

# Superior temporal gyrus and insula provide response and outcome-dependent information during assessment and action selection in a decision-making situation

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Decision-making is a complex process that comprises the assessment of a situation, the selection of an action, and the evaluation of an outcome. Distinct neural systems may contribute differentially during various stages within a decision-making situation. This study investigated whether neural activation during assessment or action selection is critically dependent on previous outcomes or actions. Twelve healthy, right-handed subjects (6 females) played a Rock Paper Scissors (RPS) computer game during functional magnetic resonance imaging. Bilateral insula and medial prefrontal cortex (including the anterior cingulate) were specifically engaged during the assessment and action selection stages of decision-making, whereas bilateral superior frontal gyrus and right inferior parietal lobule activated more during the outcome. Two regions of activation within the bilateral superior temporal gyrus activated only when the previous outcome was a win. Moreover, right insula and superior temporal gyrus were active more when the subject switched responses relative to staying with the same choice made on the previous trial. These findings support the hypothesis that distinct neural systems underlie different stages of the decision-making process. Furthermore, the superior temporal gyrus may play an important role in integrating previous actions and successful outcomes into one's decision-making strategy.

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## Introduction

Decision-making can be divided both temporally and functionally into distinct processes. First, individuals assess and form preferences among possible options; second, an action has to be

selected and executed; and third, the individual experiences or evaluates the outcome or consequence of the action. During the first stage, individuals attribute value to the available options, and select one of them. During the second stage, individuals initiate, perform, and complete an action according to the preferences established during the first stage. During stage three, a signal is generated comparing the expected to the experienced outcomes. This signal provides a means of linking actions to outcomes and is a key to adjusting the value attributed to options during the first stage of the next decision. Finally, decision-making is an iterative process, such that a given stage of decision-making is influenced by the history of preceding stages and directly influences subsequent stages of processing.

The key question that arises from the complexity of the decision-making process is which brain areas contribute to the different processes that underlie decision-making? It is assumed here that there is no single decision-making area in the brain; instead, it is hypothesized that different regions are involved in assessment, action selection, and outcome evaluation. In particular, two factors play a critical role in repeated decision-making situations. First, was the previous action successful, that is, led to a desired outcome and second, should one continue with the same action or switch to a different option? In combination, the assessment and action selection aspect of decision-making critically depends on the previous outcome and action.

Functional neuroimaging provides strong evidence that outcome processing involves hedonic evaluation, which activates limbic (Kahn et al., 2002) and paralimbic areas (Breiter and Rosen, 1999). Moreover, the medial prefrontal cortex has been implicated in preference judgment (Paulus and Frank, 2003), assessment of pleurability (Mitterschiffthaler et al., 2003), tracking of rewarding outcomes (Knutson et al., 2003), formation of hedonic associations (Passingham et al., 2000), and nonlinear assessment of reward values (Elliott et al., 2003). Similarly, different areas of the anterior cingulate have been implicated during action selection and outcome processing stages of decision-making (Bush et al., 2002; Rogers et

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al., 2004; Williams et al., 2004). Finally, differential activation in superior temporal gyrus in non-speech related processing has been related to temporal action planning (Kircher et al., 2004), judgment tasks (Luo et al., 2003), and processing complex configurations of symbolic information (Grossman et al., 2002).

In a previous investigation with a different group of healthy volunteers, we showed that the inferior prefrontal cortex activated selectively during acquisition of advantageous action selection during a simple repeated decision-making task, the Rock Paper Scissors (RPS) game, and that the magnitude of this activation was predicted by a modified temporal difference model that included trend detection (Paulus et al., 2004). In contrast, this investigation was aimed at determining whether different neural substrates contribute to assessment and action selection versus outcome evaluation during a decision-making situation. Moreover, we explored whether neural activation during assessment and action selection is critically dependent on previous actions and outcomes. We hypothesized that areas which are important for the temporal integration of decision-making differentially activate depending on previous outcome (win, loss or tie) or previous actions (continue with the same action or switch). Specifically, based on our previous study with a different task (Paulus et al., 2001), which showed that posterior parietal cortex and superior temporal gyrus activation changes were proportional to the win-stay/lose-shift consistent responses, we hypothesized that activation in these structures would differ based on previous outcomes.

## Methods

### Subjects

Twelve healthy, right-handed subjects (6 females and 6 males) with a mean age of  $35.1 \pm 2.6$  years (range 24–53), an average education level of  $15.3 \pm 0.4$  years (range 13–18), and no lifetime history of Axis I DSM-IV disorders based on a structured clinical interview for DSM-IV diagnosis (Spitzer et al., 1992), participated in this study, which was approved by the UCSD Human Research Protection Program. Handedness was determined by a series of questions about hand use during daily activities. These subjects gave written informed consent and performed an event-related Rock Paper Scissors Task within an MRI scanner during a functional magnetic resonance imaging (fMRI) scanning protocol.

### Task

The Rock Paper Scissors (RPS) task has been described in detail elsewhere (Paulus et al., 2004). Briefly, this task is based on the well-known Rock Paper Scissors game. For the task, the typical rules apply: rock beats scissors, paper beats rock, and scissors beat paper. The subjects were instructed that they were playing against the computer and were told to maximize their total point count (1 point for a win, 0 points for a tie, and  $-1$  point for a loss). The probability of beating the computer and thus being reinforced (e.g.,

