Decision-making under Risk: An fMRI Study

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Abstract

■ Recent research has focused on decision-making under risk and its neural bases. Two kinds of bad decisions under risk may be defined: too risky decisions and too cautious decisions. Here we show that suboptimal decisions of both kinds lead to increased activity in the anterior cingulate cortex in a Blackjack gambling task. Moreover, this increased activity is related to the avoidance of the negatively evaluated decision under risk. These findings complement other results suggesting an important role of the dorsal anterior cingulate cortex in reward-based decision-making and conflict resolution. ■

INTRODUCTION

Difficult decisions are often associated with risks. In some cases, risk involves limited knowledge about the outcome of one option while the outcome of the alternative option is known. Alternatively, risk may imply that highly valuable options have a low probability of occurrence or that such valuable options are probabilistically accompanied by adverse outcomes. In the present study, participants played Blackjack and had to decide whether they wanted to increase their point score with an unknown card value, either improving their chance of winning or leading to an immediate loss. In this context, ''risk'' refers to the fact that the value of the additional card is unknown and the participants can either decide to run the risk of encountering this unknown card value or to keep their current point score. Under risky circumstances, two kinds of suboptimal decisions can be made. On the one hand, risks might be overvalued, leading to overly cautious decisions. On the other hand, risks can be devalued, leading to overly risky decisions. The focus of the present study was the evaluation of these two kinds of suboptimal decisions. Such an evaluative stage of decision-making has to be separated from preceding stages of preparing or executing a decision or an action.

In a recent study, Kuhnen and Knutson (2005) examined the neural antecedents of too risky and too cautious decisions with fMRI and administered a three-choice paradigm. One option was a safe win of $1. The two other options were either a good one (with a 50% probability of winning $10, and 25% probabilities of winning nothing or losing $10) or a bad one (with a 50% probability of losing $10, and 25% probabilities of losing nothing or winning $10). These options varied randomly from trial to trial. Positive absolute outcomes were associated with activation of the nucleus accumbens (NAcc), the medial prefrontal cortex, the lateral orbito-frontal cortex (OFC), the anterior cingulate cortex (ACC), the posterior cingulate cortex, and the precuneus, whereas negative outcomes activated the anterior insula. Relative gains, when the outcome of the chosen option was better than the outcome of the alternative option (e.g., a win when the other option would have been a zero outcome or a loss), activated the caudal anterior cingulate, medial prefrontal cortex, caudate, putamen, dorsomedial thalamus, and frontal areas. Relative negative outcomes (e.g., a zero outcome when the alternative option would have been a win) activated the anterior insula. Further analyses of the anticipatory period before choice suggested that increased NAcc activity before a choice represented a shift in behavior toward higher risk (not choosing the safe option), whereas increased anterior insula activation was observed when behavior shifted toward more cautious decisions. Further, NAcc activity preceded risky mistakes and anterior insula activation preceded too cautious mistakes (see also other work by Knutson, Rick, Wimmer, Prelec, & Loewenstein, 2007). Dorsal ACC activity in the anticipatory period of decision-making was related to uncertainty and conflict (unsure to choose safe opportunity or not). Thus, the dorsal ACC was activated in the anticipation period whenever the participants had difficulties in making a decision. This might be due to the need for additional control or for activating resources to resolve a conflict successfully.

Recently, Amodio and Frith (2006) suggested that the function of the dorsal or posterior rostral medial prefrontal cortex (also denoted as the rostral cingulate zone) is to

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represent and update the value of possible actions and to regulate behavior. In particular, ACC neurons might shift decision-making toward optimal behavior. In line with this idea, the ACC may be an important structure for the formation of stimulus–response sets or intentions to action in difficult situations (Mitchell, 2006). If ACC neurons contribute to biasing a response selection signal toward optimal outcomes, these neurons also need information about the outcomes of previous behavior or the success of previous decision-making. The ACC may then use this feedback information to shift decision-making in future trials.

It has been suggested that the dopamine signal provides a feedback signal about the goal-directed behavior in the form of a temporal difference error according to learning theory (Holroyd & Coles, 2002; Schultz, 2002). In particular, recent findings suggest that the dopamine signal is specifically related to an action-oriented temporal difference (TD) error, in the context of a reinforcement learning method called Q-learning (Kennerley, Walton, Behrens, Buckley, & Rushworth, 2006), which complements suggestions that the feedback is goal oriented or related to the deviation from an intention (Hewig et al., 2007, 2008; Hajcak, Moser, Holroyd, & Simons, 2006, 2007; Holroyd & Krigolson, 2007; Holroyd, Hajcak, & Larsen, 2006; Holroyd & Coles, 2002). Furthermore, it has been suggested that an electrophysiological component in the event-related brain activity, namely the error-related negativity (ERN), is related to a negative TD error (Holroyd & Coles, 2002). Moreover, recent findings suggest that an electrophysiological positive potential in the same time frame, the P2a, might indicate a positive TD error (for converging findings, see also Hewig et al., 2008; Holroyd, Pakzad-Vaezi, & Krigolson, 2008; Potts, Martin, Burton, & Montague, 2006).

