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The Neural Basis of Financial Risk Taking

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Summary

Investors systematically deviate from rationality when making financial decisions, yet the mechanisms responsible for these deviations have not been identified. Using event-related fMRI, we examined whether anticipatory neural activity would predict optimal and suboptimal choices in a financial decision-making task. We characterized two types of deviations from the optimal investment strategy of a rational risk-neutral agent as risk-seeking mistakes and risk-aversion mistakes. Nucleus accumbens activation preceded risky choices as well as risk-seeking mistakes, while anterior insula activation preceded riskless choices as well as risk-aversion mistakes. These findings suggest that distinct neural circuits linked to anticipatory affect promote different types of financial choices and indicate that excessive activation of these circuits may lead to investing mistakes. Thus, consideration of anticipatory neural mechanisms may add predictive power to the rational actor model of economic decision making.

Introduction

Individual investors systematically deviate from optimal behavior, which could influence asset valuation (Daniel et al., 2002; Hirshleifer, 2001; Odean, 1998). The causes of these deviations have not been established, but emotion may have some influence. While some research has examined the role of emotion in decision making (Camerer et al., 2005; Loewenstein et al., 2001) and economists have begun to incorporate emotion into models of individual choice (Bernheim and Rangel, 2004; Caplin and Leahy, 2001), scientists still lack a mechanistic account of how emotion might influence choice. Understanding such mechanisms might help theorists to specify more accurate models of individual decision making, which could ultimately improve the design of economic institutions so as to facilitate optimal investor behavior.

Here, we sought to examine whether neural activation linked to anticipatory affect would predict financial choices. At least two hypotheses have been put forth regarding the role of affect in decision making. According to one account, undifferentiated arousal might be related to both risk seeking and risk aversion (Lo and Repin, 2002). However, according to a second account, positive aroused feelings associated with anticipation of gain (e.g., "excitement") may promote risk taking, whereas negative aroused feelings associated with anticipation of loss (e.g., "anxiety") may promote risk aversion (Knutson et al., 2005; Paulus et al., 2003).

Recent evidence from human brain imaging implies that affect evoked by the anticipation of gain and loss may carry distinct neural signatures. Specifically, the nucleus accumbens (NAcc) of the ventral striatum shows proportional activation during anticipation of monetary gains (Breiter et al., 2001; Knutson et al., 2001), and this activation correlates with positive aroused affect (Bjork et al., 2004; Knutson et al., 2005; Martinez et al., 2003). Neural markers of anticipatory negative affect have not been as clearly delineated, but the anterior insula provides a candidate substrate for a number of reasons. First, brain imaging studies have consistently reported activation of the anterior insula during anticipation of physical pain, which correlates with self-reported state anxiety (Buchel and Dolan, 2000; Chua et al., 1999; Ploghaus et al., 1999). Second, the anterior insula shows activation during anticipation of aversive visual stimuli (Simmons et al., 2004). Third, the anterior insula shows activation during risky choice in games involving nonmonetary incentives, which correlates with subsequent risk-aversion and trait measures of negative aroused affect (Paulus et al., 2003). Although the anterior insula is also sensitive to attentional and other demands (Phan et al., 2002), a recent review suggests that activation in this region is more common under negative than positive affective circumstances (Wager et al., 2003).

The goals of this experiment were, first, to determine whether anticipatory activity in the NAcc and anterior insula would differentially predict risk-seeking versus risk-averse choices and, second, to examine whether activation in these regions would precede both suboptimal and optimal choices. Two studies have correlated anticipatory neural activation with choice, but both involved choices that occurred in the context of social interactions (which might prove more susceptible to affective biases) rather than financial decisions (Fehr et al., 2004; Sanfey et al., 2003). Another study demonstrated a correlation between neural activation and immediate versus delayed reward choices, but did not investigate risky choices (McClure et al., 2004).

To investigate the influence of anticipatory neural activation on financial risk taking, we combined a dynamic investment task with event-related fMRI. We compared subjects' actual investment choices during the task to those of a rational risk-neutral agent who maximizes expected utility. Suboptimal choices were defined as deviations from this model and included both "risk-seeking mistakes" (in which people take risks when they should not) and "risk-aversion mistakes" (in which people do not take risks when they should).

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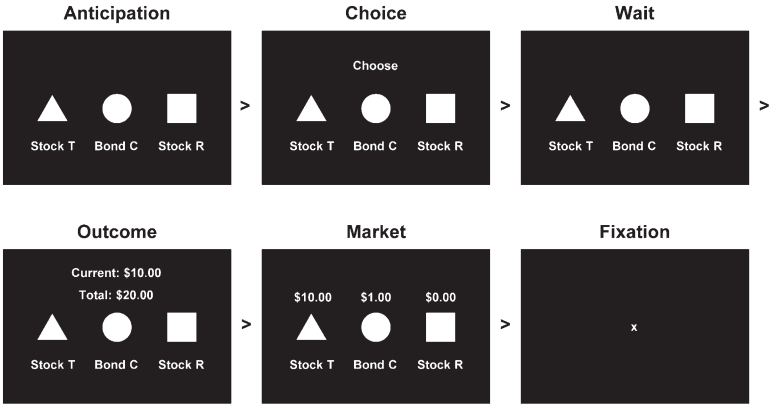

Figure 1. Trial Structure

2 s per panel.