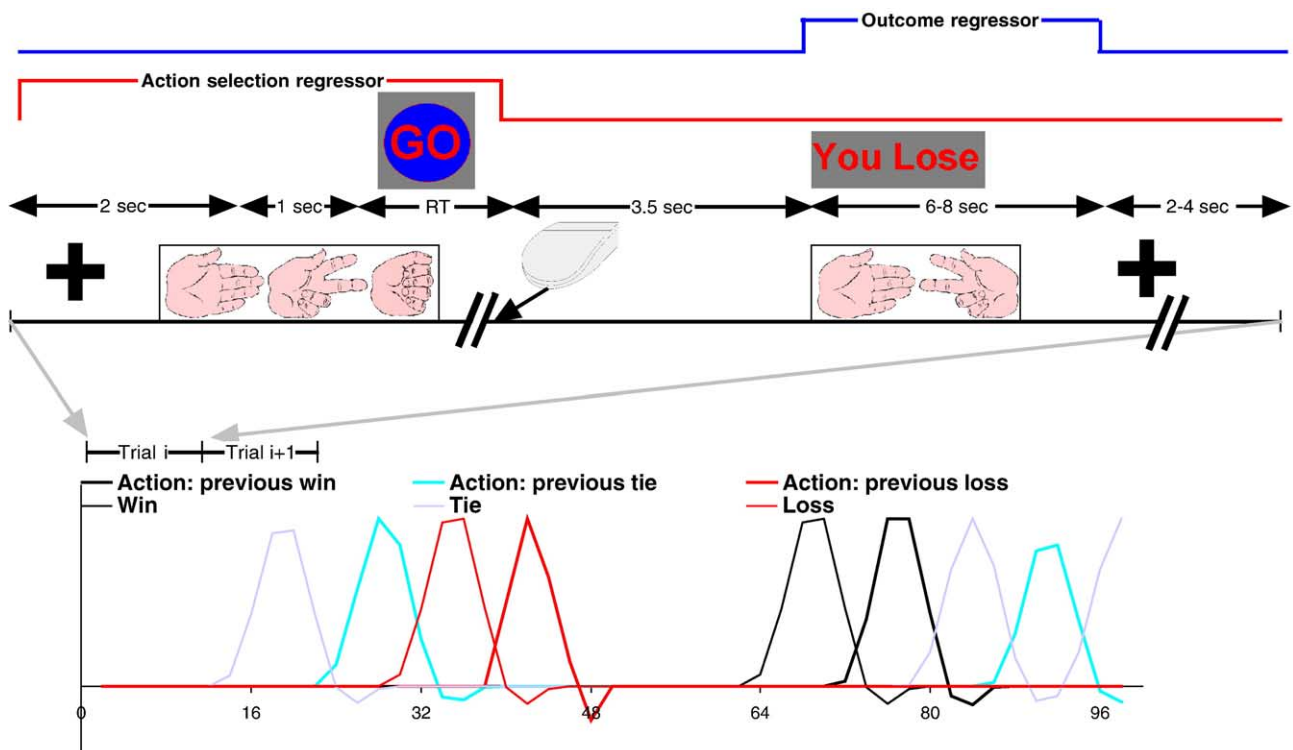


Fig. 1. This figure shows the event-related Rock Paper Scissors design. The action selection regressors were defined from the onset of the trial until the subject made a response. Outcome regressors were defined from the onset of the outcome presentation until the fixation cross. Outcome-dependent and response-dependent selection regressors were generated based on the outcome of the previous trial, that is, whether the previous trial was a win/tie/loss or whether the subject selected the same action or switched to a different action. These regressors were convolved with a modified gamma-variate function to account for the hemodynamic delay. For example, the  $i$ th trial resulted in a tie, which determined a tie-dependent action selection regressor at the  $i + 1$ st trial. Appropriate linear contrasts were computed to determine the main effect of action selection, outcome, and the difference between action selection and outcome, respectively.

subject chooses paper, computer selects rock, paper beats rock, subject gains one point) was pre-determined for each response option. Unbeknownst to the subject and without changing trial duration or inter-trial interval, the preferred, even, and worst response were switched every 16 trials. There were 4 sets of 16 trials (64 trials total). Within each set, the 3 possible selections (rock, paper, scissors) were given pre-determined probabilities of having a winning, tying or losing outcome. The “preferred response” wins on 90% of the trials, the “neutral” response wins 50% of the time, and the “worst response” wins on 10% of the trials. Thus, if rock were the preferred response and scissors were the worst response in a particular block, then selecting rock would result in a win 90% of the time and selecting scissors would result in a win 10% of the time.

The task was modified to measure outcome and assessment or action selection processing separately (see Fig. 1). After an initial fixation lasting 2 s, subjects saw pictures of a hand forming paper, scissors, and rock on the computer screen for 1 second and heard the instruction “one, two, three” over headphones. Three seconds into the trial, subjects were presented with a “Go” sign in the center of the screen, which provided the cue to select paper, scissors, or rock by pushing the left, middle, or right button with the index, middle or ring finger of the right hand, respectively. Subjects had 3.5 s to respond, after which the trial timed out. Once a response was selected, a 3.5-s delay occurred before the outcome was presented on the computer screen. At that time, the subjects saw the computer’s response, heard “you win,” “you lose,” or “a tie,” which lasted 6–8 s, and saw the score incremented, reduced by one, or left unchanged. The total score was displayed on the top of the screen. Between trials, a fixation cross was presented for 2–4 s. The number of trials with a certain trial duration were as follows (*n*, *s*): (10, 14); (14, 15); (16, 16); (18, 17); (6, 18). The order of the trial durations was fixed and optimized to estimate activation during assessment and action selection and outcome processing, respectively, using AFNI (Cox, 1996) software tools. The responses were obtained using a three-button opto-isolated computer mouse. All auditory signals were presented using MRI compatible, pneumatic, sound-insulated headphones.

### Behavioral measures

The behavioral response was obtained from the button press and recorded by a PC computer during each trial and was used to determine (1) response latency, that is, the duration from presentation of the stimulus to selection of a response, and (2) response selection, that is, whether rock, paper, or scissors was selected, resulting in a win, tie, or loss. To quantify the relationship between the current decision and previous outcome or action selection, mutual information functions were obtained. Mutual information functions (Herzel and Grosse, 1997) are based on the logarithmic likelihood ratio between the observed frequency of an event and the expected frequency of an event. These functions quantify the deviation of the co-occurrence of two events in units of bits.

### Functional magnetic resonance imaging

During the RPS task, two functional imaging runs (512 volumes) sensitive to blood oxygenation level dependent (BOLD) contrast were collected for each subject using a 1.5 Tesla Siemens (Erlangen, Germany) scanner (T2\*-weighted echo planar imaging, TR = 2000 ms, TE = 40 ms, 64 × 64 matrix, 20 4-mm axial slices,

256 scans). During the same experimental session, a T1-weighted image (MPRAGE, TR = 11.4 ms, TE = 4.4 ms, flip angle = 10°, FOV = 256 × 256, 1 mm<sup>3</sup> voxels) was obtained for anatomical reference. For preprocessing, voxel time series were interpolated to correct for non-simultaneous slice acquisition within each volume and corrected for three-dimensional motion.