The ERN was initially observed in experiments involving response errors in reaction time tasks. The potential becomes maximal around 80 msec after the response (Gehring, Goss, Coles, Meyer, & Donchin, 1993; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991) and can be termed the response-locked error-related negativity (RERN). Further studies by Miltner, Braun, and Coles (1997) and others (Nieuwenhuis, Slagter, Alting von Geusau, Heslenfeld, & Holroyd, 2005; Mars, De Bruijn, Hulstijn, Miltner, & Coles, 2004) suggested that an ERN, the feedback ERN (FERN), might also be elicited by negative performance feedback (peaking at about 250 msec; Holroyd & Coles, 2002), or losses in gambling (Gehring & Willoughby, 2002). This potential reaches its maximum at around 250 msec post feedback. As noted, it has been suggested that the RERN and the FERN are both related to reinforcement learning, indicating a decrease in reward expectation because the outcome is worse than expected (Hajcak et al., 2006, 2007; Hewig et al., 2007; Holroyd & Krigolson, 2007; Holroyd et al., 2006; Holroyd & Coles, 2002). Dipole analyses of ERP and magnetoencephalographic studies provided some evidence for a source in the ACC for the RERN and FERN (e.g., Miltner et al., 1997, 2003; Ruchsow, Grothe, Spitzer, & Kiefer, 2002; Dehaene, Posner, & Tucker, 1994). In a recent study, Debener et al. (2005) have provided convincing evidence with a parallel recording of EEG and fMRI that the RERN to errors is generated by the ACC. Several fMRI studies also provided converging evidence for an activation in Brodmann's areas 24c and 32 (posterior rostral or dorsal ACC) in response to errors, conflict, or negative feedback (y-coordinates of activated areas ranging from 4 to 34 mm and z-coordinates ranging from 22 to 48 mm; e.g., Erickson et al., 2004; Fiehler, Ullsperger, & von Cramon, 2004; Holroyd et al., 2004; Kerns et al., 2004; Ullsperger & von Cramon, 2001, 2003; Ursu, Stenger, Shear, Jones, & Carter, 2003; Bush et al., 2002; Menon, Adleman, White, Glover, & Reiss, 2001; Carter et al., 2000; Kiehl, Liddle, & Hopfinger, 2000; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999).

In a recent study, we used a realistic Blackjack gambling task to further examine the function of the RERN and FERN in reinforcement learning (Hewig et al., 2007). We observed an RERN at the time of high-risk hit decisions, and an FERN both following losses of money and following the presentation of cards that indicated an impending loss of money. Our findings were consistent with the idea that the ERN process is related to reinforcement learning. In particular, increased ERN amplitudes were associated with decreases in reward expectation. Furthermore, larger ERN amplitudes led to the future avoidance of unsuccessful behavior. In summary, ERN activity appears to reflect the negative evaluation of an event or behavior and may lead to avoidance of the eliciting event or behavior in the future. In particular, our results showed an RERN at the time of the decision, suggesting an early negative evaluation of high-risk hit decisions. A similar negativity was found for low-risk sit decisions in preliminary results, that is, too cautious decisions (see supplementary data of Hewig et al., 2007).

The aim of the present study was to examine whether this negative evaluation is indeed present in both of these kinds of trials (too risky and too cautious) in a naturalistic gambling task with ecological validity. In addition, we asked whether the source of the negativity in EEG is indeed the dorsal or posterior rostral ACC. We used fMRI to determine whether the ACC receives an assessment of the value of an action whenever that action is too risky or too cautious, confirming and extending previous ERP results.

METHODS

Participants

Participants were recruited from the student population of the Friedrich-Schiller-University (Jena, Germany). A total of 17 right-handed students took part in the experiment (8 women; mean age = 22.58 years, *SD* =

±3.1 years, range = 19–28 years). All were paid €6 per hour for participation plus an extra bonus that varied between €2.90 and €6.50 (mean = €5.12, *SD* = €1.05, starting amount of 2.50) according to the participant's performance in a German version of the Blackjack gambling task. The studies were approved by the local ethics committee.

Procedure

Prior to the experiment, participants were informed that the purpose of the experiment was to investigate cortical activity during gambling, and a physician informed them about the fMRI recordings. Subsequently, they gave written consent for participation in the experiment.

After receiving verbal instruction about the basic rules of Blackjack, and after performing 32 practice trials of a German version called ''Seventeen and Four'' (Hewig et al., 2007, 2008), participants played four blocks of 88 single-game trials against a computer opponent. The game was played with the following cards of each suit: 11, 10, 9, 8, 7, 4, 3, and 2 (each counting as many points). As in Blackjack, the goal of the game was to get 21 points or to approach 21 points as closely as possible by successively drawing single cards from the bank, but to avoid getting over 21 points. In the present experiment, a computer simulated the opponent. Each game started with the simultaneous presentation of two cards for the player and two cards for the opponent with the starting point value of each pair of cards varying between 13 and 18. The range of starting values was more restricted than in our previous study (11–21) in order to increase the number of trials around the decision threshold (point score where decision-making shifts from sit to hit decisions). Furthermore, starting points of each pair were balanced between player and opponent across the experiment (including the practice trials). The computer generated a large deck of cards for the third card/additional card and randomly assigned a card to each trial. Because the additional card was not revealed in most trials, it was impossible for the participants to profit from knowledge of cards presented in previous trials. The cards of the player were depicted with the front side up on the left side of the horizontal midline of a video screen positioned in front of the participant and cards of the opponent were presented with the back side up at a small distance above the cards of the player. Together with this opening, players were presented a third card to the right of the first two cards with face down. Immediately after card presentation, participants had to either accept (hit) or reject (stay) this card. The maximum time for participant's decision was 2500 msec (one participant was excluded due to an extreme number of slow responses.) If the participant chose a hit, the front side of the chosen card was displayed (for 500 msec). If the participant rejected the card (or if total points exceeded 21), the game continued with the opponent's turn (after 400 msec). The strategy of the opponent was set to hit always at 14 or lower points and to stay whenever the sum of the cards was 15 or higher. At the end of the trial, the hand of the opponent was shown on the screen by turning all of the opponent's cards from the back to its front sides (400 msec after opponents turn). At the same time, feedback was given to the player indicating whether he or she had won or lost 10 Eurocent on the trial by presenting the words ''won'' (''gewonnen'') or ''lost'' (''verloren'') on the screen. Finally, the next trial started 2.5 TR (6.3 sec) after the beginning of the current trial by showing the initial cards for the next game trial.