We designed a task to elicit a range of investment behaviors, including risk-seeking and risk-averse financial choices. The Behavioral Investment Allocation Strategy (BIAS) task consisted of 20 blocks of 10 trials each (see Figure 1). During each trial, subjects first saw two stocks and a bond (Anticipation) and then chose one when the word "Choose" appeared above the assets (Choice). Then subjects waited for a brief period (Wait), after which their earnings for that trial and total earnings were displayed (Outcome). These were followed by a display of the outcomes of all assets on that trial (Market) and a fixation cross (Fixation; see Figure 1).

At the beginning of each block (indicated by a cue), one of the two stocks was randomly assigned to be the "good" stock, while the other was assigned to be the "bad" stock, without the subject's knowledge. The good stock dominated the bad stock in the sense of first-order stochastic dominance (Huang and Litzenberger, 1988). Specifically, outcomes of the good stock (i.e., +$10 with 50% probability, +$0 with 25% probability, and –$10 with 25% probability) were better than outcomes of the bad stock (i.e., +$10 with 25% probability, +$0 with 25% probability, and –$10 with 50% probability) on average for each trial. The bond paid $1 with 100% probability on each trial. Earnings were drawn independently from these distributions for each trial, and subjects were informed about the distributions before performing the task.

Based on prior research, we first predicted that gain versus loss outcomes would activate the NAcc and mesial prefrontal cortex (MPFC) (Knutson et al., 2003) and that loss versus gain outcomes would instead activate the anterior insula (Paulus et al., 2003). We then examined whether NAcc activation preceded both optimal and suboptimal stock (i.e., risky) choices, as well as whether anterior insula activation instead preceded both optimal and suboptimal bond (i.e., riskless) choices.

Results

Analyses of brain imaging data focused on changes in activation during outcome, market, and anticipation periods prior to a given choice. Analyses proceeded through two stages. In the first "localization" stage, we constructed group statistical maps to identify foci of interest and then verified the predicted patterns of activation with multivariate regressions. In the second "prediction" stage, we used activation extracted from these foci during the anticipation period to predict both optimal and suboptimal subsequent investment choices with logit regression models.

In localization analyses of the outcome period, stock gain versus loss outcomes were associated with NAcc and MPFC activation at both the small volume-corrected and global thresholds, as predicted (Knutson et al., 2003) (see Table 1 and Figure 2). Although the anterior insula did not show significant deactivation at the global threshold, bilateral foci did show the only deactivations in the brain for this contrast that passed the small volume-corrected threshold (TC = –39, 19, 7; Z = –2.99; TC = 38, 19, 11; Z = –2.99). Other regions that passed the global threshold included right orbitofrontal cortex, left anterior cingulate, left precuneus, and left posterior cingulate, replicating prior findings (Knutson et al., 2003). Multiple regression of VOI data (hemodynamic lag = 4 s) verified that, after prior stock choice, gain outcomes were associated with increased NAcc and MPFC activation (all p values < 0.05; see Table S1 in the Supplemental Data available online).

In analyses of the market period, relative gain outcomes (i.e., larger difference between the outcome of the chosen versus unchosen stock) were also associated with MPFC activation at the small volume-corrected and global thresholds, as predicted (see Table 2 and Figure 2). Other areas that passed the global threshold included left middle frontal gyrus, bilateral caudate, left putamen, and dorsomedial thalamus. Mul-

Table 1. Activation Foci for Choice Outcome: Contrast of Gain versus Loss following Stock Choice

Region	Z Score	Talairach Coordinates
L MPFC	5.34	–3, 56, 4
L MPFC	5.47	–3, 49, 0
R OFC	3.89	22, 36, –8
R NAcc	6.41	11, 12, –3
L NAcc	5.82	–13, 8, –4
L Ant. Cing	4.07	–1, –1, 34
L Precuneus	4.71	–1, –33, 43
L Post. Cing.	5.11	–3, –34, 27

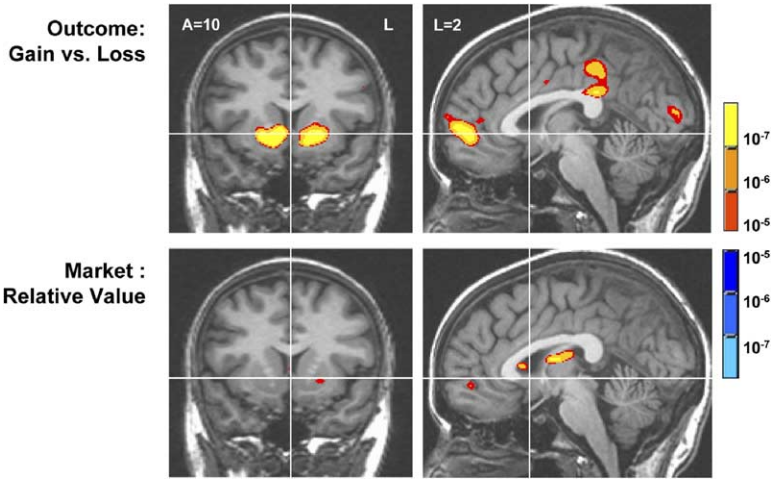

Figure 2. Effect of Actual and Relative Outcomes on Neural Activation

The top panels depict the contrast of large gains versus large losses during the Outcome period following stock choice. The bottom panels depict the contrast of chosen versus unchosen outcomes during the Market period following stock choice. n = 19.

tivariate regression of VOI data verified that, after a stock choice, relative gain outcomes increased NAcc and MPFC activation. Conversely, relative loss outcomes increased anterior insula activation (see Table S2). After a bond choice, relative gain outcomes (i.e., either of the stocks performed worse than the bond) increased MPFC activation (see Table S3).