### fMRI analysis pathway

The data were preprocessed and analyzed with the software AFNI (Cox, 1996). The preprocessed time series data for each individual was analyzed using a multiple regression model. This model consisted of regressors for assessment and action selection as well as regressors for outcomes. For each subject, three assessment and action selection regressors were created based on whether the previous outcome was a win, tie, or loss and two assessment and action selection regressors were created based on whether the subject changes the selection of an action (e.g., chose scissors previously and selected rock on the current trial) or stayed with the same action. Similarly, three subject-specific outcome regressors were created for wins, ties, or losses, respectively. Three regressors were used to account for residual motion (in the roll, pitch, and yaw direction). Lastly, regressors for baseline and linear trends were used to eliminate slow signal drifts. Thus, the total model consisted of 13 regressors, eight regressors of interest and five nuisance regressors, respectively. The regressors of interest for assessment and action selection consisted of 0–1 delta functions, which started at the beginning of the trial and ended once the subject had made a response. Similarly, outcome regressors started

Table 1  
Center of mass for volume-thresholded clusters for the assessment and action selection versus outcome contrast

Volume (μL)	x	y	z	R/L	t value	Area
<i>Assessment or action selection &gt; Outcome</i>						
29632	-48	-23	31	L	7.56	Postcentral gyrus, superior parietal lobule, temporal gyrus
10496	-2	-7	48	L	6.11	Medial frontal gyrus/anterior cingulate
3840	36	-8	48	R	5.84	Precentral gyrus
15168	49	-18	13	R	5.44	Insula/temporal gyrus
4608	-37	8	13	L	3.84	Insula
<i>Outcome &gt; Assessment or action selection</i>						
1088	-16	46	39	L	3.70	Superior frontal gyrus
4928	40	-55	42	R	4.26	Inferior parietal lobule
7488	39	-66	-5	R	4.42	Inferior temporal gyrus
4032	41	34	28	R	4.96	Superior frontal gyrus
11328	-41	-76	-4	R/L	5.26	Inferior occipital gyrus
1280	-49	-8	-17	L	5.81	Inferior temporal gyrus

when the individual was presented with the outcome and ended when the fixation cross was presented. These regressors were convolved with a modified gamma variate function modeling a prototypical hemodynamic response prior to inclusion in the regression model.

The AFNI program 3dDeconvolve was used to calculate the estimated voxel-wise response amplitude. A Gaussian filter with

FWHM 6 mm was applied to the voxel-wise percent signal change data to account for individual variations of the anatomical landmarks. Data of each subject were normalized to Talairach coordinates. Two different within-subject contrasts were carried out. First, a linear contrast was obtained between assessment and action selection regressors and outcome regressors. Second, contrasts were obtained for assessment and action selection

