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Science 312, 1047 (2006);
DOI: 10.1126/science.1125596

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Agent-Specific Responses in the Cingulate Cortex During Economic Exchanges

Damon Tomlin,1* M. Amin Kayali,1* Brooks King-Casas,1 Cedric Anen,3 Colin F. Camerer,3 Steven R. Quartz,7 P. Read Montagu1,2

Interactions with other responsive agents lie at the core of all social exchange. During a social exchange with a partner, one fundamental variable that must be computed correctly is who gets credit for a shared outcome; this assignment is crucial for deciding on an optimal level of cooperation that avoids simple exploitation. We carried out an iterated, two-person economic exchange and made simultaneous hemodynamic measurements from each player’s brain. These joint measurements revealed agent-specific responses in the social domain (“me” and “not me”) arranged in a systematic spatial pattern along the cingulate cortex. This systematic response pattern did not depend on metrical aspects of the exchange, and it disappeared completely in the absence of a responding partner.

Social exchange occurs in species ranging from insects to humans (1–3). In primates, reciprocal interactions with nonkin occur repeatedly, thus necessitating the capacity to assign social credit or blame for shared outcomes and to act appropriately according to these assignments (4–6). In humans, reciprocity is a central feature of the collection of psychological mechanisms necessary to support social exchange (3); yet, the underlying neural representations of these mechanisms remain murky. In almost all social exchanges, one must detect and accurately track which social agent (who) gets credit for an outcome. Should credit for an outcome be assigned to one’s own actions or those of one’s partner? Perhaps such assignments are more a matter of degree—assigning the degree-of-credit to some shared outcome. Understanding such agent-specific mechanisms is important, because the assignment of social agency (7–13) appears to break down in a range of mental illnesses (14–16).

Social agency computations are also a prerequisite for generating models of others’ mental states. This latter capacity, called theory-of-mind, is highly developed in humans and has been shown to activate a consistent set of brain regions in neuroimaging experiments (17–20). Recent work has complemented these theory-of-mind experiments by using interactive economic games as ecologically realistic models for human exchange (21–31). These experiments have elicited not only brain responses in previously described theory-of-mind networks (27–29), but also have elicited formerly unreported activations along the cingulate cortex that correlate with the revelation of a social partner’s decision (29). Although evoked during an economic exchange with another human, these cingulate activations did not modulate as a function of the fairness of the exchange, nor did they occur in exchanges with computer partners (28).

This lack of sensitivity to measures of outcome suggests that these responses do not encode some metrical aspect of the trade; instead, they are consistent with the social agency computation described above. To test this possibility directly, we scanned both brains of two subjects interacting in a 10-round trust game (32, 33). This game has been used to identify neural correlates of reputation building and reciprocity (25). Because the trust game is a multiround economic exchange, it allows us to estimate brain responses in both subjects to multiple revelations of a partner’s choice and multiple instances of one’s own choice.

The trust game is illustrated in Fig. 1A. In each round, one player (investor) invests some amount I (investment phase) that is tripled and sent to the other player (trustee) who decides to repay some fraction f of the tripled amount (repayment phase) (33). Players maintain their roles for 10 consecutive rounds, and information about outcomes within each phase is presented simultaneously to both subjects. We parameterized social context within the trust game by implementing two separate versions of the task in different subject cohorts: personal (n = 104 subjects) and impersonal [n = 96; previously reported in (25)]. In the personal version, subjects met before the task, were instructed together, saw a picture of their partner during each round of the game, and met their partner afterward, where they were paid in front of each other. In the impersonal version, subjects never met, had no chance of subsequent encounter, and received no information about one another.

Given the previously reported activations in the anterior and posterior portions of the medial cingulate during a social exchange (28), a detailed analysis of the cingulate cortex in each pair of subjects was performed using independent component analysis on the same data (fig. S5).

Fig. 1. Cross-cingulate correlations reveal complementary activity patterns across investment and repayment phase of game. (A) 10-round trust game. In each round the investor contributes some amount I (investment phase) that is tripled (3 × I) and sent to the trustee who then repays some fraction f of the tripled amount (f × 3 × I). (B) Cross-cingulate principal component analysis (PCA) revealed distinct, but complementary patterns when applied to the cross-correlations between cingulate cortices of investor and trustee (34). A similar result was found using independent component analysis on the same data (fig. S5).
formed. We segmented the medial cingulate and the surrounding paracingulate cortex into separate spatial domains (33), computed cross-cingulate and cross-paracingulate correlation matrices for different lags in each phase of the task (investment phase and repayment phase), and carried out temporal principal component analysis (PCA) on the resulting three-dimensional correlation matrix (Fig. 1B) (34, 35). Analysis yielded complementary spatial patterns for cingulate cortices (Fig. 1B)—that is, patterns of activation in one phase were transposed across role when analysis was performed for the other phase. Similar results were found using independent component analysis (ICA) on the cross-cingulate correlation matrix (fig. S5) (33).

