

# Error-rate-related caudate and parietal cortex activation during decision making

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The role of cortical and subcortical structures in processing success or failure in decision-making situations is unclear. Functional neuroimaging (fMRI) during a two-choice prediction task was used to investigate the relationship between error-rate-related behavioral changes during decision-making and activation patterns in the caudate and parietal cortex. Success-related activation was found in caudate and parietal cortex during a two-choice prediction task. At low error rates, participants utilized success-related

behavioral strategies rate by decreasing switching responses and increasing response predictability, which were associated with activation changes in the caudate and parietal cortex. Therefore, less response switching and increased response predictability during decision making can be directly related to the degree of activation in the caudate and posterior parietal cortex. *NeuroReport* 14:923-928 © 2003 Lippincott Williams & Wilkins.

**Key words:** Caudate; Decision-making; Error-rate; fMRI; Parietal cortex; Predictability; Reward

## INTRODUCTION

Decision making is an important process in every-day life. The success rate of an action, i.e. the degree to which selected actions result in a preferred outcome, is an important determinant of decision making. Therefore, when an outcome is uncertain, anticipated reinforcement, i.e. the degree of anticipated success, often predicts which action will be selected [1].

Functional neuroimaging studies have shown that decision making is critically dependent on the activation of inferior prefrontal cortex [2], ventromedial and ventrolateral frontal cortex [3-5], anterior cingulate [3], insula [6] and parietal cortex [2]. Others have implicated activation in the ventral striatum to prediction errors or to the anticipation of success (reinforcement [3,7]), as well as dorsal striatum activation to a rewarding outcome [8]. Finally, both nucleus accumbens and extended ventral striatum were found to activate during the expectancy phase [9] and reward phase of decision making [10], and when there is a significant divergence between expected and observed reward [11]. Neurophysiological studies suggest that a critical interplay occurs between the parietal and prefrontal cortex during decision making and that the likelihood of success associated with an action may constitute the critical variable that determines the selection of action in a decision making situation [12]. Nevertheless, the relationship between behavioral characteristics and neural activation patterns during decision making as a function of success or uncertainty is not well understood.

This study aimed to extend previous findings [13] by determining how success-related response selection is related to activations during the two-choice prediction task. We expected success-related changes in four key structures that are relevant for decision making: (1) the anterior cingulate; (2) the posterior parietal cortex; (3) the prefrontal cortex; (4) the striatum. Consistent with our previous findings, we hypothesized that cingulate, parietal, and prefrontal cortices would be activated differentially across the error-rate conditions, with the low error-rate condition eliciting increased activation. If these areas differentially process success or failure of the ongoing response strategy and the uncertainty of the environment, it was hypothesized that subcortical areas would be primarily involved in reward [9,10] and posterior parietal cortex, which has been associated with outcome mapping [14], would be primarily involved in success-related response selection.

Error-rate specific contrast functions were used to differentiate the effect of success, failure, and predictability during decision making. When considering a sequence of choices, predictability refers to the subject's ability to determine the outcome irrespective of success or failure. Thus, relative to 50% error rate, at 20% or 80% error rate the outcome of the trial is more predictable (i.e. more often either right or wrong). The distinction between examining the effects of success and predictability corresponds statistically to determining the linear and quadratic contrasts of activation patterns as a function of error rate. Specifically, a positive quadratic contrast identifies areas

that are more active with uncertain outcome. In comparison, a positive (or negative) linear contrast of activation patterns with error rate indicates that these areas differentially activate with success (or failure). The success or uncertainty-related behavioral processes can be related to the brain activations by calculating the correlations between the magnitudes of the linear and quadratic contrast vectors for both behavioral and neural activation. For example, if a certain brain structure were involved in cognitive processes associated with the uncertainty of a situation, then it would be expected that a quadratic vector coefficient (i.e. action > 50% than at 20 and 80% error rates) of the activation pattern found in this brain structure would be correlated with a quadratic vector coefficient of a behavioral response pattern across the error rate conditions. Therefore, these analyses directly link success, uncertainty, or failure related behavioral patterns with the success, uncertainty, and failure related patterns occurring in specific brain structures during decision-making.