While not the focus of this study, uncertainty correlated maximally and negatively with bilateral anterior cingulate foci, easily exceeding the global threshold (TC = +4 16, 45; Z = –5.37; TC = –4, 16, 45; Z = –6.99). Further analysis of anticipatory activation extracted from these foci revealed that activation was not greatest with maximal uncertainty (i.e., uncertainty = 0.5, corresponding to minimal information about which stock to choose), but rather with maximal conflict (i.e., uncertainty = 0.3, corresponding to minimal information about whether to choose the stock or the bond). Specifically, activation in this region was –0.08 ± 0.01 (mean ± SEM, n = 2100) when uncertainty was less than 0.25; –0.05 ± 0.01 (n = 868) when uncertainty was between 0.25 and 0.35; and –0.15 ± 0.02 (n = 832) when uncertainty was greater than 0.35. Additionally, anterior cingulate anticipatory activation robustly predicted subjects' subsequent reaction time [$t(3718) = 7.92$, $R^2 = 0.15$ in a linear regression model that included subject fixed effects]. Thus, anticipatory anterior cingulate activation correlated most robustly not with uncertainty, which was greatest when it was unclear which stock to choose, but rather with conflict, which was greatest when it was unclear whether to choose a stock or the bond. However, anticipatory anterior cingulate activation did not correlate with subsequent choice, as described below.

Table 2. Activation Foci for Market Outcome: Contrast of Chosen Stock versus Unchosen Stock Value

Region	Z Score	Talairach Coordinates
L MFG	3.93	–3, 56, 8
L MPFC	4.26	–3, 49, –5
L Caudate	4.46	–7, 19, 8
R Caudate	4.59	7, 19, 8
L Putamen	4.14	–20, 9, –2
DM Thalamus	5.00	–1, –7, 12

In prediction analyses, we included anticipatory NAcc, MPFC, and anterior insula activation (lag = 4 s) in logistic regression models of subsequent choice, after incorporating relevant behavioral variables (see Tables 3–5). Adding activation from control regions (i.e., bilateral anterior cingulate, orbitofrontal cortex, medial caudate, and amygdala) did not increase explanatory power, and so, data from these regions were not included in subsequent prediction analyses.

Logistic regressions indicated that anticipatory NAcc and anterior insula activation were correlated with subsequent choice and that these associations critically depended upon prior choice. For all choices, anticipatory NAcc activation increased the likelihood of choosing a stock only when the prior choice was a bond (a 0.1% increase in NAcc activation led to a 0.06% increase in the odds of choosing a stock; $p < 0.05$). When the prior choice was a stock, anticipatory anterior insula activation increased the likelihood of choosing the bond (a 0.1% increase in anterior insula activation led to a 0.08% increase in the odds of choosing a bond; $p < 0.05$; see Table 3 and Figure 3). MPFC activation did not correlate with subsequent choice. Thus, high NAcc activation preceded switching to risk-seeking choices, while high anterior insula activation preceded switching to risk-averse choices.

Logistic regressions also indicated that anticipatory NAcc and anterior insula activation were correlated with the types of mistakes that subjects made. When the prior choice was riskless (i.e., the bond), anticipatory NAcc activation increased the likelihood of making a risk-seeking mistake (a 0.1% increase in NAcc activation led to a 0.07% increase in the odds of making a risk-seeking mistake; $p < 0.05$). Also, anticipatory NAcc activation decreased the likelihood of making a risk-aversion mistake (a 0.1% increase in NAcc activation led to a 0.06% decrease in the odds of making a risk-aversion mistake; $p < 0.05$). When the prior choice was risky (i.e., a stock), anterior insula activation increased the likelihood of making a risk-aversion mistake (a 0.1% increase in insula activation led to a 0.11% increase in odds of making a risk-aversion mistake; $p < 0.05$; see

Table 3. Logit Estimation of the Probability of Choosing a Stock or Bond in Trial *t*

	Previous Choice Was a Stock	Previous Choice Was the Bond	All Data
$StockChoice_t$	Coef	Coef	Coef
$INAcc_t^{ANT}$	−0.0498	0.5889	0.3192
	(0.24)	(3.21)***	(2.70)***
$IMPFC_t^{ANT}$	−0.0461	−0.0222	−0.0137
	(0.26)	(0.15)	(0.14)
$linsula_t^{ANT}$	−0.7875	0.1910	−0.2359
	(3.04)***	(0.89)	(1.69)*
$RelEarnings_{t-1}$	−0.0550	0.0447	−0.0360
	(5.18)***	(4.08)***	(6.65)***
$Outcome_{t-1}$	−0.0253		−0.0452
	(1.88)*		(4.65)***
$Uncertainty_t$	−4.7256	−8.8818	−8.1441
	(7.68)***	(12.89)***	(21.42)***
$CumEarnings_{t-1}$	−0.0036	−0.0017	−0.0031
	(3.43)***	(1.99)**	(5.51)***
Constant	2.7542	1.8624	2.7986
	(7.37)***	(5.30)***	(12.33)***
Observations	1578	1595	3367
Pseudo R-sq	0.27	0.31	0.33