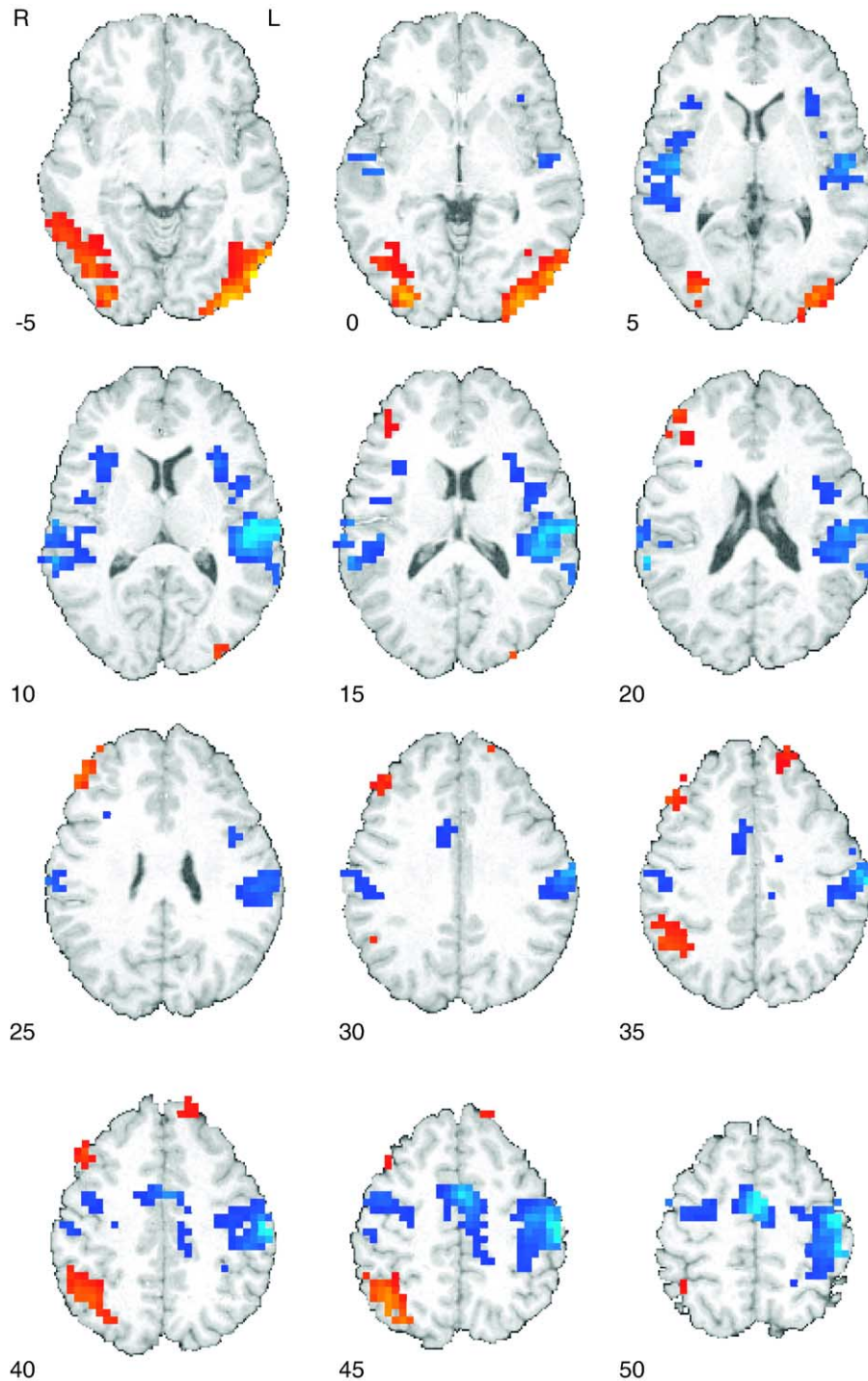


Fig. 2. Outcome-decision effect: task-related activation-differences between outcome and decision-making during the RPS task. Outcome activation is the combination of activation during the outcome presentation, that is, from onset of the outcome to the presentation of the fixation cross, of win, tie, or loss trials. (numbers represent Talairach  $y$  coordinates). Blue: decision-making > outcome, red: outcome > decision-making. For coordinates, see Table 1.

regressors based on previous outcome or previous action. However, in order to be considered for an action or outcome-dependent action selection area, brain regions had to show significant activation during the action selection stage of RPS task and differ significantly from outcome-related processing areas. To assure that these analyses were not biased by reduced estimation efficiency, covariances were computed for the design matrices of each subject. These analyses showed that the estimated normalized standard deviation for outcome-dependent action regressors ( $0.2 \pm 0.4$ ) did not differ significantly from those for action ( $0.18 \pm 0.4$ ) or outcome ( $0.19 \pm 0.4$ ) regressors.

### Statistical analyses

The voxel-wise percent signal change data were used in planned contrast analyses. Specifically, the contrasts defined above were evaluated using *t* tests. A threshold adjustment method based on Monte-Carlo simulations (Forman et al., 1995) was used, which determined that a voxel-wise a priori probability of one-sided  $P < 0.05$  would result in a corrected cluster-wise activation probability of 0.05 if a minimum volume of 1024  $\mu\text{L}$  (or 16 contiguous voxels) and a connectivity radius of 4.0 mm was considered. All analyses for the behavioral data were carried out with SPSS 10.0 (Norusis, 1990). A mixed model ANOVA (fixed factor: task conditions, random factor: subjects) was used to analyze the behavioral measures.

### Results

Based on post-task questionnaires, individuals reported attempting to win more often than the computer but did not indicate that they observed any patterns of responses by the computer. Subjects took 790 ms ( $\pm 110$  ms) after seeing the GO sign to select one of the three responses. There was no significant acquisition of selecting the preferred response ( $F(2,24) = 0.14$ , NS), which results in winning 90% of the time, or avoiding the worst response ( $F(2,24) = 0.18$ , NS), which results in winning 10% of the time, in this version of the paradigm. Overall, individuals were more likely to select a shift response ( $P < \text{shift} = 0.71 + 0.03$ ,  $F(1,12) = 33.6$ ,  $P < 0.01$ ) (e.g., choose paper one trial and choose scissors next trial) than a stay response (e.g., choose paper one trial and choose paper the next trial). However, the selection of a stay or shift response was not significantly influenced by the prior outcome ( $F(2,24) = 0.92$ , NS). The overall response selection was significantly determined by the previous response (mutual information = 0.082 bits/response  $\pm 0.02$ ,  $t(12) = 4.18$ ,  $P < 0.01$ ) but not by the previous outcome (win-stay/lose-shift mutual information = 0.01 bits/response  $\pm 0.01$ ,  $t(12) = 0.80$ , NS). Specifically, individuals tended to generate sequences of switch between different actions more often than expected by chance.

As shown in Table 1 and Fig. 2, neural substrates activated differentially during assessment or action-selection versus outcome processing. Whereas, bilateral insula, anterior cingulate and medial prefrontal cortex, bilateral superior/inferior temporal gyrus were more active during assessment or action selection relative to outcome processing, the right inferior parietal lobule, bilateral superior frontal gyrus, and bilateral occipital/inferior temporal areas were more active during outcome processing relative to assessment or action selection.

Only bilateral superior temporal gyrus (STG) was found to differentially activate during action selection as a function of prior outcome (Table 2). The activation in bilateral STG was mostly due to the fact that these structures activated in particular when the prior outcome was a win as opposed to a loss (Fig. 3). The time course of the BOLD-fMRI signal is consistent with the involvement of this structure in an outcome-dependent action selection process of the RPS task. Moreover, the decision-making related activation after a previous win in the left STG ( $r = 0.60$ ,  $P < 0.05$ ) but not in the right STG ( $r = 0.14$ , NS) was correlated with the number of win-stay consistent responses. No other significant correlations were observed. Moreover, the transition area between insula and STG showed differential activation during action selection as a function of the prior response (Table 2). Specifically, this area activated when the subject switched responses relative to the condition when the subject selected the same action (Fig. 4). Moreover, the degree of response predictability as measured by the mutual information was inversely related to the difference between the activation during a switch and the activation during a stay response ( $r = -0.68$ ,  $P < 0.05$ ). In other words, a greater activation difference in this area was associated with a less predictable response.

### Discussion

This investigation yielded two main results. First, distinct neural substrates activated during assessment and action selection versus outcome evaluation. Second, response and outcome-dependent activation occurred in bilateral STG and right insula during the assessment and action selection stage of decision-making. The degree of activation in left STG was related to an increase in win-stay consistent responding. Moreover, the degree of response predictability, as measured by mutual information, was associated with less activation in the right insula and STG. In combination, these results provide evidence that the STG and insula are important for integrating the previous response and previous outcome to the subsequent assessment and action selection stage of decision-making.

Posterior brain structures, including the STG and middle temporal gyrus, are involved in lexical-semantic processing

Table 2  
Center of mass for volume-thresholded clusters of outcome and action related decision-making

Volume ( $\mu\text{L}$ )	<i>x</i>	<i>y</i>	<i>z</i>	R/L	<i>t</i> value	Area
<i>Outcome-dependent decision-making</i>						
1984	-54	-47	15	L	3.38	Superior temporal gyrus
1600	49	-36	15	R	4.94	Superior temporal gyrus
<i>Action-related decision-making</i>						
1792	51	7	1	R	5.04	Insula/superior temporal gyrus

The outcome-dependent action selection areas show differential activation depending on whether the previous outcome was a win or a loss. The action-dependent action selection areas show different activation depending on whether the subject switched responses or chose the same response as on the previous trial.