The cross-cingulate analysis led us to examine the hemodynamic time series in each cingulate segment. This region-of-interest analysis revealed three distinct response types (Fig. 2A). The first followed the submission of a subject’s own decision (unimodal “own”-dominated response); the second followed the visual presentation of a partner’s decision (unimodal “other”-dominated response). This is a remarkable finding, because visual presentation of the subject’s own decision elicited little response in the cingulate cortex. The third response type was bimodal, yielding approximately equal responses after submission of one’s own decision and revelation of the partner’s decision. However, the peak amplitude of these distinct response types was not uniform across the anterior-posterior axis of the cingulate. Instead, they displayed a systematic spatial variation that was complementary across the basic response types (“own” and “other”). Specifically, the submission of one’s own decision elicited maximal activation in middle cingulate regions (Fig. 2A, segment G), whereas viewing the revelation of a partner’s decision yielded maximal activation in anterior and posterior cingulate (an example of an anterior response is shown in Fig. 2A, segment K). This result was in stark contrast to the results of the paracingulate analysis, which indicated that, although the dorsal anterior cingulate cortex was highly activated during the experiment, there was no spatial selectivity for either stimulus. In fact, the dorsal anterior cingulate cortex responded strongly to the submission of decisions and the revelation of partner choices, and it was the only paracingulate region significantly activated by either (Fig. S6) (33).

The distinct response types and the systematic spatial variation of peak amplitudes across the anterior-posterior axis disappeared completely in motor control (n = 15; Fig. 2C) and sensory control experiments (n = 17; Fig. 2E) not involving exchange with another agent (33). In the motor control, subjects reiterated the motor responses of randomly selected investors. We applied the same region-of-interest analysis to the control data (Fig. 2 and fig. S2). Statistical comparison of responses in each of the cingulate domains showed that responses differed significantly between the normal trust task and the control tasks (33). In particular, no significant response was present in the middle cingulate (Fig. 2C), ruling out the possibility that middle cingulate activation in the trust game was the result of motor activity produced by button tapping. In the sensory control, partner reveal screens from the trust game were viewed passively by a separate cohort of subjects (n = 17). Because partner reveal screens

Fig. 2. Agent-specific responses and their pattern disappear outside of economic exchange. (A) Calculation of response pattern diagrams. Traces are the average magnetic resonance (MR) signal during subject decision phases (magenta lines) and during partner decision phases (black lines); error bars represent the standard error of the mean (n = 200 subjects). To compute the magnitude of responses to submitting a decision, MR values were selected from the time of peak response and the peak’s two flanking points (teal boxes). These values, when averaged, represent the responsiveness of a segment to the submission of the decision. This measure was performed for all segments, and a pseudo color image was produced, as depicted in Figs. 2 and 3. For responses to partner reveal screens, MR values corresponding to the peak activity after screen onset and the peak’s two flanking points (red boxes) were averaged and compiled into a similar pseudo color map. (B) The average response to submitting a decision is shown for subjects playing the linked trust game (n = 200), and a predominance of the middle cingulate is apparent. (C) Average response profile to submitting decisions in the unlinked motor control experiment (n = 15). No significant differentiation was observed across the cingulate of subjects in this task, but response levels in the middle cingulate were significantly different than those in the linked trust game (P = 0.00003). (D) Subjects from the linked trust experiment (n = 200) demonstrate the average response to viewing a social partner’s decision. The predominance of responses in the anterior and posterior poles of the cingulate is apparent in this group. (E) Average response to viewing screens in the unlinked visual control experiment (n = 17). No significant differentiation was observed across cingulate domains, but responses in both anterior and posterior regions were significantly different than those in the linked trust game (P < 0.01). Maximum activation in (B) and (C) is 0.21% change in MR signal; maximum activation in (D) and (E) is 0.12%; minimum activation for each is 0.00%.
in the trust game had novel content and had been generated by an external agent, we could not use the original data set to separate responses to social or novel stimuli. Thus, subjects in the sensory control task were informed that their compensation depended on money shown under the “gave” label on the screen, but were not told about the social task from which this screen was derived (fig. S1). This manipulation was performed so that a screen’s content still held novel and valuable information, but was devoid of social interaction. In each of the 11 cingulate domains, BOLD responses after each of 10 outcome screens did not resemble those obtained during the analogous presentation in the linked experiment (Fig. 2E and fig. S3). There was no systematic spatial variation in response amplitudes across the cingulate gyrus. To verify that motor control and sensory control effects were not due to the smaller number of subjects involved in the control manipulations, we confirmed this finding by using random samples of the existing 200-subject database (fig. S3).