## MATERIALS AND METHODS

**Participants:** Seventeen healthy participants without a lifetime history of Axis I mental disorders based on a structured clinical interview [15] (10 females; 16 right-handed) with a mean ( $\pm$  s.d.) age of  $36.2 \pm 7.8$  years and education level of  $14.9 \pm 1.7$  years signed informed consent (UCSD Human Research Protection Program 000730) and participated in this fMRI study.

**Task:** In this task [16], a house is presented on the computer screen, which is flanked by a person to the left and right. The goal for the subject is to decide on which side of the house a car will be presented. Each trial is self-paced to maximize self-determined action [17], thus the subject determines the number of trials by the latency to select a response. Immediately following the subject's response, the car is presented for 300 ms on the far left or right side of the screen, which provides the feedback whether the prediction was correct, i.e. the person and car are on the same side, or incorrect, i.e. the person and car are on opposite sides. Immediately, after the presentation of the car, the next trial begins. Unknown to the participants, the computer determined the response based on the participant's selection. Three error-rate block types were presented: a high (20% of responses were correct), a chance-level (50% of responses were correct), and a low (80% of responses were correct) error-rate block type. Because error-rates are a property of sequences of trials, a parametric fMRI block design was used. The three task conditions (20%, 50%, or 80% error rate) were presented four times and yielded 12 blocks, which lasted between 21 and 24 s to minimize expectation effects. Each block type occurred in a pseudorandom order (R = rest, 50%, R, 20%, R, 80%, R, 20%, R, 50%, R, 80%, R, 50%, R, 20%, R, 50%, R, 80%, R, 20%, R, 80%) and was separated by a resting condition (presentation of the background stimulus, no response required) lasting 6–12 s.

**Behavioral measures:** For each trial, the selection by the participant (right or left), computer-selected response (right or left), and response latency was obtained. The strategies of decision-making in the presence of uncertainty were

assessed by two sets of measures: (1) General response biases: the number of left or right responses or stay (e.g., left followed by left response) versus switch responses (e.g., left followed by right response). (2) The degree to which the current response is determined by the previous response, the previous stimulus, or a combination of both is quantified by mutual information measures [18]. Mutual information functions [19] are based on the logarithmic likelihood ratio between the observed frequency and the expected frequency of an event. These functions quantify the deviation of the co-occurrence of two events in units of bits. For example, if the subject always selects the LEFT after the previous stimulus occurred on the LEFT side, the mutual information will measure the degree to which these two occurrences co-occur more frequently than expected by chance.

**fMRI protocol and image analysis pathway:** Magnetic resonance images were obtained using a 1.5 T whole-body system (Siemens, Erlangen). Anatomical T1-weighted images of the whole brain (MPRAGE, TR = 11.4 ms, TE = 4.4 ms, flip angle = 10°, FOV 256 × 256, 1 mm<sup>3</sup> voxels) were obtained sagittally. Thirty-two slices of T2\*-weighted images were obtained in the axial plane using gradient-recalled echo-planar imaging (TE = 40 ms, flip angle 90°, 64 × 64 pixel FOV = 256 × 256 mm, 4 mm contiguous slice thickness) every 3000 ms for 128 repetitions yielding a voxel size of 4 mm<sup>3</sup>.

The Analysis of Functional Neuroimages (AFNI) software package [20] was used to process all structural and functional images. The measure of task-related activation was the percentage signal change between the two-choice prediction task and the rest condition. Multiple regression analysis as previously described in [13] was used to quantify the fMRI time-series data [21]. A Gaussian filter with FWHM 4 mm was applied to voxel-wise percentage signal change data to account for individual variations of the anatomical landmarks. Data from each subject were normalized to Talairach coordinates. The percentage signal difference between the two-choice prediction task and rest was entered into a mixed-model (fixed factor: error rate, random factor: subjects) ANOVA. A threshold adjustment based on Monte-Carlo simulations was used to guard against identifying false-positive areas of activation [22]. The Talairach Demon software [23] was used to determine brain labels for activation clusters.

