscience*, 31(11), 4178–4187. doi: 10.1523/jneurosci.4652-10.2011
- Hayden, B. Y., & Platt, M. L. (2010). Neurons in anterior cingulate cortex multiplex information about reward and action. *Journal of Neuroscience*, 30(9), 3339–3346. doi: 10.1523/jneurosci.4874-09.2010
- Henson, R., & Rugg, M. D. (2001). Effects of stimulus repetition on latency of BOLD impulse response [Meeting Abstract]. *NeuroImage*, 13(6), S683–S683.
- Henson, R. N. A., Price, C. J., Rugg, M. D., Turner, R., & Friston, K. J. (2002). Detecting latency differences in event-related BOLD responses: Application to words versus nonwords and initial versus repeated face presentations. *NeuroImage*, 15(1), 83–97. doi: 10.1006/nimg.2001.0940
- Holroyd, C. B., Nieuwenhuis, S., Yeung, N., Nystrom, L., Mars, R. B., Coles, M. G. H., et al. (2004). Dorsal anterior cingulate cortex shows fMRI response to internal and external error signals. *Nature Neuroscience*, 7(5), 497–498. doi: 10.1038/nn1238
- Hooker, C. I., Verosky, S. C., Germine, L. T., Knight, R. T., & D'Esposito, M. (2008). Mentalizing about emotion and its relationship to empathy. *Social Cognitive and Affective Neuroscience*, 3(3), 204–217. doi: 10.1093/scan/nnn019
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology*, 3(3), 529–535. doi: e7910.1371/journal.pbio.0030079
- Jabbi, M., Bastiaansen, J., & Keysers, C. (2008). A common anterior insula representation of disgust observation, experience and imagination shows divergent functional connectivity pathways. *PLoS ONE*, 3(8), 8. doi: e2939 10.1371/journal.pone.0002939
- Jackson, P. L., Meltzoff, A. N., & Decety, J. (2005). How do we perceive the pain of others? A window into the neural processes involved in empathy. *NeuroImage*, 24(3), 771–779. doi: 10.1016/j.neuroimage.2004.09.006
- Kennerley, S. W., Dahmubed, A. F., Lara, A. H., & Wallis, J. D. (2009). Neurons in the frontal lobe encode the value of multiple decision variables. *Journal of Cognitive Neuroscience*, 21(6), 1162–1178.
- Kennerley, S. W., & Wallis, J. D. (2009). Evaluating choices by single neurons in the frontal lobe: Outcome value encoded across multiple decision variables. *European Journal of Neuroscience*, 29(10), 2061–2073. doi: 10.1111/j.1460-9568.2009.06743.x
- Kilner, J. M., Neal, A., Weiskopf, N., Friston, K. J., & Frith, C. D. (2009). Evidence of mirror neurons in human inferior frontal gyrus. *Journal of Neuroscience*, 29(32), 10153–10159. doi: 10.1523/jneurosci.2668-09.2009
- Lau, H. C., Rogers, R. D., & Passingham, R. E. (2006). On measuring the perceived onsets of spontaneous actions. *Journal of Neuroscience*, 26(27), 7265–7271. doi: 10.1523/jneurosci.1138-06.2006
- Matsumoto, M., Matsumoto, K., Abe, H., & Tanaka, K. (2007). Medial prefrontal cell activity signaling prediction errors of action values. *Nature Neuroscience*, 10(5), 647–656. doi: 10.1038/nn1890
- Palomero-Gallagher, N., Mohlberg, H., Zilles, K., & Vogt, B. (2008). Cytology and receptor architecture of human anterior cingulate cortex. *Journal of Comparative Neurology*, 508(6), 906–926. doi: 10.1002/ene.21684
- Pandya, D. N., Vanhoesen, G. W., & Mesulam, M. M. (1981). Efferent connections of the cingulate gyrus in the rhesus-monkey. *Experimental Brain Research*, 42(3–4), 319–330.
- Petrides, M., & Pandya, D. N. (2007). Efferent association pathways from the rostral prefrontal cortex in the macaque monkey. *Journal of Neuroscience*, 27(43), 11573–11586. doi: 10.1523/jneurosci.2419-07.2007
- Porrino, L. J., Crane, A. M., & Goldman-Rakic, P. S. (1981). Direct and indirect pathways from the amygdala to the frontal-lobe in rhesus-monkeys. *Journal of Comparative Neurology*, 198(1), 121–136.
- Ramnani, N., & Miall, R. C. (2003). Instructed delay activity in the human prefrontal cortex is modulated by monetary reward expectation. *Cerebral Cortex*, 13(3), 318–327.