The results provide strong support for three new findings: (i) agent-specific response types localized on the medial bank of cingulate cortex, (ii) a systematic spatial variation of each response type across the anterior-posterior axis of cingulate cortex, and (iii) a dependence of both signals on the presence of a responding agent. Despite the relative simplicity of this economic exchange game, other variable(s) related to this task may have been the underlying cause of the different response types, the spatial variation across the cingulate, and the difference in response to visual revelation of one’s own decision and one’s partner’s decision. However, the different response types and their systematic but complementary spatial variation across the cingulate did not change as a function of a range of dimensions (Fig. 3). The most dramatic dimensions tested in Fig. 3 are reciprocity and social context (personal versus impersonal). In previously published work, reciprocity, expressed as degree of tit-for-tat behavior across rounds, acted as a powerful behavioral signal to one’s partner and elicited strong, measurable neural correlates (25). Yet, as illustrated in Fig. 3 (bottom three rows), differences in reciprocity had no effect on the response types or on their spatial variation along the cingulate. The same result held for the difference in social context (personal, n = 104; impersonal, n = 96), where prior exposure to one’s partner, the sight of their picture in each round, and the knowledge of an imminent encounter afterward had no effect. Likewise, no differences were observed when comparing subject role (investor or trustee), sex of subject, or amount of money sent or received.

Using an iterated economic exchange task, we found two distinct response types along the cingulate cortex consistent with agent-specific responses that signal “me” and “not me.” Rather than residing in strictly demarcated functional zones, these complementary responses types exhibited smooth transitions across the entire medial bank of the cingulate gyrus. It is difficult to probe the extent to which a subject is considering outcomes for oneself or a social partner; individuals in a social exchange must necessarily model the actions of both agents as decisions are made and revealed. Despite this obstacle, the pattern of activation observed in these data was clearly sensitive to which participant was responsible for a given action. The response types and their variation through the tissue space disappeared in control experiments where money sent, actions taken, and money received were matched to those experienced during the normal multiround exchange (Fig. 2 and fig. S3) (35). These controls provided strong evidence that the response types were due to neither motor and premotor responses nor to sensory responses to outcome screens.

One question deserves separate consideration: Did the reveal screens generate simple surprise or novelty responses along cingulate that were not related to the social element of the exchange? Although this reasonable interpretation is possible, the control experiments suggest otherwise. The response pattern along the cingulate disappeared in the control experiments where subjects received stimuli that were visually identical to those in the trust game and were composed of novel, reward-related information. This manipulation used novel stimuli with economically meaningful content to probe the reveal response and showed neither an “other” response anywhere along the cingulate nor the spatial variation so prominent in the linked trust task. We take these data as strong support that the responses observed in the linked trust game were not the mere result of surprising content.

The response types and their spatial variation along the cingulate were remarkably stable across a range of variables. All responses to decision submission are shown in the left column, whereas those responses to partner reveal screens are shown in the right column. With the exception of the reciprocity and amount diagrams, all responses were averaged across rounds before compilation. Rows labeled “Personal” and “Impersonal” separate activity across social context: the personal (n = 104 individuals) and impersonal (n = 96 individuals) tasks. Rows labeled “Investors” and “Trustees” demonstrate the consistency of the responses across the two different roles (n = 100 for each). Rows labeled “Males” and “Females” demonstrate that these responses do not differ across gender (n = 100 for each). Rows labeled “Small amount” and “Large amount” show that these patterns do not depend upon the amount of resource sent or received by the player (upper 25% versus lower 25% of payments; n = 454 and 161, respectively). Finally, the rows labeled “Positive,” “Neutral,” and “Negative” reciprocity depict responses across different valences of a behavioral variable of already known interest (25). These diagrams correspond to average BOLD responses to positive (values > 0.1; n = 377 choices), neutral (−0.1 ≤ values ≤ 0.1; n = 865 choices), and negative (values < −0.1; n = 458 choices) values of the reciprocity index. Left column maximum is 0.25% change in MR signal; right column maximum is 0.16%; minimum activation for both is 0.00%.