Robust Z statistics are in parentheses. *significant at 10%; **significant at 5%; ***significant at 1%. The dependent variable, $StockChoice_t$, is an indicator variable equal to 1 if a stock was chosen and 0 if the bond was chosen on trial *t*. $INAcc_t^{ANT}$, $IMPFC_t^{ANT}$, and $linsula_t^{ANT}$ are activations in the left NAcc, MPFC, and anterior insula in the Anticipation period of trial *t*. $RelEarnings_t$ is equal to the difference between the dividends on trial *t* of the stock not chosen and those of the chosen stock. If the asset chosen in trial *t* was the bond, $RelEarnings_t$ is equal to the maximum dividend paid by the two stocks on that trial. $Outcome_t$ is equal to the earnings made on trial *t*. $Uncertainty_t$ is the uncertainty of the choice and defined as min(Pr{Stock T = Good | History}, Pr{Stock R = Good | History}). $CumEarnings_t$ is wealth accumulated during the task up to and including trial *t*. Subject fixed effects are included, with robust standard errors. Inclusion of brain variables increases R-sq by 1% in each regression.

Table 4. Logit Estimation of the Probability of Making a Risk-Aversion Mistake in Trial *t*

	Previous Choice Was a Stock	Previous Choice Was the Bond	All Data
RAM_t	Coef	Coef	Coef
$INAcc_t^{ANT}$	0.2962	−0.5787	−0.1973
	(1.11)	(2.34)**	(1.21)
$IMPFC_t^{ANT}$	−0.1224	−0.1361	−0.1578
	(0.52)	(0.61)	(1.11)
$linsula_t^{ANT}$	1.0985	0.1027	0.4973
	(3.22)***	(0.34)	(2.56)**
$RelEarnings_{t-1}$	0.0474	−0.0511	0.0384
	(3.45)***	(3.20)***	(5.02)***
$Outcome_{t-1}$	0.0495		0.0497
	(2.47)**		(3.89)***
$Uncertainty_t$	3.9333	11.6122	11.7142
	(2.25)**	(7.52)***	(11.86)***
$CumEarnings_{t-1}$	0.0019	0.0016	0.0026
	(1.40)	(1.58)	(3.67)***
Constant	−2.3645	−2.4798	−3.3136
	(5.27)***	(5.11)***	(10.64)***
Observations	1015	694	1857
Pseudo R-sq	0.26	0.21	0.25

Robust Z statistics are in parentheses. *significant at 10%; **significant at 5%; ***significant at 1%. The dependent variable, RAM_t (Risk-Aversion Mistake), is an indicator variable equal to 1 if the bond was chosen on trial *t* while the optimal choice was one of the stocks. $INAcc_t^{ANT}$, $IMPFC_t^{ANT}$, and $linsula_t^{ANT}$ are activations in the left NAcc, MPFC, and anterior insula in the Anticipation period of trial *t*. $StockChoice_t$ is an indicator variable equal to 1 if a stock was chosen and 0 if the bond was chosen on trial *t*. $RelEarnings_t$ is equal to the difference between the dividends on trial *t* of the stock not chosen and those of the chosen stock. If the asset chosen in trial *t* was the bond, $RelEarnings_t$ is equal to the maximum dividend paid by the two stocks on that trial. $Outcome_t$ is equal to the earnings made on trial *t*. $Uncertainty_t$ is the uncertainty of the choice and defined as min(Pr{Stock T = Good | History}, Pr{Stock R = Good | History}). $CumEarnings_t$ is wealth accumulated during the task up to and including trial *t*. Subject fixed effects are included, with robust standard errors. Inclusion of brain variables increases R-sq by 1% in each regression.

Tables 4 and 5 and Figure 3). MPFC activation was not correlated with subsequent mistakes. Thus, anticipatory neural activation correlated with both optimal and suboptimal subsequent choices, even *after* controlling for behavioral variables that should have been the primary determinants of those choices.

Finally, we investigated whether individual differences in average anticipatory activation correlated with subsequent choice, after establishing that average anticipatory activation varied across individuals. Because regression of anticipatory NAcc activation on subject fixed effects yielded no significant differences, relationships between individual differences in anticipatory NAcc activation and choice were not examined further. On the other hand, regression of anticipatory anterior insula activation on subject fixed effects did yield significant differences in 8 (all p values < 0.05) of 19 subjects, suggesting some individual differences in anticipatory insula activation. Individual differences in average anterior insula activation during anticipation were significantly correlated with the frequency of choosing a bond after having chosen a stock [$t(17) = 2.14$, $p < 0.05$; $R^2 = 0.21$]. Additionally, individual differences in average anterior insula activation during anticipation were also significantly correlated with the frequency of risk-aversion mistakes after having chosen a stock [$t(17) = 2.10$, $p < 0.05$, $R^2 = 0.21$]. Thus, individual differences in anticipatory anterior insula activation were related to making subsequent riskless choices and risk-aversion mistakes.