- Ramnani, N., & Miall, R. C. (2004). A system in the human brain for predicting the actions of others. *Nature Neuroscience*, 7(1), 85–90. doi: 10.1038/nn1168
- Reithler, J., van Mier, H. I., Peters, J. C., & Goebel, R. (2007). Nonvisual motor learning influences abstract action observation. *Current Biology*, 17(14), 1201–1207. doi: 10.1016/j.cub.2007.06.019
- Rilling, J. K., Goldsmith, D. R., Glenn, A. L., Jairam, M. R., Elfenbein, H. A., Dagenais, J. E., et al. (2008). The neural correlates of the affective response to unreciprocated cooperation. *Neuropsychologia*, 46(5), 1256–1266. doi: 10.1016/j.neuropsychologia.2007.11.033
- Rilling, J. K., Gutman, D. A., Zeh, T. R., Pagnoni, G., Berns, G. S., & Kilts, C. D. (2002). A neural basis for social cooperation. *Neuron*, 35(2), 395–405.
- Rilling, J. K., Sanfey, A. G., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2004). The neural correlates of theory of mind within interpersonal interactions. *NeuroImage*, 22(4), 1694–1703. doi: 10.1016/j.neuroimage.2004.04.015
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192. doi: 10.1146/annurev.neuro.27.070203.144230
- Rudebeck, P. H., Bannerman, D. M., & Rushworth, M. F. S. (2008). The contribution of distinct subregions of the ventromedial frontal cortex to emotion, social behavior, and decision making [Review]. *Cognitive Affective and Behavioral Neuroscience*, 8(4), 485–497. doi: 10.3758/cabn.8.4.485
- Rudebeck, P. H., Buckley, M. J., Walton, M. E., & Rushworth, M. F. S. (2006). A role for the macaque anterior cingulate gyrus in social valuation. *Science*, 313(5791), 1310–1312. doi: 10.1126/science.1128197
- Rushworth, M. F. S., & Behrens, T. E. J. (2008). Choice, uncertainty and value in prefrontal and cingulate cortex [Review]. *Nature Neuroscience*, 11(4), 389–397. doi: 10.1038/nn2066
- Rushworth, M. F. S., Behrens, T. E. J., Rudebeck, P. H., & Walton, M. E. (2007). Contrasting roles for cingulate



- and orbitofrontal cortex in decisions and social behaviour [Review]. *Trends in Cognitive Sciences*, 11(4), 168–176. doi: 10.1016/j.tics.2007.01.004
- Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision-making in the ultimatum game. *Science*, 300(5626), 1755–1758.
- Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people – the role of the temporo-parietal junction in “theory of mind”. *NeuroImage*, 19(4), 1835–1842. doi: 10.1016/s1053-8119(03)00230-1
- Saxe, R., & Powell, L. J. (2006). It’s the thought that counts: Specific brain regions for one component of theory of mind. *Psychological Science*, 17(8), 692–699.
- Schubotz, R. I. (2007). Prediction of external events with our motor system: Towards a new framework [Review]. *Trends in Cognitive Sciences*, 11(5), 211–218. doi: 10.1016/j.tics.2007.02.006
- Schubotz, R. I., & von Cramon, D. Y. (2009). The case of pretense: Observing actions and inferring goals. *Journal of Cognitive Neuroscience*, 21(4), 642–653.
- Schultz, W., & Dickinson, A. (2000). Neuronal coding of prediction errors. *Annual Review of Neuroscience*, 23, 473–500.
- Seltzer, B., & Pandya, D. N. (1989). Frontal-lobe connections of the superior temporal sulcus in the rhesus-monkey. *Journal of Comparative Neurology*, 281(1), 97–113.
- Singer, T., Seymour, B., O’Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science*, 303(5661), 1157–1162.
- Vogt, B. A., Nimchinsky, E. A., Vogt, L. J., & Hof, P. R. (1995). Human cingulate cortex – surface-features, flat maps, and cytoarchitecture. *Journal of Comparative Neurology*, 359(3), 490–506.
- Vogt, B. A., & Pandya, D. N. (1987). Cingulate cortex of the rhesus-monkey. II. Cortical afferents. *Journal of Comparative Neurology*, 262(2), 271–289.
- Walton, M. E., & Mars, R. B. (2007). Probing human and monkey anterior cingulate cortex in variable environments. *Cognitive Affective and Behavioral Neuroscience*, 7(4), 413–422.
- Wise, S. P., & Murray, E. A. (2000). Arbitrary associations between antecedents and actions [Review]. *Trends in Neurosciences*, 23(6), 271–276.
- Yeterian, E. H., & Pandya, D. N. (1991). Prefrontostriatal connections in relation to cortical architectonic organization in rhesus-monkeys. *Journal of Comparative Neurology*, 312(1), 43–67.