**Fig. 3.** Cingulate pattern of “me” and “not me” remains constant across a range of variables. All responses to decision submission are shown in the left column, whereas those responses to partner reveal screens are shown in the right column. With the exception of the reciprocity and amount diagrams, all responses were averaged across rounds before compilation. Rows labeled “Personal” and “Impersonal” separate activity across social context: the personal (n = 104 individuals) and impersonal (n = 96 individuals) tasks. Rows labeled “Investors” and “Trustees” demonstrate the consistency of the responses across the two different roles (n = 100 for each). Rows labeled “Males” and “Females” demonstrate that these responses do not differ across gender (n = 100 for each). Rows labeled “Small amount” and “Large amount” show that these patterns do not depend upon the amount of resource sent or received by the player (upper 25% versus lower 25% of payments; n = 454 and 161, respectively). Finally, the rows labeled “Positive,” “Neutral,” and “Negative” reciprocity depict responses across different valences of a behavioral variable of already known interest (25).
changed as a function of sex, role, amount sent, or amount received. Lastly, these signals were clear even in individual subject pairs, as shown in fig. S4 for a single interacting dyad.

The observed lack of change as a function of reciprocity is extremely important because it reduces the likelihood of two alternate interpretations of these data. The average behavior in this game is initial cooperation followed by tit-for-tat moves, a strategy conjectured to be optimal in a reciprocal interaction (3, 6). To play such a tit-for-tat strategy, a player’s brain must compute the expected next move of their partner and compare this to the actual outcome. Consequently, large deviations in reciprocity would also carry large prediction error error signals, a signal type known to show up near or around dorsal anterior cingulate cortex (dACC) (36, 37). Two possibilities arise. The error signals could activate dACC because they reflect directly an error response. Alternately, large deviations in reciprocity represent a signal with a large amount of uncertainty and might engage an output conflict response typical for this brain region (36–44). However, neither of these interpretations would anticipate an important feature of the data actually observed. There was no difference in response types or their spatial variation as a function of positive, negative, or neutral reciprocity. One would at least expect both alternate explanations to show responses that differentiated neutral reciprocity from the other two categories (positive and negative). One possibility is that our current analysis missed the error signals altogether for some unidentified reason. However, by using this same behavioral task, we have previously identified such error-related signals elsewhere in the brain and have shown these regions to be sensitive to reciprocity (25). Consequently, our capacity to detect these error signals elsewhere makes it less likely that we simply missed error signals in cingulate related to strong deviations in reciprocity. However, it remains a possibility that some unprobed behavioral dimension generated an error signal along cingulate cortex during this task.

In a two-person social exchange, it is crucial for each agent to know how to credit an outcome. Failure to assign this credit accurately will compromise an agent’s capacity to decide on an appropriate level of cooperation with the partner—a mistake that could prove extremely costly when averaged over multiple encounters (1–6). Consequently, we suspect that these data derive from a neural mechanism dedicated to distinguishing “me” outcomes from “not me” outcomes. The systematic spatial progression of responses suggests to us that this social agency variable may be arrayed as a map; however, the current experiment cannot adequately test this provocative possibility. It is important, therefore, to note that the assignment of credit (or agency) within a social interaction necessarily implicates a variety of cognitive and emotional mechanisms. Thus, although agency parsimoniously characterizes the activations seen with these data, it may not necessarily be congruent to the underlying functions represented along the cingulate.

Extant data support a multifunctional role for the cingulate cortex, particularly in light of the extreme diversity of information that impinges on this region. Cingulate and paracingulate cortices have long been hypothesized as sites of integration of information sources that include cognitive, emotional, and interoceptive signals. Consequently, a range of functions has been ascribed to cingulate cortex (38–51), and there are disagreements over the exact variables processed and represented in these regions. However, it is reasonably clear that cingulate and paracingulate cortices contribute to normal social cognition and adaptive decision-making (17–19). The results of this paper add the important possibility that many other variables in the social domain may be arranged in such a systematic fashion through the spatial domain, a phenotype that could be disturbed in afflictions (positive and negative). One possibility is that deviations in reciprocity represent a signal with the social domain may be arranged in such a systematic fashion through the spatial domain, a phenotype that could be disturbed in afflictions.
Supporting Online Material for

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This PDF file includes:

Materials and Methods
Figs. S1 to S6
References
Supporting Online Material

**Scanning and image analysis** - Scanning was performed on a 3.0 Tesla Siemens Allegra scanner. First, high-resolution T1-weighted anatomical scans were acquired using an MPRage sequence (Siemens). Subjects then played the trust game while undergoing continuous whole-brain functional imaging. Functional run details: echo-planar imaging, gradient recalled echo; repetition time (TR) = 2000 msec; echo time (TE) = 40 msec; flip angle = 90°; 64 x 64 matrix, 26 4 mm axial slices acquired parallel to anteroposterior commissural line for measurement of the blood oxygenation level-dependent (BOLD) effect (1-3). This yielded functional voxels with dimensions 3.3mm x 3.3mm x 4.0 mm. Head movement was minimized by padding and head restraints.

The data were analyzed using Statistical Parametric Mapping (4-5). Motion correction to the first functional scan was performed within subjects using a six-parameter rigid-body transformation. The average of the motion-corrected images was co-registered to each individual’s structural MRI using a 12-parameter affine transformation. The images were then spatially normalized to the Montreal Neurological Institute (MNI) template (6) by applying a 12-parameter affine transformation, followed by a nonlinear warping using basis functions following the method of Ashburner and Friston (7). Images were subsequently smoothed with an 8 mm isotropic Gaussian kernel and bandpass filtered in the temporal domain.

**Task design** - In the personal version of the trust game, subject pairs (n = 52 pairs) were strangers, met briefly before the task, were instructed on the task (fig. S1) while sitting next to one another and walked to adjacent scanner rooms together just before being placed in identical Siemens Allegra 3T scanners. Each subject pair carried out the entire experiment while in the scanner. After the experiment, subjects exited the scanners and met at the junction of two adjoining control rooms, where they were paid in front of each other after learning of their performance on the task. Subjects were paid in cash and the total amount received ranged from $20 to $40 depending on how well they performed during the task; while the exact mechanism of the pay scale was not divulged to subjects, they were informed of the range of payments that they could receive, and that their compensation depended upon their accrued point level in the task. The payment schedule is listed below where ‘points’ is the number of dollars earned during the experiment. Notice the perfectly selfish Nash equilibrium strategy (in which the investor keeps all $20 each round) results in 200 points – no subject adopted this strategy.

<table>
<thead>
<tr>
<th>POINTS</th>
<th>MONEY</th>
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<tbody>
<tr>
<td>0-67</td>
<td>$20</td>
</tr>
<tr>
<td>68-133</td>
<td>$25</td>
</tr>
<tr>
<td>134-200</td>
<td>$30</td>
</tr>
<tr>
<td>201-300</td>
<td>$35</td>
</tr>
<tr>
<td>301+</td>
<td>$40</td>
</tr>
</tbody>
</table>

There were no statistical differences in earnings between investors and trustees. The same scheme held for the impersonal task (n = 48 pairs), except that players never met or communicated except through their offers and splits during the game. The pay scale and instructions were exactly the same at each institution. Volunteers for the personal task were drawn from the subject pool of Baylor College of Medicine in Houston, TX. For the impersonal task, separate subject pools at BCM and The California Institute of Technology in Pasadena, CA were used. Volunteers never met and were instructed separately at each institution. Furthermore, subjects were never deceived regarding their social partner or the payoffs they would receive. Although the time between screens within a round (excepting those whose timing depended upon the subjects’ free response) was consistent across rounds, 10 inter-round delays were drawn from a uniform distribution between 12 and 42 seconds quantized at half second boundaries. The
exact values of inter-round delays in seconds were: \(33, 13.5, 22.5, 33.5, 17, 18, 33.5, 16.5, 27.5, 30\).

**Cingulate and paracingulate segmentation** - Since we used h-fMRI for each dyad studied, we were able to relate the BOLD responses in both interacting brains directly to asynchronous behavioral events. Consequently, the cingulate cortices for each player in all dyads were examined using a detailed region-of-interest (ROI) analysis. The cingulate gyrus was designated by hand using the canonical T1 image included with SPM 2; this image has a resolution of 1.6 mm x 1.6 mm x 1.5 mm. After selection, structural voxels were converted into the analogous voxels for a functional image. The conversion was designed such that any functional voxel overlapping a designated structural voxel caused the functional voxel to be included, regardless of adjacent areas that the voxel may have contained. The resulting mask was comprised of 398 voxels for the entire cingulate gyrus.