**Statistical analysis:** All behavioral analyses were carried out with SPSS 10.0 [24]. A repeated measures multivariate ANOVA, with error rate (20, 50, or 80%) as the within-subjects factor, was used to analyze the behavioral measures and neural activation areas. For both behavioral responses and neural activation patterns, the effect of success (low vs high error rate) and uncertainty (50% error vs low and high error rate) was examined by linear and quadratic contrasts, respectively. In order to determine the relationship between behavioral response on the task and activation pattern, we obtained a linear and quadratic fit of the behavioral change as a function of error rate. These fit coefficients were then related to the linear and quadratic fit coefficients of the activation patterns using correlational analyses. This ap-

proach utilizing linear and quadratic vector coefficients allows us to relate in a processing-specific manner behavioral and neuroimaging data (i.e., the behavioral response patterns depicting success, failure, and uncertainty can be related directly to the neural activation patterns depicting success, failure, and uncertainty).

A threshold adjustment method based on Monte-Carlo simulations was used to guard against identifying false-positive areas of activation [22]. Based on these simulations, it was determined that a voxel-wise *a priori* probability of 0.05 would result in a corrected cluster-wise activation probability of 0.05 if a minimum volume of 512  $\mu\text{l}$  (or eight connected voxels) was considered. Hemispheric laterality effects were analyzed with a 2 (hemisphere region of interest) by 3 (error rate condition) multivariate ANOVA [25].

## RESULTS

**Behavioral measures:** The probability of a switching response differed significantly across conditions ( $F(2,15) = 16.84, p < 0.01$ ; quadratic contrast,  $F(1,16) = 6.55, p = 0.02$ ). Subjects were more likely to switch their response from the last trial in the 80% error-rate condition ( $56.2 \pm 9.8\%$ ) than in either the 50% ( $47.9 \pm 11.2\%$ ) or the 20% ( $44.3 \pm 13.9\%$ ) conditions. The subjects' responses during the two-choice prediction task were most predictable at low error rates. Specifically, mutual information measures (in bits) between the current response and the previous response (stimulus right or left;  $MI_{20\%} = 0.14 \pm 0.08, MI_{50\%} = 0.10 \pm 0.05, MI_{80\%} = 0.11 \pm 0.06$ ;  $F(2,15) = 3.24, p = 0.07$ ), previous stimulus ( $CMI_{20\%} = 0.24 \pm 0.19, CMI_{50\%} = 0.24 \pm 0.12, CMI_{80\%} = 0.16 \pm 0.10$ ;  $F(2,15) = 6.32, p = 0.01$ ; quadratic contrast,  $F(1,16) = 6.91, p = 0.02$ ), and the combination of previous stimulus and response ( $SMI_{20\%} = 0.38 \pm 0.17, SMI_{50\%} = 0.42 \pm 0.15, SMI_{80\%} = 0.29 \pm 0.10$ ;  $F(2,15) = 11.36, p < 0.01$ ; quadratic contrast,  $F(1,16) = 11.17, p < 0.01$ ) showed that responses were more predictable at 20% or 50% error rate relative to 80% error rate. Similar to our previous study [13], subject responses across the three error-rate conditions did not differ significantly for response rate ( $RESPNB_{20\%} = 21.5 \pm 4.8, RESPNB_{50\%} = 22.1 \pm 4.8, RESPNB_{80\%} = 22.5 \pm 4.3$ ;  $F(2,15) = 2.40, p = 0.12$ ), right vs left responses ( $FreqRIGHT_{20\%} = 36.7 \pm 8.9\%, FreqRIGHT_{50\%} = 38.3 \pm 9.7\%, FreqRIGHT_{80\%} = 40.8 \pm 10.5\%$ ;  $F(2,15) = 1.73, p = 0.21$ ), or response time ( $RESPTIME_{20\%} = 770 \pm 343\text{ ms}, RESPTIME_{50\%} = 770 \pm 340\text{ ms}, RESPTIME_{80\%} = 733 \pm 300\text{ ms}$ ;  $F(2,15) = 1.37, p = 0.33$ ).