Discussion

While NAcc activation preceded both risky choices and risk-seeking mistakes, anterior insula activation preceded both riskless choices and risk-aversion mistakes. These findings are consistent with the hypothesis that NAcc represents gain prediction (Knutson et al., 2001), while anterior insula represents loss prediction (Paulus et al., 2003). One of the contributions of this paper is the BIAS task, as it provides a way to operationalize optimal choices, which by extension allows the identification of suboptimal choices. According to financial models, one can define risk-neutral choices based on Bayesian updating as rational and deviations from these choices as irrational. The results therefore

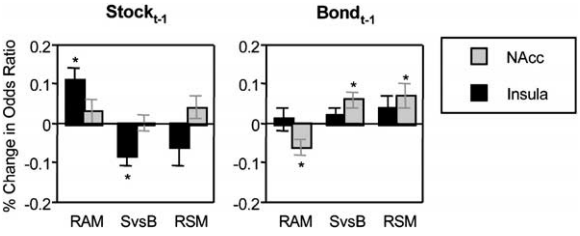

Figure 3. Association of Anticipatory Neural Activation with Subsequent Choice

The left panel indicates a significant effect of anterior insula activation on the odds of making riskless (bond) choices and risk-aversion mistakes (RAM) after a stock choice (Stock$_{t-1}$). The right panel indicates a significant effect of NAcc activation on the odds of making risk-aversion mistakes, risky choices, and risk-seeking mistakes (RSM) after a bond choice (Bond$_{t-1}$). The odds ratio for a given choice is defined as the ratio of the probability of making that choice divided by the probability of not making that choice. Percent change in odds ratio results from a 0.1% increase in NAcc or anterior insula activation. Error bars indicate the standard errors of the estimated effect. *coefficient significant at $p < 0.05$.

Table 5. Logit Estimation of the Probability of Making a Risk-Seeking Mistake in Trial *t*

	Previous Choice Was a Stock	Previous Choice Was the Bond	All Data
RSM_t	Coef	Coef	Coef
$INAcc_t^{ANT}$	0.3998	0.7395	0.4868
	(0.93)	(2.63)***	(2.69)***
$IMPFC_t^{ANT}$	−0.4330	−0.1108	−0.1210
	(1.44)	(0.50)	(0.81)
$linsula_t^{ANT}$	−0.6024	0.4430	−0.0577
	(1.19)	(1.30)	(0.27)
$RelEarnings_{t-1}$	−0.0838	0.0395	−0.0152
	(3.81)***	(2.34)**	(1.67)*
$Outcome_{t-1}$	0.0037		−0.0416
	(0.16)		(2.49)**
$Uncertainty_t$	−12.4172	−14.6378	−8.8036
	(6.20)***	(5.37)***	(8.07)***
$CumEarnings_{t-1}$	−0.0089	−0.0008	−0.0038
	(4.32)***	(0.58)	(4.22)***
Constant	7.1203	3.1759	2.9538
	(5.93)***	(2.58)***	(5.24)***
Observations	353	874	1295
Pseudo R-sq	0.30	0.34	0.25

Robust Z statistics are in parentheses. *significant at 10%; **significant at 5%; ***significant at 1%. The dependent variable, RSM_t (Risk-Seeking Mistake), is an indicator variable equal to 1 if a stock was chosen on trial *t* while the optimal choice was the bond. $INAcc_t^{ANT}$, $IMPFC_t^{ANT}$, and $linsula_t^{ANT}$ are activations in the left NAcc, MPFC, and anterior insula in the Anticipation period of trial *t*. $StockChoice_t$ is an indicator variable equal to 1 if a stock was chosen and 0 if the bond was chosen on trial *t*. $RelEarnings_t$ is equal to the difference between the dividends on trial *t* of the stock not chosen and those of the chosen stock. If the asset chosen in trial *t* was the bond, $RelEarnings_t$ is equal to the maximum dividend paid by the two stocks on that trial. $Outcome_t$ is equal to the earnings made on trial *t*. $Uncertainty_t$ is the uncertainty of the choice (or uncertainty of the environment) and defined as min(Pr{Stock T = Good | History}, Pr{Stock R = Good | History}). $CumEarnings_t$ is wealth accumulated during the task up to and including trial *t*. Subject fixed effects are included, with robust standard errors. Inclusion of brain variables increases R-sq by 1% in each regression.

indicate that, above and beyond contributing to rational choice, anticipatory neural activation may also promote irrational choice. Thus, financial decision making may require a delicate balance—recruitment of distinct circuits may be necessary for taking or avoiding risks, but excessive activation of one mechanism or the other may lead to mistakes.