As in our previous studies (Hewig et al., 2007, 2008), the logistic response pattern of each participant's decisions to hit or sit was analyzed with models from Item Response Theory (see Fischer & Molenaar, 1995; Hambleton & Swaminathan, 1985). This provides a parameter for the degree of risk taking of each participant (indicating the score for which the probability of accepting a hit or a sit was equal to 0.5), which may be called the risk threshold.

fMRI: Recording and Quantification

Participants were scanned using a 1.5-T magnetic resonance scanner (''Magnetom Vision plus''; Siemens Medical Systems). Four runs of 132 echo-planar volumes were acquired using a T2*-weighted sequence (TE = 50 msec, flip angle = 90°, matrix = 64 × 64, FOV = 192 mm, TR = 2.52 sec). Each volume comprised 25 axial slices with 4 mm thickness and an in-plane resolution of 3 × 3 mm. The slices covered the whole brain except for the most superior part of the cortex. In addition, a high-resolution T1-weighted anatomical scan was acquired (1 × 1 × 1 mm). The first four volumes were discarded to ensure that steady-state tissue magnetization was reached. Preprocessing and analysis of the functional data were performed using the software Brain Voyager QX (Version 1.8.6; Brain Innovation, Maastricht, The Netherlands). Data were realigned to the first volume in order to minimize the effects of head movements on data analysis. Subsequently, anatomical and functional images were normalized to the Talairach and Tournoux (1988) space and were spatially smoothed using an 8-mm full-width half-maximum isotropic Gaussian kernel filter and temporally smoothed using a high-pass filter with 2.8 cycles per run.

Statistical analyses were performed with a random effects model using multiple linear regression of the signal time course at each voxel. The expected blood oxygen level-dependent signal change was modeled by a canonical hemodynamic response function. In the first step, voxelwise statistical maps were generated and the relevant, planned contrasts of predictor estimates (beta-weights) were computed for each individual. In the second step, a random effect group analysis of these

Table 1. Number of Trials in Each Condition and Definition of Contrasts

Point Score	*13/14*					*15–18*					
Decision	*Sit*		*Hit*			*Sit*		*Hit*			*All*
Outcome	*Win*	*Loss*	*Win*	*Loss*	*Bust*	*Win*	*Loss*	*Win*	*Loss*	*Bust*	*Error*
Number of trials	1	9.2	50.1	15.7	47.8	126.8	53.3	28.1	1.8	17.2	1.2
Contrasts	–	a	c/f	f	b	e	a/e	c	–	b	–

Average number of trials in each condition. The two conditions compared with each other in each of the contrasts are indicated by a, b, c, d, and e.

individual contrasts was performed. Eleven predictors were included in the general linear model (see Table 1 for the number of trials). Ten predictors represented 10 different trial types: 5 each for starting scores of 13/14 versus 15–18 (sit decision and win, sit decision and loss, hit decision and bust, hit decision and final win, hit decision and final loss). One error trial predictor was used for trials where participants did not show a response or showed a late response. The grouping of the point scores followed two criteria. First, Table 2 reveals that for scores of 13 and 14, a hit decision was clearly favorable, whereas for trials between 16 and 18, a sit was more favorable. A score of 15 is on the threshold between sit and hit concerning optimal behavior and participant behavior as well. In order to optimize the number of trials in different conditions, and thus, increase the power of the analyses, a score of 15 was included in the group of higher point scores.

A first group of three contrasts compared trials with suboptimal decision-making with comparable trials with optimal decision-making in order to test the main hypothesis of increased ACC activity in response to suboptimal decision-making. First, trials with a sit decision and a loss at a point score of 13/14 (low risk) were contrasted with trials with a sit decision and a loss at a point score of 15–18 (high risk). Second, trials with a hit decision and a bust at high risk (15–18) were compared with that same trials at low risk (13/14). Third, trials with a hit decision and a final win at high risk (15–18) were compared with that same trials at low risk (13/14). Another group of two contrasts examined the role of final feedback (win vs. loss) for a comparison of these results with previous ERP findings. First, trials with a hit decision and a final win were compared with trials with a hit decision and final losses at starting scores of 13/14 and, second, a contrast was calculated for trials with a sit decision and a win versus trials with a sit decision and a loss at starting scores of 15–18.