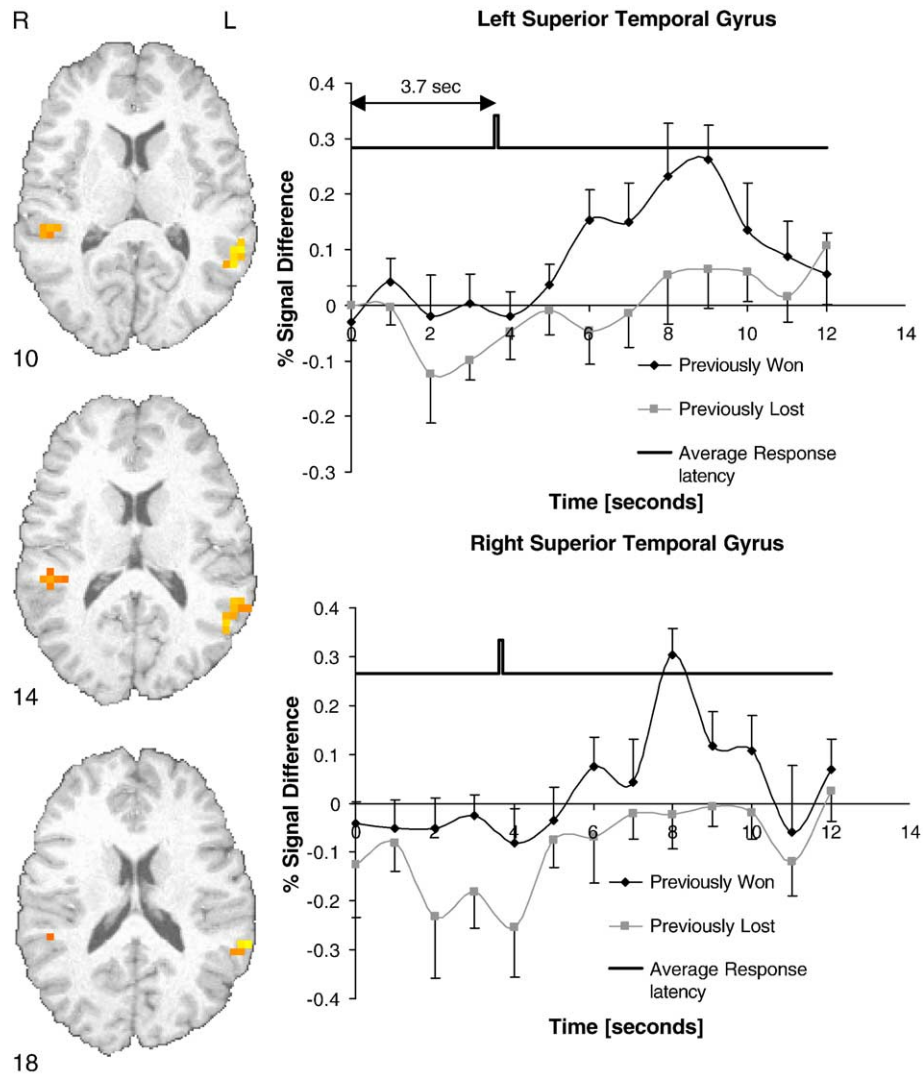


Fig. 3. Outcome-contingent action selection: bilateral STG activation during assessment and action selection is larger following a previous win relative to a previous loss. The average latency to select a response (Paper, Rock, or Scissors) is shown to indicate the relationship between action selection and the hemodynamic response.

(Rissman et al., 2003). The STG has primarily been implicated in semantic processing (Friederici et al., 2000; Luo et al., 2003), in particular of spoken words (Booth et al., 2002), object-naming (Hirsch et al., 2001), and other semantic processing components. However, the role of these structures in non-speech-related processing has only recently been appreciated. Specifically, the role of the STG in non-speech related processing has been described as a correlate of temporal action planning (Kircher et al., 2004), semantic judgment (Luo et al., 2003), processing complex configurations of symbolic information (Grossman et al., 2002), hand imitation (Leslie et al., 2004), cross-modal integration (Booth et al., 2003), and artificial grammar learning (Skosnik et al., 2002). In addition, this structure is thought to identify salient events in the sensory environment both within and independent of the current behavioral context (Downar et al., 2003). Thus, the STG appears to be critical for providing information that occurs over time in order to identify, process, or prepare for actions, which have to be integrated over time. In the context of this investigation, distinct portions of the STG differentially activate as a function of prior response and prior outcome.

The activation areas observed here are located more superior and posterior than traditional auditory processing areas. The STG has also been shown to be involved in target and deviant processing during odd-ball paradigms (Kiehl and Liddle, 2001; Lieberthal et al., 2003) and episodic memory encoding (Lee et al., 2002). In a recent review, the STG was found to be extremely sensitive to biological motion (Adolphs, 2003). This area plays an important role in explaining and predicting the behavior of others during theory of mind scenarios (Fletcher et al., 1995) and may also be involved in decision-making about complex ethical dilemmas (Heekeren et al., 2003). Thus, the current finding of activation during assessment or action selection that differs on the basis of prior outcome is consistent with the idea that the superior temporal gyrus provides contextual information, that is, the presence of a previous win or loss or whether to continue with the ongoing action, to areas of the brain that are important for assessment and action selection such as the insula.