**fMRI measures:** Table 1 presents the volume-thresholded cluster results from the 2 (two-choice prediction task vs resting baseline) by 3 (error rate condition) ANOVA along with significant error rate pattern of activation results (linear or quadratic trend contrast). The right medial (BA 9) and left superior frontal gyri (BA 8) were most active when the outcome was most predictable (i.e. quadratic contrast resulting in 20% and 80% error rate > 50% error rate). Activations in bilateral inferior and left superior parietal lobules (BA 7, 40), right middle and superior frontal gyri (BA 6), bilateral caudate and caudate body, left precuneus, and left lentiform nucleus and putamen were proportional to error rate, i.e. success (linear contrast

resulting in 20% > 80% error rate; Table 1). Activation in the left middle and superior temporal gyri, left precentral gyrus, middle occipital gyrus, and left precuneus were proportional to failure (linear contrast resulting in 80% > 20% error rate).

Task-related hemispheric laterality interactions were analyzed for the primary regions of interest (i.e. caudate and parietal areas) with a 2 (hemisphere region of interest)  $\times$  3 (error rate condition). A multivariate ANOVA to determine if the caudate and parietal areas exhibited significantly different error rate functions dependent upon hemisphere revealed an effect of hemisphere in the caudate (hemisphere,  $F(1,16) = 6.1, p < 0.05$ ) error rate ( $F(2,15) = 17.27, p < 0.01$ ), but no hemisphere  $\times$  error rate interaction ( $F(2,15) = 2.81, ns$ ). Despite the error-rate effect in the parietal cortex ( $F(2,15) = 7.33, p < 0.01$ ), there was no effect of hemisphere ( $F(1,16) = 0.44, ns$ ) or hemisphere  $\times$  error-rate interaction ( $F(2,15) = 0.80, ns$ ). The lack of a hemisphere  $\times$  error-rate interaction in these areas is consistent with the hypothesis that these areas functioned similarly across the error rate conditions in the two hemispheres.


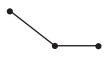

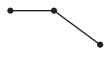

**fMRI-behavior relationships:** Success-related decrease in the response switching (Fig. 1a) vector was related to success-related increase in activation in the right inferior parietal ( $r = -0.52, p = 0.032$ ), left caudate ( $r = -0.56, p = 0.019$ ), and left lentiform nucleus and putamen vectors ( $r = -0.52, p = 0.032$ ; Fig. 1b). The increase in success-related predictability of the response vector during the two-choice prediction task (Fig. 1c) was related to a success-related increase in activation in the right caudate ( $r = -0.59, p = 0.013$ ), and left superior parietal lobule and left precuneus vectors ( $r = -0.66, p = 0.003$ ; Fig. 1d).

Success-related neural activations that were related to error-rate-related changes in the behavioral response (Fig. 1b) were subjected to a (region of interest (right inferior parietal, left caudate, left lentiform, and putamen)  $\times$  error rate) MANOVA. There was a significant region  $\times$  error-rate interaction ( $F(4,13) = 7.6, p = 0.05$ ), which is consistent with the observation that the lentiform nucleus and putamen are relatively deactivated when error rates are high while the caudate and parietal areas are relatively more activated when error rates are low.

## DISCUSSION

This investigation yielded two main results. First, at low error rates (80% correct predictions), subjects switched responses less frequently, which was associated with an increased activation in the right inferior parietal gyrus and left caudate, lentiform, and putamen. Second, at low error rates responses were more predictable, which was associated with increased activation in the right caudate and left superior parietal lobule and precuneus. In combination, success-related decrease in response switching and increase in response predictability can be directly related to the degree of activation in the posterior parietal cortex and striatum, which is consistent with current theories about the role of anticipation in reward processing [10]. Therefore, these structures may provide top-down modulation of the ongoing response strategies as a function of success in decision-making situations [9,11].