In order to examine separate functional domains within the cingulate and dependent on the elements of the trust game, the mask was subdivided into 11 distinct zones running along the anterior-posterior axis. This was done using a selection method in which voxels were grouped according to their angle relative to a particular origin \((x = 0, y = -3.5, z = 13)\). This point was selected because it was equidistant from the anterior and posterior extremes of the cingulate mask; its location along the dorsal-ventral axis (on a level one voxel below the posterior cingulate) was aligned to an anatomical landmark: the ventral edge of the posterior cingulate. The angular boundaries for the zones were designated such that each area contained approximately the same number of voxels. The boundary angles and number of voxels for each segment are detailed in the table below. Each of these segments was then used as a separate mask for region-of-interest analysis for which the raw MR response was compiled. Because there were no notable differences in activity between the left and right cingulates in either GLM contrasts or ROI analyses, the voxels for each side were pooled for every area.

<table>
<thead>
<tr>
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<th>Lower Bound (\theta) (deg)</th>
<th>Upper Bound (\theta) (deg)</th>
<th>Voxels</th>
<th>Bin Centers</th>
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<tbody>
<tr>
<td>A</td>
<td>20.6</td>
<td>29.8</td>
<td>35</td>
<td>(0,-43,23))</td>
</tr>
<tr>
<td>B</td>
<td>29.8</td>
<td>40.6</td>
<td>36</td>
<td>(0,-41,32))</td>
</tr>
<tr>
<td>C</td>
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<td>36</td>
<td>(0,-31,36))</td>
</tr>
<tr>
<td>D</td>
<td>50.2</td>
<td>63.4</td>
<td>38</td>
<td>(0,-29,44))</td>
</tr>
<tr>
<td>E</td>
<td>63.4</td>
<td>80.5</td>
<td>35</td>
<td>(0,-18,43))</td>
</tr>
<tr>
<td>F</td>
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<td>104</td>
<td>38</td>
<td>(0,-7,39))</td>
</tr>
<tr>
<td>G</td>
<td>104</td>
<td>135</td>
<td>38</td>
<td>(0,2,38))</td>
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<tr>
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<td>35</td>
<td>(0,14,33))</td>
</tr>
<tr>
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<td>33</td>
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</tr>
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<tr>
<td>K</td>
<td>180</td>
<td>192.5</td>
<td>34</td>
<td>(0,45,2))</td>
</tr>
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</table>

Figure S2 illustrates the method used to segment the cingulate cortex. By deliberately specifying equal-sized regions before performing the analysis presented here, the test conservatively underestimates the extent of own-other differential activity. An alternative procedure is to choose areas which demonstrate the largest activations for ‘own’ and ‘other’; this latter method necessarily biases segmentation toward these effects, while choosing equally-sized regions a priori does not. On average, each domain contained 36.2 ± 2.1 voxels and extended 4 voxels bilaterally from the midline; a detailed breakdown is also shown in figure S2. For the analysis detailed in figure 3, minimum activation represents a 0% change in MR signal; maximum activation for the left column is .25%, while that for the right column is .16%.
So as not to overlook activity in adjacent regions of the brain, the cingulate segments were supplemented with a mask containing the paracingulate gyrus (fig. S6). In this case, fifteen zones of 35 voxels each were designated such that the mask from the cingulate analysis was surrounded along the anterior-posterior axis; none of the voxels in this new mask had been previously included in the cingulate mask. Included in this second mask are regions such as the sub parietal sulcus, dorsal anterior cingulate cortex, and medial prefrontal cortex, all of which abut the original cingulate domains. The 22 cingulate regions-of-interest (11 from each brain) and 30 paracingulate regions-of-interest (15 from each brain) were entered into cross-brain principal components analysis and independent components analysis, as described below.

**PCA and ICA procedure** - The cross-brain correlation analysis was applied to both personal and impersonal versions of the task. Our data sets consisted of 52 and 48 subject pairs from the personal and impersonal versions of the task, respectively.