The results of the analysis within our main region of interest (ROI), the ACC, were considered statistically significant for t values with $p < .005$ as in our previous studies (e.g., Straube, Weiss, Mentzel, & Miltner, 2007; Straube, Glauer, Dilger, Mentzel, & Miltner, 2006). For interindividual correlation analyses, average beta values across active clusters were used to increase reliability. The ROI was defined using Talairach daemon software (www.ric.uthscsa.edu/projects/talairachdaemon.html). For further exploratory analyses outside of the ACC, thresholds were set at $p < .0005$. In all analyses, a cluster threshold of 100 contiguously activated voxels ($1 \times 1 \times 1$) was used to minimize false-positive results.

Table 2. Probabilities of Winning for Different Starting Points

Total Points	*13*	*14*	*15*	*16*	*17*	*18*
p(win|sit)	.08	.11	.30	.52	.77	.93
p(win|hit)	.41	.40	.34	.33	.34	.21

p(win|sit) denotes the empirical probability of winning given a sit decision and p(win|hit) denotes the probability of winning given a hit decision for each starting score.

RESULTS

Behavioral Data

The participants' average decision-making behavior is shown in Figure 1. As indicated by the graph, the probability of taking another card decreased as the player's current total points increased. The risk threshold ranged from 14.38 to 15.97 (mean = 15.17, *SD* = 0.49). The

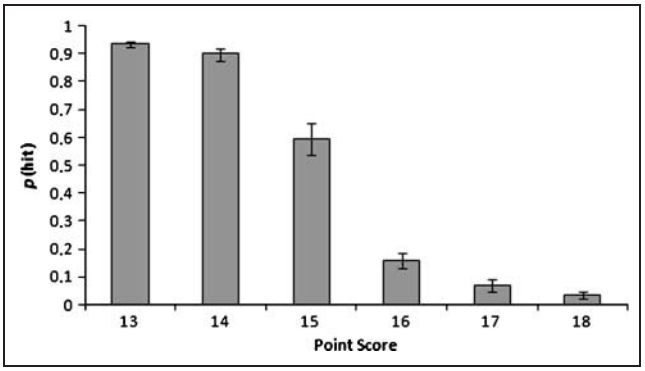

Figure 1. Average decision-making behavior. The figure shows the response characteristic averaged across all participants and decisions. The *y*-axis represents the mean probability of hit decisions (taking another card) across all participants at each current amount of points (*x*-axis, 11–21 points) with two and three cards (error bars indicate standard error).

Table 3. Significant Activation for the Contrast of Low-risk Sits minus High-risk Sits

Region		Talairach x	Talairach y	Talairach z	Max. t Value	n Voxel
ROI						
Anterior cingulate (BA 32/24)	R	9	11	37	4.42	277
Exploratory						
Lateral OFC (BA 46)	R	45	44	7	7.90	651

Talairach coordinates (x, y, z) of maximal activated voxel. R = right; Activation threshold: $p < .005$ for ROI, uncorrected; clusters > 99 voxels.

linear correlation between the risk threshold and the amount of money participants won was not significant ($r = -.23$, $p = .392$), yet the quadratic regression effect was significant [$F(2, 13) = 6.32$, $p = .012$, $R^2 = .49$], showing an inverse U-shaped relation, which indicates that some participants played more cautiously and others more riskily than was optimal.

fMRI Data

Analysis of Too Risky and Too Cautious Decisions

A first analysis addressed the question whether too cautious (sit at scores of 14 and lower) and too risky (hit at scores of 15 and higher) decisions would be associated with activations in the ACC as predicted by EEG evidence in our previous experiment.

A first contrast compared trials with a point score of 13/14 (low risk) to trials with a point score of 15–18 (high risk) subsequent to a sit decision (low-risk sits vs. high-risk sits). Only trials leading to a final loss could be used because there were almost no low-risk sit decisions that lead to a win. These decisions may be defined as too cautious because, according to optimal play, the appropriate decision is to hit. ROI analysis showed significant activations in the right ACC (BA 24) as predicted (see Table 3). Thus, as expected, too cautious decisions led to ACC activation (Figure 2). In addition, the right lateral OFC showed activation in the exploratory analysis. A second contrast compared high-risk hit decisions (15–18) with low-risk hit decisions (13/14). This analysis was performed separately both for hits leading to a bust and for hits leading to a win (see Table 4). First, an ROI