The superior temporal gyrus is bi-directionally connected to the insula (Augustine, 1985), which activated bilaterally during the assessment and action selection stage of decision-making. How-

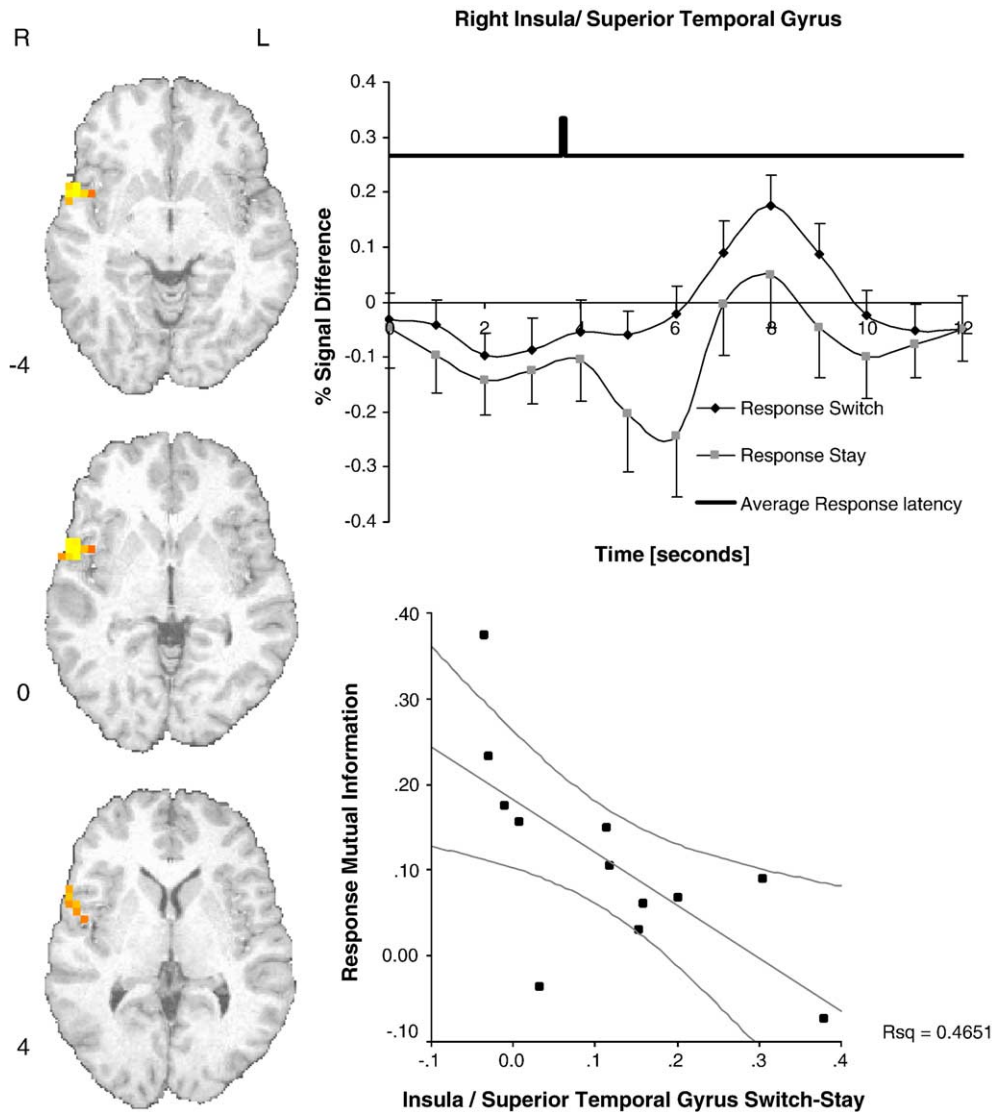


Fig. 4. Response-contingent action selection: right insula/STG activation during assessment and action selection is larger if individual switches to a different response than when the individual stays with the same choice. Moreover, greater activation during the switch response was correlated with less predictable response sequences.

ever, the bilateral activation of the insula during the action selection stage of decision-making was not differentially affected by the previous outcome. Instead, we observed differential activation as a function of previous action selection. This structure has been shown to activate during the assessment of emotionally aversive states. Specifically, functional neuroimaging studies have shown insula related activation during the processing of fearful (Morris et al., 1998) or disgusted (Phillips et al., 1998) faces, during the anticipation of electric shocks (Chua et al., 1999), as well as during script-evoked sad mood induction (Liotti et al., 2000). Moreover, insula activity has been related to the awareness of threat (Critchley et al., 2002), or the internal state of the body (Critchley et al., 2004), alterations of sympathetic tone (Nagai et al., 2004), extent of self-relatedness (Phan et al., 2004), empathic pain perception (Singer et al., 2004). Within the context of decision-making, the ventromedial prefrontal cortex, amygdala, and insular have been proposed to be part of a neural system involved in somatic state activation and decision-making (Bar-On

et al., 2003). For example, in interactional games, anterior insula activation has been observed during “unfair” offers (Sanfey et al., 2003). Some investigators have proposed that anterior insula and lateral orbitofrontal cortex may signal a change in reward contingencies (O’Doherty et al., 2003). In combination, the activation of the anterior insula during the assessment or action selection stage of decision-making may provide a “gut” feeling aid in the selection of the most advantageous option.

Previous investigations have differentiated different parts of the anterior cingulate during action selection and outcome processing stages of decision-making (Rogers et al., 2004). Specifically, these authors have attributed an evaluative role of pregenual anterior cingulate and dorsal medial prefrontal cortex. Others have shown that the dorsal anterior cingulate differentially activated with varying the amount of reward (Bush et al., 2002). The focus of our activation during the assessment or action selection stage of decision-making is consistent with the findings of dorsal cingulate activation during conflict monitoring paradigms (Bush et al., 2000;

Carter et al., 2001). Recently, using direct recording from the anterior cingulate, many neurons of the dorsal anterior cingulate, activity increased in response to a diminished reward, and was also predictive of the movement ultimately made (Williams et al., 2004). This is consistent with the observation that medial frontal cortex is involved in performance monitoring (Ridderinkhof et al., 2004), whereas lateral and orbitofrontal divisions of prefrontal cortex are involved in subsequently implementing appropriate adjustments. Others have shown that there is a negative correlation between the activation in the anterior cingulate and the orbitofrontal cortex during decision-making (Walton et al., 2004). The lack of differential ventral cingulate activation in this study and orbitofrontal activation is most likely due to partial volume coverage and some susceptibility artifact due to axial slice acquisition.