While the observation that NAcc activation is correlated with subsequent risk taking and risk-seeking mistakes agrees with a gain prediction account of NAcc function (Knutson et al., 2001), the current findings are not as consistent with alternative accounts. Motor preparation accounts predict equal activation prior to motor acts of equal force (Mogenson et al., 1980) and so cannot explain the NAcc's prediction of risk-seeking but not risk-averse choices, since both required active choices indicated by button presses. Similarly, a saliency account predicts equal activation during anticipation of both large gains and losses (Zink et al., 2003) and so cannot account for the NAcc's prediction of risk-seeking but not risk-averse choices. Finally, a behavioral switching account predicts that NAcc activation will increase prior to any switch from a repeated behavior to a novel behavior (Robbins et al., 1986). While the influence of the NAcc in biasing choice was most pronounced when subjects switched from risk-averse to risk-seeking choices, NAcc activation did not predict switches in the opposite direction (from risk-seeking to risk-averse choices). The same arguments apply in reverse to the anterior insula predicting risk-averse choices. In either case, theories that fail to include the anticipated subjective value of an outcome cannot easily account for the observed pattern of results.

Although both actual and relative gain outcomes increased activation in the MPFC, MPFC activation did not predict subsequent risk-taking behavior, consistent with its proposed role in representing gain prediction error rather than gain prediction (Knutson et al., 2003). Gain outcomes also activated other regions implicated in decision making (e.g., orbitofrontal cortex, medial caudate, anterior cingulate cortex), but activation in these regions also did not predict subsequent risk-taking behavior. While activation in these regions do not correlate with subsequent risk taking, these regions may still play other important roles in decision making (O'Doherty et al., 2003). For instance, anterior cingulate foci showed increased activation under conditions of increased response conflict, consistent with the postulated role of this region in conflict monitoring (Ridderinkhof et al., 2004).

The BIAS task offers a number of advantages in eliciting financial choice behavior. First, because the BIAS task utilizes monetary incentives in a dynamic setting, our findings may generalize to real-world trading scenarios. Second, the BIAS task enables identification of both optimal choices and suboptimal choices. Third, the BIAS task elicits a range of behaviors from each individual, including both risk-seeking and risk-averse choices. Fourth, the event-related design of the study allowed us to correlate anticipatory rather than concurrent neural activation with choice by temporally isolat-

ing anticipatory activation and controlling for key antecedent behavioral variables (i.e., earnings, uncertainty).

While the event-related analyses ensured that both anticipatory activation and decision making occurred prior to actual choice, the dynamic nature of the BIAS task leaves open the question of whether anticipatory activation preceded decision making or the reverse. Some of the present findings support the idea that activation preceded decision making. Specifically, the link between activation and subsequent choice critically depended upon prior choice. For example, if NAcc activation simply reflected the decision to pick a stock, then the relationship between NAcc activation and the likelihood of choosing a stock should not depend upon prior choice. However, anticipatory NAcc activation significantly predicted the likelihood of subsequent stock choice only if the bond was picked on the previous trial (see Table 3). The same argument also applies to insula activation. Future research that specifically manipulates anticipatory activation could further establish whether such activation influences decisions.

The dynamic nature of the BIAS task may have obscured stable individual differences in NAcc activation, which might influence subsequent choice, but are more evident in stationary tasks (Knutson et al., 2005). However, even during this dynamic task, significant individual differences were evident in insula activation during anticipation, and these predicted switching from risky to riskless choices as well as the likelihood of making risk-aversion mistakes while doing so. The link between individual differences in anterior insula activation and subsequent risk-averse choices replicates and extends prior findings (Paulus et al., 2003).

While experts and nonexperts who differed in terms of prior coursework in finance and statistics did not significantly differ in behavior in this experiment, future research should also examine the influence of individual differences in trading experience on financial risk taking, since psychophysiological evidence suggests that experienced traders may show less emotional responsiveness to market events than inexperienced traders (Lo and Repin, 2002). While many psychophysiological measures (e.g., skin conductance, heart rate, pupillary dilation) index anticipatory arousal, the current results suggest that measures that probe anticipatory valence will also be necessary to predict the likelihood of subsequent risky choice.

Overall, these findings suggest that risk-seeking choices (such as gambling at a casino) and risk-averse choices (such as buying insurance) may be driven by two distinct neural circuits involving the NAcc and the anterior insula. The findings are consistent with the notion that activation in the NAcc and anterior insula, respectively, index positive and negative anticipatory affective states and that activating one of these two regions can lead to a shift in risk preferences. This may explain why casinos surround their guests with reward cues (e.g., inexpensive food, free liquor, surprise gifts, potential jackpot prizes)—anticipation of rewards activates the NAcc, which may lead to an increase in the likelihood of individuals switching from risk-averse to risk-seeking behavior. A similar story in reverse may apply to the marketing strategies employed by insurance companies.

Consideration of risk necessarily involves weighing potential gains against potential losses. The notion that distinct neural mechanisms anticipate gain versus loss suggests a novel componential view of risk taking. Combined with such a view, these findings provide neural targets for investigating complex risk phenomena such as loss aversion, in which people weigh losses more than gains of equivalent size (Kahneman and Tversky, 1979). These findings further imply that neuroeconomic research may foster a more comprehensive theory of individual decision making than the rational actor model and thus may ultimately yield new insights relevant to economic policy and institutional design.