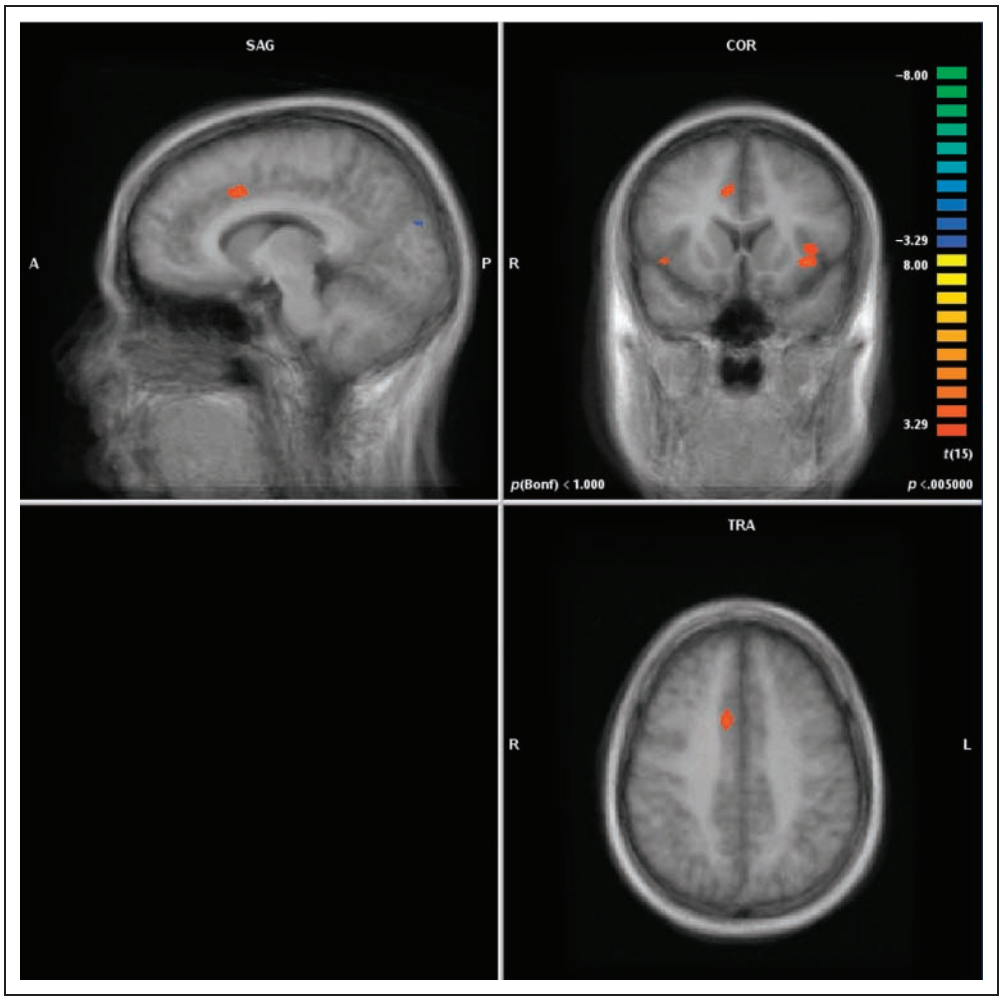

Figure 2. Too cautious decisions. Low-risk sit decisions as compared to high-risk sit decisions lead to significant ACC activation.

Table 4. Significant Activation for the Contrast of High-risk Hits minus Low-risk Hits

		Bust					*Win*				
		TAL					*TAL*				
Region		*x*	*y*	*z*	*Max t*	*n*	*x*	*y*	*z*	*Max t*	*n*
ROI											
ACC (BA 32/24)	R	9	20	34	3.98	183	6	5	40	4.70	340

R = right; TAL = Talairach coordinates (x, y, z) of maximal activated voxel; Max t = t level at this voxel; n = number of activated voxels; ACC = anterior cingulate cortex. Activation threshold: $p < .005$ for ROI, uncorrected; explorative clusters > 99 voxels.

analysis revealed significant activation of the right ACC for high-risk as compared to low-risk busts (Figure 4). Moreover, the ROI analysis revealed a significant activation in the right ACC (BA 32/24) for high-risk hits that lead to a win (Figure 3). Thus, ACC activation was independent of final outcome but was triggered by high-risk hit decisions. Exploratory analyses did not reveal further significant activations.

Thus, right ACC activation was observed for both too cautious and too risky decisions.

Analyses of Final Feedback

There was no increased activation for losses as compared to wins in ROI analyses or exploratory analyses. Exploratory analyses revealed greater activation after wins as compared to losses widespread across regions (see Table 5).

Interindividual Differences

We further analyzed whether activity in the ROIs was associated with risk-taking behavior. The correlations between beta values for each subject and the individual risk threshold revealed a significant positive relation between the risk threshold and ACC activity to low-risk sits as compared to high-risk sits ($r = .49$, $p = .028$). Thus, riskier participants showed relative greater ACC activity for too cautious decisions as compared to more reasonable sit decisions. In addition, there was a significant negative correlation between risk threshold and ACC activity