In contrast to our previous investigation (Paulus et al., 2004), which showed robust learning of the preferred responses and avoidance of the worst responses, no such learning was evident during this version of the task. Accordingly, there was no significant activation of the inferior prefrontal cortex in relation to action selection or outcome processing. The differences in acquisition of the advantageous response selecting on this task between the previous and the current study could be due to several important differences in the implementation. First, whereas the previous version of the task provided a frequent feedback (every 3.5 s), this version of the task yielded a win, tie, or loss every 14–18 s. Second, the number of trials sets with the same preferred, even or worst response was shortened to 16 trials to evaluate learning across different conditions within this event-related design. In combination, these differences point toward the importance of frequent and quick feedback to establish associative learning in this paradigm. Future investigations will, therefore, utilize a fast event-related design to examine both the acquisition of advantageous response selection and the contribution of different neural systems during assessment and action selection versus outcome evaluation in a decision-making situation. Moreover, although individual variation in response latency create temporal jitter, which helps to distinguish assessment and action selection from outcome processing during decision-making in this slow event-related paradigm, these stages are still temporally contingent on one another. Therefore, future experiments may need to introduce outcome presentation as a variable in order to separate these two components.

In summary, the current investigation shows that bilateral insula, superior/inferior temporal cortex, and medial prefrontal cortex (including the anterior cingulate) were differentially activate during assessment or action selection versus outcome processing. The activation in the superior temporal cortex and right insula were dependent on the previous response and bilateral STG for previous outcome. Thus, the activation in this area may be critical for establishing a response and outcome dependent response strategy in decision-making situations.

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#### References

- Adolphs, R., 2003. Cognitive neuroscience of human social behaviour. *Nat. Rev., Neurosci.* 4, 165–178.
- Augustine, J.R., 1985. The insular lobe in primates including humans. *Neurol. Res.* 7, 2–10.
- Bar-On, R., Tranel, D., Denburg, N.L., Bechara, A., 2003. Exploring the neurological substrate of emotional and social intelligence. *Brain* 126, 1790–1800.
- Booth, J.R., Burman, D.D., Meyer, J.R., Gitelman, D.R., Parrish, T.B., Mesulam, M.M., 2002. Functional anatomy of intra- and cross-modal lexical tasks. *NeuroImage* 16, 7–22.
- Booth, J.R., Burman, D.D., Meyer, J.R., Gitelman, D.R., Parrish, T.B., Mesulam, M.M., 2003. Relation between brain activation and lexical performance. *Hum. Brain Mapp.* 19, 155–169.
- Breiter, H.C., Rosen, B.R., 1999. Functional magnetic resonance imaging of brain reward circuitry in the human. *Ann. N. Y. Acad. Sci.* 877, 523–547.
- Bush, G., Luu, P., Posner, M.I., 2000. Cognitive and emotional influences in anterior cingulate cortex. *Trends Cogn. Sci.* 4, 215–222.
- Bush, G., Vogt, B.A., Holmes, J., Dale, A.M., Greve, D., Jenike, M.A., Rosen, B.R., 2002. Dorsal anterior cingulate cortex: a role in reward-based decision making. *Proc. Natl. Acad. Sci. U. S. A.* 99, 523–528.
- Carter, C.S., MacDonald, A.W., Ross, L.L., Stenger, V.A., 2001. Anterior cingulate cortex activity and impaired self-monitoring of performance in patients with schizophrenia: an event-related fMRI study. *Am. J. Psychiatry* 158, 1423–1428.
- Chua, P., Krams, M., Toni, I., Passingham, R., Dolan, R., 1999. A functional anatomy of anticipatory anxiety. *NeuroImage* 9, 563–571.
- Cox, R.W., 1996. AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. *Comput. Biomed. Res.* 29, 162–173.
- Critchley, H.D., Mathias, C.J., Dolan, R.J., 2002. Fear conditioning in humans: the influence of awareness and autonomic arousal on functional neuroanatomy. *Neuron* 33, 653–663.
- Critchley, H.D., Wiens, S., Rotshtein, P., Ohman, A., Dolan, R.J., 2004. Neural systems supporting interoceptive awareness. *Nat. Neurosci.* 7, 189–195.
- Downar, J., Mikulis, D.J., Davis, K.D., 2003. Neural correlates of the prolonged salience of painful stimulation. *NeuroImage* 20, 1540–1551.
- Elliott, R., Newman, J.L., Longe, O.A., Deakin, J.F., 2003. Differential response patterns in the striatum and orbitofrontal cortex to financial reward in humans: a parametric functional magnetic resonance imaging study. *J. Neurosci.* 23, 303–307.
- Fletcher, P.C., Happe, F., Frith, U., Baker, S.C., Dolan, R.J., Frackowiak, R.S., Frith, C.D., 1995. Other minds in the brain: a functional imaging study of “theory of mind” in story comprehension. *Cognition* 57, 109–128.
- Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A., Noll, D.C., 1995. Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. *Magn. Reson. Med.* 33, 636–647.
- Friederici, A.D., Opitz, B., von Cramon, D.Y., 2000. Segregating semantic and syntactic aspects of processing in the human brain: an fMRI investigation of different word types. *Cereb. Cortex* 10, 698–705.
- Grossman, M., Cooke, A., DeVita, C., Chen, W., Moore, P., Detre, J., Alsop, D., Gee, J., 2002. Sentence processing strategies in healthy seniors with poor comprehension: an fMRI study. *Brain Lang.* 80, 296–313.
- Heekeren, H.R., Wartenburger, I., Schmidt, H., Schwintowski, H.P., Villringer, A., 2003. An fMRI study of simple ethical decision-making. *NeuroReport* 14, 1215–1219.
- Herzel, H., Grosse, I., 1997. Correlations in DNA sequences: the role of protein coding segments. *Phys. Rev., E* 55, 800–810.
- Hirsch, J., Moreno, D.R., Kim, K.H., 2001. Interconnected large-scale systems for three fundamental cognitive tasks revealed by functional MRI. *J. Cogn. Neurosci.* 13, 389–405.