In every round there were two sets of \( N_e = 26 \) time series, representing the cingulate and paracingulate regions-of-interest of each player. For every time series there were \( N_T = 22 \) observations in each investment and repayment phase, an epoch ranging from 16 seconds prior to the submission of a choice to 26 seconds afterward. The same steps of analysis were applied to both versions of the task; hence we outline our method for the personal version. The data were averaged over all rounds, yielding time series for each pair and segment over the “average round” of the task. We subtracted the mean from every time series and then calculated the cross correlation matrix for all possible time lags. For every pair and phase we got a 3-D correlation matrix \( C_p \) of size \( 2^*N_e \times 2^*N_e \times (2^*N_T - 1) \), or 52x52x43, and then calculated the ensemble-average of \( C_p \) for 52 pairs. The large number of dimensions made the ensemble-averaged correlation matrix \( C \) difficult to visualize; therefore, we thought of looking for a lower dimensional representation of the cross correlation data. A well known dimensional reduction technique is principal components analysis (PCA). To perform PCA on our cross correlation data we reshaped \( C \) into a 2704x43 matrix \( M \) for which we calculate the covariance matrix \( \text{Cov}(M) \). Next, we calculate the eigenvalues and eigenvectors of \( \text{Cov}(M) \) and identify the eigenvector \( V_G \) associated with the largest eigenvalue \( \lambda_G \). The largest eigenvalue \( \lambda_G \) accounted for almost 85% of the variance. The largest principal component was then obtained by multiplying the \( M \) by \( V_G \), which gave us a vector which we reshaped into a 52x52 matrix \( P \). Given our interest in the cross brain correlations, we extracted the cross cingulate and cross paracingulate pieces, then z-scored and smoothed them with a box kernel. Results from the cross correlation PCA are shown in (Fig. 1B; S5 and S6).

Our second approach to study the interaction between the investor and trustee cingulate and paracingulate cortices used independent component analysis ICA (8). In this approach, slices of \( C \) were treated as a mixture of independent source matrices which we needed to estimate. Such a problem is known as Blind Source Separation (BSS) (9), because neither the sources nor the way in which they are mixed (mixing matrix) are known. ICA is a practical approach widely used in estimating sources and their mixing matrix. The process seeks a set of sources such that the joint probability distribution function for the set can be factored out as a product of the probability distribution functions for each source. In the language of ICA, the matrix \( C \) in each phase can be written as a linear sum of the independent components \( S \):

\[
C_{ij}(t) = \sum_{\tau=1}^{N_D} A(t, \tau) S_{ij}(\tau)
\]

where \( C_{ij}(t) \) is the value of the ensemble-averaged cross correlation function between the time series in the investor’s \( f^i \) segment and the trustee’s \( f^j \) segment at time lag \( t \) between the two series. The independent components \( S_{ij}(\tau) \) and their mixing coefficients \( A(t, \tau) \) are unknowns to be estimated blindly. The ICA approach not only decomposes the mixture into its sources but it also allows for the possibility of reducing the dimensionality of the data; the number of source
signals, \( N_D \), is less than the number of mixed signals. By applying ICA, we found that only one independent component was necessary to account for our threshold value of 85% of the variance in \( M \). We extracted this component, denoted by \( S_i(1) \), and the corresponding mixing coefficients \( A(t,1) \). We reshaped \( S_i(1) \) into a 52x52 matrix, then z-scored the cross cingulate and cross paracingulate blocks independently before smoothing them with a box kernel. The results for the cross cingulate temporal ICA are shown in (fig. S5). In both versions of the task these analyses yielded strong correlations between the middle cingulate of the subject making a decision and the anterior and posterior portions of the partner's cingulate cortex. However, both analyses revealed no such structure in the cross paracingulate analysis.

**Motor and visual control tasks** – Separate cohorts of subjects, unfamiliar with the linked trust experiments, participated in either the unlinked motor control task (\( n = 15 \)) or unlinked visual control task (\( n = 17 \)). Subjects in the control tasks underwent fMRI scanning identical to that performed for the linked task.

Every subject in the motor control task experienced ten simulated choices. For each choice, the subject was shown an instruction screen indicating the “investment level” to which they should toggle (participants were not told anything about the original linked task, the source of the instructed levels, or the significance of the choices). After the instruction was given, a slider bar identical to that used during the linked trust task was presented; the subject then used the same button box procedure utilized in the linked task to toggle the bar to the instructed level and submit the selection. As in the linked task, the submission of a decision was followed by a blank screen. The timing between choice epochs varied randomly from 21.5 to 46 seconds. The sequences of instructed levels were taken directly from the choices of randomly selected investors, with each control subject reiterating the selections made by an investor from the linked task. Response levels in the unlinked motor task can be compared to the linked trust task in figure 2 and SOM 3. For figure 2, minimum activation represents a 0% change in MR signal; maximum activation for rows B & C is .21%, while that for rows D & E is .12%. In addition, \( p \) values indicating the degree of statistical difference between activity levels in the two tasks is shown for each segment below (two sample t test):