**Table 1.** Patterns of activation, i.e. relative activation as a function of error rate, and contrasts for the 20%, 50% and 80% error rate conditions and center of mass for volume-thresholded mixed ANOVA clusters of task-related (two-choice prediction—resting baseline) activation.

Pattern of error rate activation	ANOVA <sup>a</sup> F(2,15)	Contrast <sup>b</sup> F(1,16)	Volume ( $\mu$ l)	Talairach coordinates and anatomical description					
				X	Y	Z	L/R	Structure	BA
<b>Certainty</b> 	20.65**	42.29**	1792	2	51	34	R	Medial frontal gyrus	9
	6.91**	14.61**	1088	-25	37	44	L	Superior frontal gyrus	8
<b>Success</b> 	9.72**	8.65**	6272	39	-57	40	R	Inferior parietal lobule	40
	16.45**	15.67**	1408	-12	2	16	L	Caudate and caudate body	
	11.74**	8.76**	1792	-29	-71	50	L	Superior parietal lobule and precuneus	7
	14.79**	23.44**	960	20	20	57	R	Superior and middle frontal gyrus	6
	16.85**	33.27**	1408	6	3	11	R	Caudate and caudate body	
	3.92**	8.26**	1344	-48	-57	46	L	Superior and inferior parietal lobule	40,7
	13.18**	8.37**	576	-16	9	1	L	Lentiform nucleus, putamen	
<b>Failure</b> 	18.50**	38.23**	3136	-24	-43	28	L	Precuneus	31
	16.76**	35.32**	1472	-28	-11	29	L	Precentral gyrus	6
	15.20**	32.16**	1152	-31	-55	12	L	Middle and superior temporal, middle occipital	