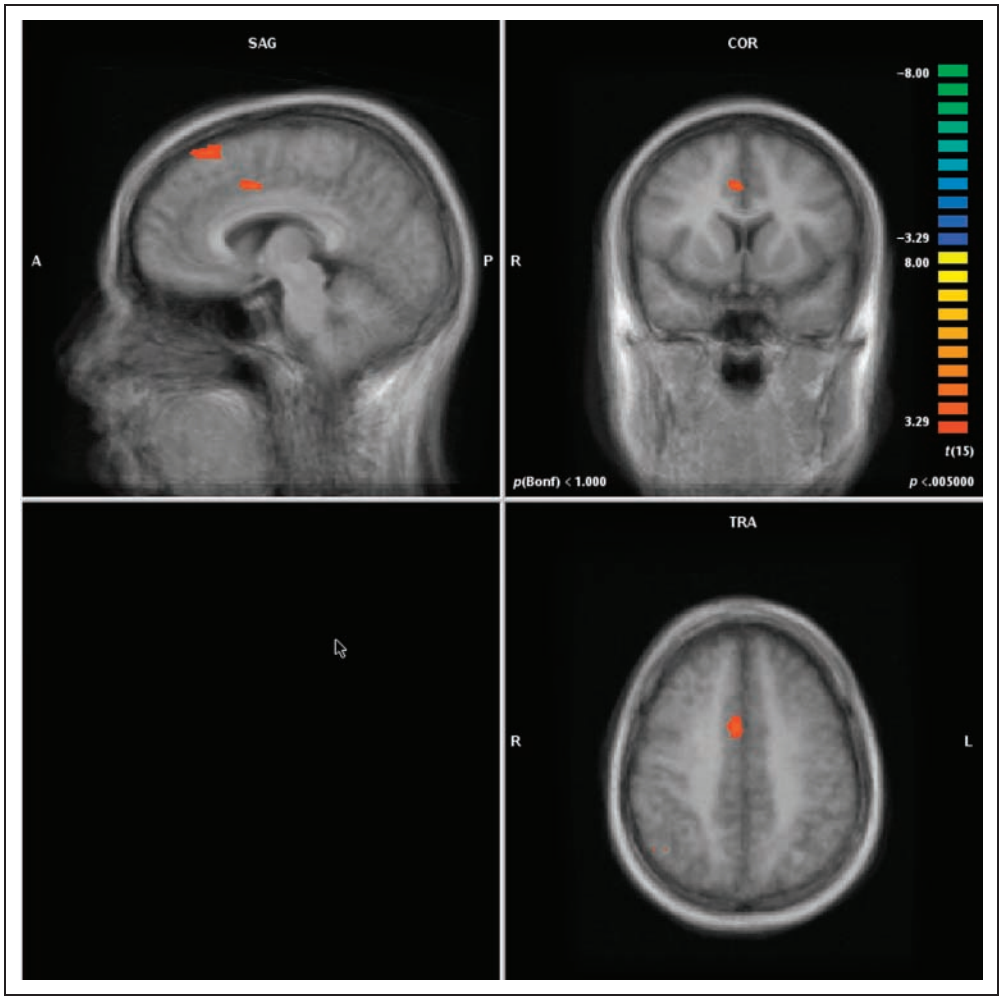

Figure 3. Too risky decisions. High-risk hit decisions as compared to low-risk hit decisions elicit significant ACC activation despite the fact that all trials resulted in final wins.

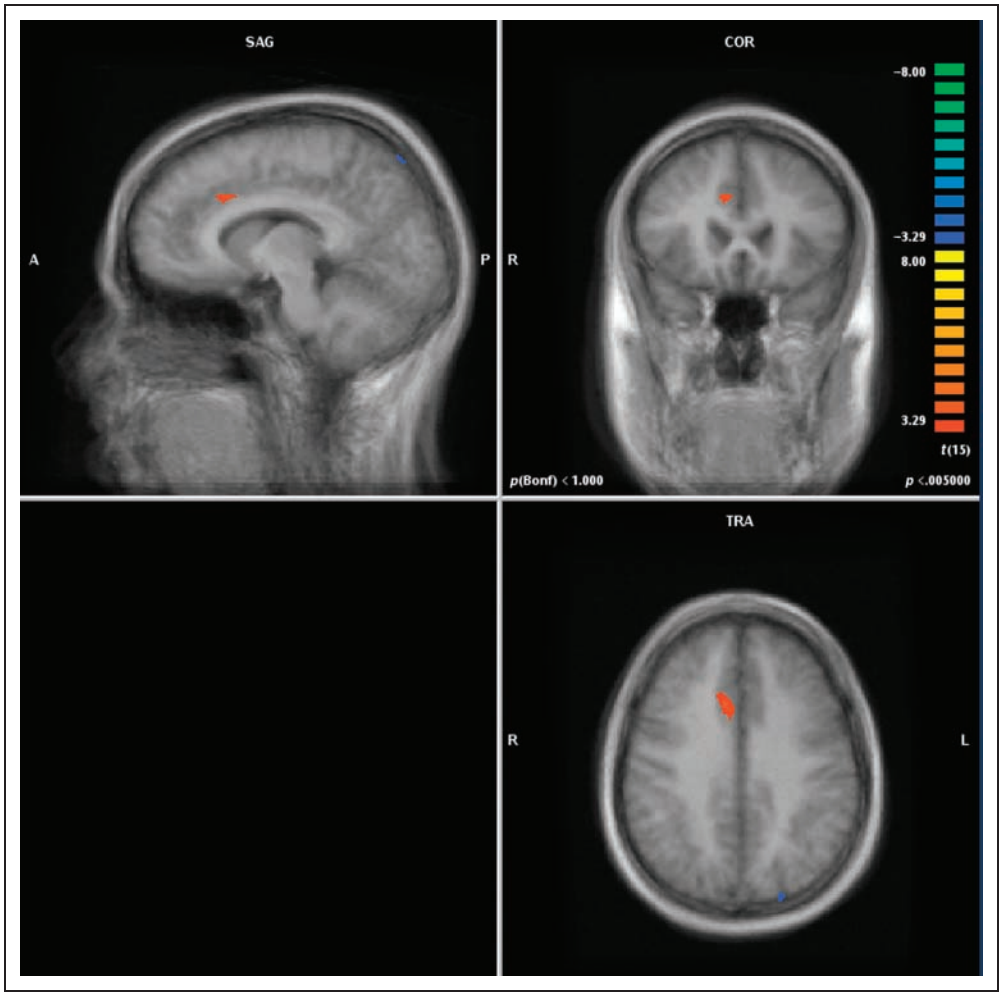

Figure 4. Too risky decisions. High-risk hit decisions as compared to low-risk hit decisions elicit significant ACC activation in trials that resulted in busts.

for high-risk hits ($r = -.66$, $p = .003$; not significant for ACC activity to busts, $r = -.16$). Thus, more cautious participants showed increased ACC activity for high-risk hits as compared to more reasonable hits.