Experimental Procedures

Nineteen healthy volunteers (10 females, mean age = 27, range = 24–39 years, right handed) participated in the study. Prior to entering the scanner, subjects played a practice version of the investment task for at least 10 min, minimizing learning effects. Subjects were then shown the cash they could earn by performing the task successfully and correctly reported believing that they would receive cash at the end of the experiment contingent upon their performance. Subjects received a fixed compensation of $20 per hour, as well as a tenth of their total task earnings. They were also informed that it was possible to lose money on the task and that any losses would be deducted from their total payment.

To elicit a range of investment behavior, subjects included both "experts" and "nonexperts," depending on whether they had taken prior graduate coursework in statistics and finance. Experts included Ph.D. students in finance, economics, or accounting, while nonexperts included Ph.D. students in humanities at Stanford University, to equate age, socioeconomic status, education, and intelligence. A 2 (expert versus nonexpert-between) × 20 (block-within) analysis of variance revealed a main effect of block [$F(19,323) = 2.35$, $p < 0.005$], indicating that subjects chose the bond more often as the experiment progressed. However, experts and nonexperts did not significantly differ in choice of stocks versus bonds, either overall (54% ± 6% versus 53% ± 6%) or across blocks. Experts and nonexperts also did not significantly differ in the proportion of risk-seeking mistakes [26% ± 6% versus 35% ± 8%; $t(17) = 0.88$, n.s.] or risk-aversion mistakes they made overall [23% ± 6% versus 29% ± 6%; $t(17) = 0.67$, n.s.; calculated as percentage of mistakes made on trials where mistakes of that type were possible], suggesting more of a performance continuum than distinct groupings. Since choices and mistakes did not significantly differ between experts and nonexperts, we combined groups in subsequent analyses.

Behavioral Analysis

In the context of the BIAS task, the optimal strategy of a rational, risk-neutral agent is to pick a stock if he or she expects to receive a dividend that is at least as large as the bond earnings. Since the actual monetary amounts at stake in each trial were small (–$1 to $1), we used risk neutrality as the baseline model of investor behavior (Rabin, 2000), a model which assumes that individuals maximize expected return. A rational actor should also update his or her beliefs about the probability of each stock being optimal according to Bayes' rule. Based on these assumptions, we derived the optimal portfolio selection strategy, which was the same for all trials (see Supplementary Data).

For each trial, the objective probability of each of the two stocks being dominant can be computed using Bayes' rule. We refer to the minimum of these two probabilities as "uncertainty" for that trial. Uncertainty is highest (and equal to 0.5) at the beginning of a block, when the probability of either stock being optimal is 50%, and decreases as more information about dividends is revealed, clarifying which stock dominates. On trials where uncertainty was 0.3 or lower, the optimal choice was one of the stocks—otherwise, the optimal choice was the bond. Thus, when uncertainty is close to the threshold value of 0.3, it is most difficult for subjects to deter-

mine the optimal strategy (i.e., whether to choose a bond versus stock), leading to maximum conflict. Thus, uncertainty is maximal when subjects cannot distinguish which of the two stocks is better, while conflict is maximal when subjects cannot distinguish whether it is better to choose a stock or the bond.

For each trial, we compared subjects' investment choices to those of a rational, risk-neutral agent. Deviations from this model were defined as different types of "mistakes." These mistakes fell into three categories. Subjects might (1) pick a stock when the bond was the optimal choice ("risk-seeking mistake"), (2) pick the bond when a stock was the optimal choice ("risk-aversion mistake"), or (3) pick a stock when the other stock is the optimal choice ("confusion mistake"). Confusion mistakes occurred in less than 1% of the trials and thus were not considered in subsequent analyses. We used logit models to predict the likelihood of choosing a stock or making either type of mistake conditional, as well as unconditional, on prior choice.

We predicted that several behavioral variables would influence subsequent choice (i.e., prior choice, prior outcome, relative earnings of chosen versus unchosen assets, cumulative earnings, and uncertainty). Logistic regressions indicated that, when the prior choice was a stock, lower relative earnings reduced the likelihood of choosing a stock again (see Table 3). When the prior choice was a bond, lower relative earnings increased the likelihood of switching to a stock. Moreover, as predicted and independent of prior choice, increasing uncertainty increased the likelihood of choosing the bond. These predicted findings provided behavioral evidence for the validity of the task.

Additionally, and independent of prior choice, increasing cumulative earnings increased the likelihood of choosing a bond (see Table 3). When the prior choice was a stock, increasing cumulative earnings also decreased the likelihood of making a risk-seeking mistake. When the prior choice was a stock, decreased relative earnings increased the likelihood of making a risk-aversion mistake (see Table 4). On the other hand, when the prior choice was a bond, decreased relative earnings increased the likelihood of making a risk-seeking mistake (see Table 5). Outcomes also influenced subsequent choice. When the prior choice was a stock, increasing outcome increased the likelihood of choosing a bond as well as the likelihood of making a risk-aversion mistake (see Tables 3 and 4). Because behavioral variables including prior outcome, relative earnings of the chosen versus unchosen asset, cumulative earnings, and uncertainty all influenced subsequent choice, we included them as covariates in prediction analyses.