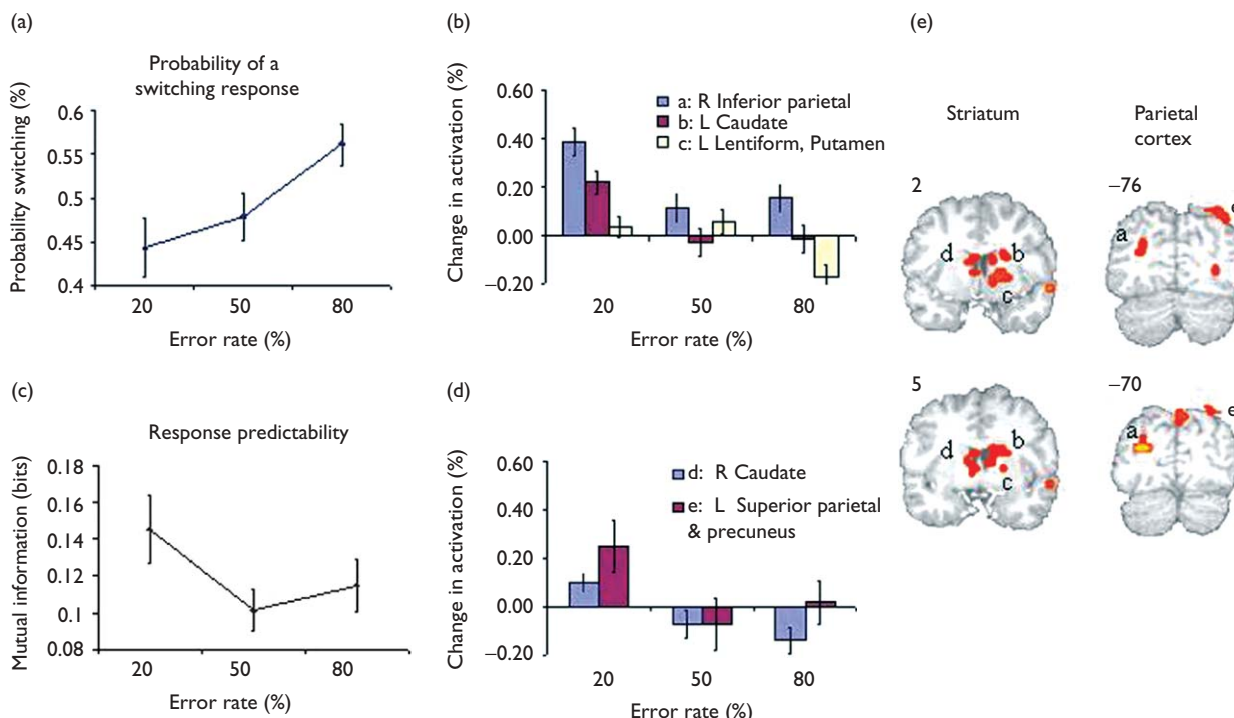
20% 50% 80%

**Error rate**

\*\* $P < 0.01$ ; \* $P < 0.05$ . Labels are based on Talairach Demon software [23].

<sup>a</sup>2 (two-choice prediction task vs resting baseline)  $\times$  3 (error-rate) ANOVA.

<sup>b</sup>Linear or quadratic trend contrast (as depicted in the pattern of error rate activation).



**Fig. 1.** Behavioral characteristics and neural activation patterns of regions of interest. The pattern of the probability of a switching response across the three error-rate conditions, 20, 50, and 80% (a), was inversely related to the error-rate pattern found in the right inferior parietal cortex, and the left caudate, lentiform and putamen (b). These areas, a, b, and c, respectively, are depicted in the brain images (e) of the striatum and parietal areas. The error-rate pattern of the mutual information measure of response predictability (c) was associated with the error-rate pattern of the right caudate and left superior parietal and precuneus (d). These areas, d and e, respectively, are also depicted in the striatum and parietal areas (e). Numbers above the image indicate the y-coordinate of the coronal slice. Error bars are 1 s.e.

The interpretation of these findings is limited by the use of a block design. Specifically, such a design does not allow the separate investigation of the experimental manipulation (error rate) with behavioral response (stay/switch). Similarly, it leaves open the possibility that incorrect predictions, or fewest errors, or both were associated with increased activation in caudate and parietal areas. Finally, response switching and success cannot be differentiated in this design. Future studies using fast event-related designs will be able to address such questions.

When faced with selecting responses in an uncertain environment that is associated with different levels of success, participants activate both subcortical and cortical structures to form an assessment of the success of the ongoing strategy. The posterior parietal cortex may maintain a representation of the success or failure of online hypotheses according to their logarithmic likelihood ratio of successful prediction [12]. The link between behavioral characteristics during the two-choice prediction task and the activation pattern in the posterior parietal cortex and the caudate supports the conclusion that these areas balance success-consistent response strategies with the exploration of novel response strategies as a function of success or failure. Specifically, at low error-rates switching rates are typically low. In this case, more activation in the right inferior parietal cortex and left caudate was associated with reduced switching rates, which is consistent with a success-related response strategy. Similarly, increased response predictability at low error-rates was associated with

increased activation in left superior parietal lobule and precuneus and right caudate, which is also consistent with the maintenance of a successful response strategy.

**CONCLUSION**

Neural activation patterns in the caudate and parietal cortex modulate, in a success-related manner, decision making during a two-choice prediction task. At low error rates, subjects generate fewer switching responses and generate response sequences that are more predictable, which is consistent with a success-related decision-making strategy. These changes were directly associated with the error-rate-related activation pattern in the parietal cortex, which is thought to maintain a representation of success or failure online [14], and the caudate, which plays an important role in reward-related processes [8–10]. In conclusion, during decision making the caudate and parietal cortex monitor and update the availability of response programs according to the history and expectation of success.

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