- Kahn, I., Yeshurun, Y., Rotshtein, P., Fried, I., Ben Bashat, D., Hendler, T., 2002. The role of the amygdala in signaling prospective outcome of choice. *Neuron* 33, 983–994.
- Kiehl, K.A., Liddle, P.F., 2001. An event-related functional magnetic resonance imaging study of an auditory oddball task in schizophrenia. *Schizophr. Res.* 48, 159–171.
- Kircher, T.T., Brammer, M.J., Levelt, W., Bartels, M., McGuire, P.K., 2004. Pausing for thought: engagement of left temporal cortex during pauses in speech. *NeuroImage* 21, 84–90.
- Knutson, B., Fong, G.W., Bennett, S.M., Adams, C.M., Hommer, D., 2003. A region of mesial prefrontal cortex tracks monetarily rewarding outcomes: characterization with rapid event-related fMRI. *NeuroImage* 18, 263–272.
- Lee, A.C., Robbins, T.W., Graham, K.S., Owen, A.M., 2002. “Pray or Prey?” dissociation of semantic memory retrieval from episodic memory processes using positron emission tomography and a novel homophone task. *NeuroImage* 16, 724–735.
- Leslie, K.R., Johnson-Frey, S.H., Grafton, S.T., 2004. Functional imaging of face and hand imitation: towards a motor theory of empathy. *NeuroImage* 21, 601–607.
- Liebethal, E., Ellingson, M.L., Spanaki, M.V., Prieto, T.E., Ropella, K.M., Binder, J.R., 2003. Simultaneous ERP and fMRI of the auditory cortex in a passive oddball paradigm. *NeuroImage* 19, 1395–1404.
- Liotti, M., Mayberg, H.S., Brannan, S.K., McGinnis, S., Jerabek, P., Fox, P.T., 2000. Differential limbic-cortical correlates of sadness and anxiety in healthy subjects: implications for affective disorders. *Biol. Psychiatry* 48, 30–42.
- Luo, Q., Perry, C., Peng, D., Jin, Z., Xu, D., Ding, G., Xu, S., 2003. The neural substrate of analogical reasoning: an fMRI study. *Brain Res., Cogn. Brain Res.* 17, 527–534.
- Mitterschiffthaler, M.T., Kumari, V., Malhi, G.S., Brown, R.G., Giampietro, V.P., Brammer, M.J., Suckling, J., Poon, L., Simmons, A., Andrew, C., Sharma, T., 2003. Neural response to pleasant stimuli in anhedonia: an fMRI study. *NeuroReport* 14, 177–182.
- Morris, J.S., Friston, K.J., Buechel, C., Frith, C.D., Young, A.W., Calder, A.J., Dolan, R.J., 1998. A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain* 121, 47–57.
- Nagai, Y., Critchley, H.D., Featherstone, E., Trimble, M.R., Dolan, R.J., 2004. Activity in ventromedial prefrontal cortex covaries with sympathetic skin conductance level: a physiological account of a “default mode” of brain function. *NeuroImage* 22, 243–251.
- Norusis, M.J., 1990. SPSS base system user’s guide. SPSS Inc., Chicago.
- O’Doherty, J.P., Critchley, H.D., Deichmann, R., Dolan, R.J., 2003. Dissociating valence of outcome from behavioral control in human orbital and ventral prefrontal cortices. *J. Neurosci.* 23, 7931–7939.
- Passingham, R.E., Toni, I., Rushworth, M.F., 2000. Specialisation within the prefrontal cortex: the ventral prefrontal cortex and associative learning. *Exp. Brain Res.* 133, 103–113.
- Paulus, M.P., Frank, L.R., 2003. Ventromedial prefrontal cortex activation is critical for preference judgments. *NeuroReport* 14, 1311–1315.
- Paulus, M.P., Hozack, N., Zauscher, B., McDowell, J.E., Frank, L., Brown, G.G., Braff, D.L., 2001. Prefrontal, parietal, and temporal cortex networks underlie decision-making in the presence of uncertainty. *NeuroImage* 13, 91–100.
- Paulus, M.P., Feinstein, J.S., Tapert, S.F., Liu, T.T., 2004. Trend detection via temporal difference model predicts inferior prefrontal cortex activation during acquisition of advantageous action selection. *NeuroImage* 21, 733–743.
- Phan, K.L., Taylor, S.F., Welsh, R.C., Ho, S.H., Britton, J.C., Liberzon, I., 2004. Neural correlates of individual ratings of emotional salience: a trial-related fMRI study. *NeuroImage* 21, 768–780.
- Phillips, M.L., Young, A.W., Scott, S.K., Calder, A.J., Andrew, C., Giampietro, V., Williams, S.C., Bullmore, E.T., Brammer, M., Gray, J.A., 1998. Neural responses to facial and vocal expressions of fear and disgust. *Proc. R. Soc. London, B Biol. Sci.* 265, 809–817.
- Ridderinkhof, K.R., van den Wildenberg, W.P., Segalowitz, S.J., Carter, C.S., 2004. Neurocognitive mechanisms of cognitive control: the role of prefrontal cortex in action selection, response inhibition, performance monitoring, and reward-based learning. *Brain Cogn.* 56, 129–140.
- Rissman, J., Eliassen, J.C., Blumstein, S.E., 2003. An event-related fMRI investigation of implicit semantic priming. *J. Cogn. Neurosci.* 15, 1160–1175.
- Rogers, R.D., Ramnani, N., Mackay, C., Wilson, J.L., Jezzard, P., Carter, C.S., Smith, S.M., 2004. Distinct portions of anterior cingulate cortex and medial prefrontal cortex are activated by reward processing in separable phases of decision-making cognition. *Biol. Psychiatry* 55, 594–602.
- 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, 1755–1758.
- 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, 1157–1162.
- Skosnik, P.D., Mirza, F., Gitelman, D.R., Parrish, T.B., Mesulam, M.M., Reber, P.J., 2002. Neural correlates of artificial grammar learning. *NeuroImage* 17, 1306–1314.
- Spitzer, R.L., Williams, J.B., Gibbon, M., First, M.B., 1992. The structured clinical interview for DSM-III-R (SCID): I. History, rationale, and description. *Arch. Gen. Psychiatry* 49, 624–629.
- Walton, M.E., Devlin, J.T., Rushworth, M.F., 2004. Interactions between decision making and performance monitoring within prefrontal cortex. *Nat. Neurosci.* 7, 1259–1265.
- Williams, Z.M., Bush, G., Rauch, S.L., Cosgrove, G.R., Eskandar, E.N., 2004. Human anterior cingulate neurons and the integration of monetary reward with motor responses. *Nat. Neurosci.* 7 (12), 1370–1375.