DISCUSSION

The aim of the present study was to examine whether the dorsal ACC is activated by suboptimal decisions that are either too risky or too cautious. Furthermore, we aimed to evaluate fMRI data in the context of previous ERP findings with the same gambling task.

Our results clearly support the notion that a negative evaluation of decision-making under risk is related to an activation of the dorsal ACC. In particular, too cautious decisions elicited dorsal ACC activity as compared to reasonably cautious choices, and too risky decisions elicited dorsal ACC activity as compared to more reasonable risk taking. Moreover, all of the observed ACC effects were localized in the same region of the dorsal ACC. Together with our recent ERP findings, the results indicate that the ACC is activated by an early evaluation of an action that reflects suboptimal decision-making—being either too cautious or too risky. This evaluation occurs before, and is independent of, the feedback indicating the outcome of the decision. The same kinds of risky decisions elicited an RERN in the same Blackjack task used here (Hewig et al., 2007). The present results are also in line with the many previous fMRI studies of errors in reaction time tasks and negative feedback in learning or gambling tasks reviewed earlier.

It may be argued that the three conditions, where we found increased ACC activity, include some confounding influence. First, for the comparison between low-risk sits and high-risk sits, it may be argued that initial point score is a confound, which would indicate that dorsal ACC activity is generally related to low risk. However, the finding of ACC activity in almost the same region for high-risk hits indicates that the initial point score, that is, the degree of risk in general, is not important. Rather it is the decision-making in relation to the degree of risk that is critical. It might further be argued that final feedback is a confounding factor. However, we found ACC activity in relation to suboptimal decision-making not only for high-risk hit trials with negative final feedback but also for those with positive final feedback. Finally, ACC activity was also not specific to the kind of decision

Table 5. Significant Activation for the Contrasts of Win versus Loss

	13/14 Hit						*15–18 Sit*					
		TAL						*TAL*				
Cluster in Region		*x*	*y*	*z*	*Max t*	*n*		*x*	*y*	*z*	*Max t*	*n*
DLPFC	B	−30	53	31	5.89	354	B	−52	26	13	5.70	284
Medial OFC	L	−30	63	22	6.41	192	B	−6	50	4	8.80	2143
Lateral OFC							B	36	30	−3	6.46	476
PMC	L	−27	44	43	5.97	106	B	−9	−10	52	7.60	1761
Somatomotor							B	60	−20	31	5.57	1146
Parietal							B	60	−28	21	7.51	759
Temporal							B	−40	−31	10	8.27	3761
Occipito-temporal							B	−55	−64	16	9.01	1091
ACC rostral							B	−5	47	4	8.32	1861
Posterior cingulate cortex							B	−3	−37	37	8.61	3741
Retrosplenial							B	−39	−30	14	6.97	855
Insula							B	−36	−22	16	7.44	1050
Parahippocampus							B	27	−1	−14	7.71	1184
Amygdala							B	18	−7	−11	8.35	1713
Thalamus							R	15	−22	4	5.43	240
Basal ganglia							B	15	8	1	10.31	6753
Cer. uvula	B	30	−82	−24	6.63	793						
Cer. declive	L	−9	−76	−20	5.48	148	L	−12	−76	−14	5.97	464
Cer. culmen							R	39	−37	−23	6.71	566

R = right; L = left; B = bilateral; TAL = Talairach coordinates (x, y, z) of maximal activated voxel; Max t = t level at this voxel; n = number of activated voxels; ACC = anterior cingulate cortex; Ant. Ins. = anterior insula; DLPFC = dorsolateral prefrontal cortex (BA 9, 46); Lat. OFC = lateral orbito-frontal cortex (BA 45, 47), medial OFC (BA 10). Somatomotor areas (BA 2–4), occipito-temporal (BA 19, 37, 39), PMC = premotor cortex (BA 6, 8), parietal (BA 7, 40), Cer. = cerebellum. Activation threshold: $p < .005$ for ROI, uncorrected; explorative clusters > 99 voxels.

(hit or sit) because we found it for high-risk hits and low-risk sits.

In summary, the consistent common factor in the three contrasts for which we find ACC activation is the suboptimality of decision-making given empirical estimates of reward expectation (see Table 2). Thus, the findings are in line with a negative TD error or reinforcement learning view of ACC activity concerning the immediate evaluation of behavior. Moreover, our analyses of interindividual differences are well in line with previous findings with ERPs (e.g., Cohen & Ranganath, 2007; Hewig et al., 2007; Frank, Woroch, & Curran, 2005). More cautious participants showed increased ACC activity to high-risk hits and more risky participants showed increased ACC activity to low-risk sits. For a particular suboptimal decision, greater ACC activity was related to avoidance of that decision.

These results relate to research on interindividual differences such as anxiety or behavioral inhibition, sensation seeking or impulsivity, and to relevant disorders such as pathological gambling. For example, increased ERN activity has been shown for high negative affect, neuroticism, and for high scorers on behavioral inhibition (Amodio, Master, Yee, & Taylor, 2008; Boksem, Tops, Wester, Meijman, & Lorist, 2006; Luu, Collins, & Tucker, 2000), a concept proposed by Gray and McNaughton (2000) reflecting strong punishment processes and good passive avoidance learning. Accordingly, it has been shown that increased ERN activity is related to superior avoidance learning (Frank et al., 2005) and increased dorsal ACC activity to the ability of quitting gambling after losses (Campbell-Meiklejohn, Woolrich, Passingham, & Rogers, 2008). The latter finding is related to pathological gambling, which includes the inability to stop gambling despite negative consequences (Campbell-Meiklejohn et al., 2008). Taken together, this might indicate that deficient dorsal ACC activity may be part of a more general deficit of medial prefrontal cortex functioning in gambling (Reuter et al., 2005; Potenza et al., 2003), which is in line with the finding of decision-making deficits in

patients with damage to the ventromedial prefrontal cortex (Clark et al., 2008). This is in agreement with the suggested role of dopaminergic innervations of the medial prefrontal cortex in both ERN processes (e.g., Holroyd & Coles, 2002) and pathological gambling (Hollander, Buchalter, & DeCaria, 2000; Comings et al., 1996, 1999).