fMRI Acquisition

Images were acquired with a 1.5T General Electric MRI scanner using a standard birdcage quadrature head coil. Twenty-four 4 mm thick slices (in-plane resolution 3.75 × 3.75 mm, no gap) extended axially from the mid-pons to the top of the skull, providing adequate spatial resolution of subcortical regions of interest (e.g., midbrain, ventral striatum). Functional scans of the whole brain were acquired every 2 s (TR = 2 s) with a T2*-sensitive in-/out- spiral pulse sequence (TE = 40 ms, flip = 90°) designed to minimize signal dropout at the base of the brain (Glover and Law, 2001). High-resolution structural scans were subsequently acquired using a T1-weighted spoiled grass sequence (TR = 100 ms; TE = 7 ms, flip = 90°), facilitating subsequent localization and coregistration of functional data.

fMRI Analysis

Localization analyses were conducted using Analysis of Functional Neural Images (AFNI) software (Cox, 1996). For preprocessing, voxel time series were sinc interpolated to correct for nonsimultaneous slice acquisition within each volume, concatenated across runs, and corrected for three-dimensional motion. Visual inspection of motion correction estimates confirmed that no subject's head moved more than 2.0 mm in any dimension from one volume acquisition to the next. Preprocessed time series were submitted to a regression model that included three regressors indexing residual motion and six regressors modeling baseline, linear, and quadratic trends for each of the two runs.

Regressors of interest were convolved with a γ-variate function that modeled a canonical hemodynamic response prior to inclusion in regression models (Cohen, 1997). Maps of t statistics for regressors of interest were transformed into Z scores, coregistered with structural maps, spatially normalized by warping to Talairach space, slightly spatially smoothed (FWHM = 4 mm) to minimize the effects of anatomical variability, resampled at 2 mm^3, and combined into a group map using a meta-analytic formula [average Z × sqrt(n)] (Knutson et al., 2000). Thresholds for statistical significance within the predicted volumes of interest (i.e., NAcc, anterior insula, and MPFC) were determined by a local small volume correction (3 4 mm radius spheres or 12.56 4 mm^3 voxels corrected at $p < 0.05$ yields a threshold Z of 2.88, $p < 0.004$, uncorrected) and required a minimum cluster of four contiguous voxels. Thresholds for statistical significance outside the predicted volumes of interest were set using a global family-wise error rate that corrected for gray matter volume in subcortical and mesial prefrontal cortical regions (approximately 500 4 mm^3 voxels corrected at $p < 0.05$ yields a threshold Z of 3.88, $p < 0.0001$, uncorrected; Knutson et al., 2000) and required a minimum cluster of four contiguous voxels.

As indicated by behavioral analyses, all fMRI analyses included covariate regressors representing cumulative earnings (defined as current wealth earned during the task, updated at each outcome period) and uncertainty (updated at each market period). For outcome analyses, regressors of interest contrasted stock versus bond choice, as well as gain versus loss outcome predicated on stock choice. Because the BIAS task is a dynamic reward learning task, we predicted that gain versus loss outcomes would activate both the NAcc (gain prediction) and MPFC (gain prediction error) (Knutson et al., 2003) and deactivate the anterior insula (Paulus et al., 2003). For market analyses, the regressor of interest contrasted amount earned on the current stock choice versus possible earnings from the unchosen stock, predicated on prior stock choice. As with actual outcomes, we predicted that better relative earnings during the market period would also activate the NAcc and MPFC.

Volumes of interest (VOIs) were specified as 8 mm diameter spheres centered on foci identified in the outcome analysis in the NAcc, MPFC, and insula (see Table 1), thereby ensuring that equal amounts of data were extracted for each subject in each region. Visual inspection confirmed that VOIs encompassed only gray matter for each individual subject (Knutson et al., 2004). Additional control volumes of interest of the same size and shape were specified in the bilateral anterior cingulate at foci correlated with uncertainty (TC = ±4, 16, 45), in the bilateral orbitofrontal cortex at foci correlated with outcome (TC = ±26, 36, −8), and in the bilateral amygdala (TC = ±22, −10, −26), and bilateral medial caudate (TC = ±10, 7, 10), based on the Talairach atlas, in order to verify local specificity of predicted effects.

Prediction analyses were conducted on activation time course data that were spatially averaged and extracted from these VOIs. Prediction analyses tested whether NAcc activation during anticipation was associated with subsequent stock choice as well as risk-seeking mistakes, after controlling for potential behavioral confounds. Prediction analyses also tested whether anterior insula activation during anticipation was associated with subsequent bond choice as well as risk-aversion mistakes, after controlling for potential behavioral confounds. Additional analyses utilized identical models, but substituted data extracted from control VOIs.

Individual differences analyses were conducted by first using logistic regressions to determine whether subject fixed effects alone had a significant influence on VOI activation during anticipation. Given sufficient variability across subjects in activation during anticipation (e.g., fixed effects were significant in over 25% of the subjects), logistic regressions were conducted that examined the effects of individual differences in average VOI activation during anticipation on the frequency of choosing the stock versus the bond, as well as on the frequency of making risk-seeking or risk-aversion mistakes.

Supplemental Data

The Supplemental Data for this article can be found online at http://www.neuron.org/cgi/content/full/47/5/763/DC1/.

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