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<td></td>
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<td>.0002</td>
<td>.0003</td>
<td>.00007</td>
<td>.000006</td>
<td>.11</td>
<td>.81</td>
<td>.82</td>
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For the unlinked visual control task, subjects lay in the scanner while passively viewing reveal screens taken from the linked trust task. In this case, the reveal screens resulting from the choice sequences of seventeen randomly selected investors were used. After each screen, a blank screen was presented for an epoch of random length between 13.5 and 38 seconds. Because we wished to remove the social component of the task without also removing the varying reward magnitude indicated by each revelation, subjects were paid according to the total number of points indicated as “given” on the various screens, and were told that this was the case prior to the experiment. Responses from the unlinked visual task can be compared to the linked trust task in figure 2 and S3. In addition, \( p \) values indicating the degree of statistical difference between activity levels in the two tasks is shown for each segment below (two sample t test):

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<td>.23</td>
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<td>.38</td>
<td>.03</td>
<td>.06</td>
<td>.48</td>
<td>.04</td>
<td>.0002</td>
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Figure S1 - Complete timeline for the trust game. Each pair of subjects played 10 rounds of the task with their roles (investor or trustee) fixed for the entire game. Except for the periods of free response, both players viewed the same visual stimulus simultaneously. Both players saw the investor prompted to “Make Initial Investment” (cue to invest); the investor then entrusted the trustee with any amount between $0 and $20. During this first free decision period, the trustee saw a blank screen. Eight seconds after the investor’s decision was submitted, the investment was revealed to both players simultaneously, along with the investor’s photo (personal task) or symbol (impersonal task). The amounts kept and given were represented both graphically (by the height of a bar graph) and numerically. After the investor’s decision was revealed, the trustee was then prompted to split 3 times the invested amount in any proportion between themselves and the investor (cue to repay = “Make repayment”). Eight seconds after the trustee repayment decision was submitted, the repayment was revealed to both players in the same graphical and numerical fashion. After another 8 second delay, the totals for the round were revealed using the same method.
Figure S2 - Cingulate segmentation. (A) The population of voxels comprising the cingulate gyrus in both hemispheres was separated into 11 non-overlapping sub-domains based upon their location relative to a predetermined origin. Each group of voxels was designated with a letter, beginning with the most posterior portion of the gyrus, and rotating through the anterior toward the most ventral part of the cingulate. The boundaries for these zones are shown. The cingulate’s width and distance from the origin were not identical for each zone, leading to small variations in the number of voxels comprising each region. The segment boundaries were selected so as to minimize these variations. (B) Total number of functional voxels for each of the 11 cingulate domains examined.
Figure S3 - **Response pattern as a function of sample number.** (A) A randomly selected group of subjects was used to compute the response patterns shown. The resulting pattern is the same as that shown in figure 2. Minimum activation = 0%; rows 1 & 2 max = .20%; rows 3 & 4 max = .19%. (B) A second randomly selected group of subjects scanned in the trust task were incorporated into the sample, and the response patterns were calculated once more. As before, the sampling of individuals does not affect the transition of the social agency signal across the cingulate. Minimum activation = 0%; rows 1 & 2 max = .18%; rows 3 & 4 max = .19%.
Figure S4 - *Response pattern in an individual dyad.* In order to demonstrate that this pattern is not simply the result of averaging across large number of subjects, and individual subject pair was selected from the impersonal task. The BOLD signals of the two subjects were averaged across rounds, and their respective responses within the cingulate were calculated. Response profiles are individually normalized. (A) The pattern from a single investor demonstrates the predominance of the middle cingulate while making decisions and the predominance of the anterior and posterior poles when viewing decisions made by a social partner – the response pattern indicated by the average across subjects. (B) This same signal profile is visible in the trustee.
Figure S5 - Cross-cingulate ICA reveals same pattern as cross-cingulate PCA. Cross correlation ICA reveals correlation pattern similar to that obtained by cross correlation PCA. Thus, this result arises under a variety of analytical methods, and is not idiosyncratic to the PCA employed in figure 1.
Figure S6 - Cross-paracingulate PCA. (A) Segmentation of the cingulate gyrus (11 segments). (B) Segmentation of the paracingulate gyrus (15 segments). (C) Cross cingulate PCA reveals correlation between the middle cingulate of the decision maker (sender) and the posterior and anterior of the cingulate in the social partner (receiver). This pattern of correlation is absent in the cross paracingulate PCA. Further analysis revealed that, while the cingulate’s spatial domains are highly selective regarding responses to decisions and reveals screens, activity in the dorsal paracingulate was significant but responsive to both types of stimuli.
References


4. http://www.fil.ion.ucl.ac.uk/spm/