It may be argued that the ACC activity we have identified was elicited by uncertainty or conflict (for further evidence for conflict effects, see Fan et al., 2007; Sohn, Albert, Jung, Carter, & Anderson, 2007; Stahl & Gibbons, 2007; Kerns et al., 2004; Ursu et al., 2003; Carter et al., 2000; Botvinick et al., 1999). For example, in the study by Kuhnen and Knutson (2005), ACC activity in the anticipatory period of decision-making was related to uncertainty and conflict (unsure whether or not to choose the safe option). Thus, the ACC was activated in the anticipation period whenever the participants had difficulties in making a decision. In the present case, it may be suggested that the highest conflict should be found for trials with scores of 15 (next highest conflict would be expected for 16), as a score of 15 (and 16) is closest to the decision threshold (15.2; see also Figure 1). Participants chose to hit and sit with equal probability at 15 (for a similar suggestion concerning high conflict in Blackjack, see Yang, Li, Zhang, Qiu, & Zhang, 2007). ACC activity in high-risk hits (comprising scores of 15) would be compatible with this expectation and with a conflict theory explanation of the present findings. However, our finding of ACC activity to low-risk sits (scores of 13/14, low conflict) is not in line with the prediction from the conflict account that scores of 15 should be accompanied by the highest ACC activity. For this reason, conflict cannot account for the present results.

A further potential problem for our position is that we failed to find increased ACC activity in response to final negative feedback. Two reasons may be given for this failure. First, there was a strong general increase in many brain regions following wins. Reinforcement processes associated with these wins seem to be very active as there was no region across the whole brain showing higher activity under negative feedback. One possibility may be that reinforcement processes generally increase the activity of the brain more than punishment processes. Another possibility might be that participants were, on average, continuously winning. This may have sensitized reward regions of the brain. A further possibility is that final feedback may result in an outcome either worse than expected or better than expected. Although these two different effects may be separated in event-related potentials due to the different polarity, ERN for negative TD error and P2a for positive TD error (Potts et al., 2006), in fMRI both TD errors might increase ACC activity, and thus, wins and losses may both elicit dorsal ACC activity. Therefore, a contrast between win and loss conditions may lead to a null finding, although the ACC might be active to a certain degree in both conditions.

The following considerations apply to the events surrounding the immediate evaluation of an action. Whenever an action is not very difficult, a successful action or decision (absence of an error) is the optimal option chosen by the action system, and thus, it is as good as expected. In these cases, no TD error results because the action is as good as was intended. Alternatively, if the optimal option is not chosen, a negative TD error may immediately be generated after the response choice. This is manifested in differential ACC activity and RERNs between optimal and suboptimal decisions. Of course, it is possible that the differential ACC activity observed in the present study is due to either increased activity for suboptimal responses or decreased activity for optimal responses or both (a suitable neutral control condition probably cannot be implemented; see Holroyd et al., 2006).

In addition, the ACC should be activated not only at the time of feedback but also in situations when information, accumulated via reinforcement learning, has to be used and the biasing function on decision-making has to be executed. This applies to difficult situations, such as those involving conflict and uncertainty. ACC activity then reflects the demand to use the reinforcement learning information stored from previous occasions. Thus, ACC activity in fMRI might be related (1) to the demand of using reinforcement learning information—that is a biasing signal—under ambiguity, conflict, or uncertainty both before and during decision-making and action; and (2) to the feedback provided by the dopamine signal in order to update the biasing signal of ACC neurons after decision-making or feedback signals. The latter reason for ACC activity seems to be the best explanation for the present findings. It has to be noted here that the design of our analyses did focus on the decision to hit or sit and its evaluation rather than on the anticipatory or preparatory period of decision-making.

In summary, the two sources of ACC activity described above are in line with results of recent research providing evidence for the importance of ACC activity in both conflict monitoring and reinforcement learning (see Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Yeung, Cohen, & Botvinick, 2004; Holroyd & Coles, 2002; Botvinick, Braver, Barch, Carter, & Cohen, 2001). In line with reinforcement learning theory, it may be suggested that a biasing signal is accumulated in the ACC during experiences of punishment (negative TD errors) and reinforcement (positive TD errors). Although the present ACC activity may not be explained by conflict theory (e.g., Yeung et al., 2004; Botvinick et al., 2001), it may be suggested that ACC activity is also elicited by the need to retrieve the biasing signal from the ACC to modulate decision-making in situations of risk, uncertainty, or conflict.

In conclusion, we have shown that suboptimal decision-making is associated with increased activity in the ACC in a Blackjack gambling task. Moreover, the increased

activity is related to avoidance of negatively evaluated decisions, and thus, can be accommodated within the principles of reinforcement learning.

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