Mini-Review

Neural Antecedents of Financial Decisions

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To explain investing decisions, financial theorists invoke two opposing metrics: expected reward and risk. Recent advances in the spatial and temporal resolution of brain imaging techniques enable investigators to visualize changes in neural activation before financial decisions. Research using these methods indicates that although the ventral striatum plays a role in representation of expected reward, the insula may play a more prominent role in the representation of expected risk. Accumulating evidence also suggests that antecedent neural activation in these regions can be used to predict upcoming financial decisions. These findings have implications for predicting choices and for building a physiologically constrained theory of decision-making.

Key words: reward; risk; finance; accumbens; striatum; prefrontal; human; FMRI; review

As a tool unique to humans, money allows individuals to consensually define value. People can conveniently exchange money for goods, which stimulates trade by removing the physical limitations of barter. According to learning theorists, money provides a "secondary reinforcer" that acquires value only after association with "primary reinforcers" such as food, drink, and shelter. Certainly, at some stage of development, humans learn that money carries value (for instance, newborns immediately smack their lips for sugar water but not dollar bills). However, after learning the value of money, it is not clear whether people treat money as a symbol representing a good or as a good itself. Different incentives might recruit distinct neural circuits, with more recent cortical circuits supporting symbolic representations of goods, whereas evolutionarily conserved subcortical circuits represent goods. Alternatively, the same neural circuits that represent goods may eventually and interchangeably come to represent money.

Recent advances in the spatial and temporal resolution of brain imaging techniques now enable researchers to track changes in the cortical and subcortical activity of humans as they make financial decisions. Specifically, event-related functional magnetic resonance imaging (FMRI) allows investigators to visualize changes in oxygen utilization (or "activation," a proxy for neural activity) in deep subcortical regions as small as 2 mm³ on the order of seconds. Importantly, these advances allow investigators to examine brain activation that occurs not only during or after decision-making, but also before decisions. These developments open up new and unique theoretical opportunities for investigating neural correlates of constructs long believed to play critical roles in financial decisions (e.g., expected reward and

risk), as well as creating practical opportunities to predict individuals' upcoming decisions.

Neural correlates of expected reward

One reductionist strategy is to break down a complex phenomenon into components, examine each separately, and then reconstitute the phenomenon. This strategy has been successfully applied to problems in both economics and neuroscience. In microeconomics, "expected value" represents a foundational component of decisions (von Neumann and Morgenstern, 1944). Commonly formulated as the magnitude of a desirable outcome multiplied by its probability, expected value provides a common metric that individuals can assign to different options and then use to choose between them. Although sometimes inferred on the basis of past choice behavior, expected value was originally conceived as being computed by an individual before the point of decision. By removing choice from the equation and systematically varying expectations, investigators might identify neural correlates of expected value. These neural correlates might then be used to predict choice in separate experiments. In recent years, a growing number of event-related FMRI studies have adopted this strategy by varying expectations related to the magnitude and/or value of anticipated monetary incentive outcomes and documenting correlated neural activation.

Although the initial studies that used financial incentives in the context of brain imaging did not separately model anticipation and outcome (Thut et al., 1997; Koepp et al., 1998; Delgado et al., 2000; Elliott et al., 2000; Knutson et al., 2000), they did collectively demonstrate that striatal and prefrontal mesolimbic dopamine target regions showed increased activity when monetary versus symbolic incentives (e.g., points) were at stake. The first studies to apply the temporal resolution of FMRI to specifically visualize anticipation of incentives critically indicated that mesolimbic activation could occur before incentive outcomes. One mixed-gamble study found greater mesolimbic activation for gains than losses but did not find obvious differences in activation during incentive anticipation versus outcome (Breiter et al., 2001). The other cued reaction time study found increased

Received April 7, 2007; revised June 3, 2007; accepted June 4, 2007.

B.K. was supported by National Institute of Health Grant RO3 DA020615, and P.B. was supported by the Swiss Finance Institute during article preparation. We thank G. Elliott Wimmer for feedback on previous drafts.

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DOI:10.1523/JNEUROSCI.1564-07.2007

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ventral striatal activation (including the nucleus accumbens) proportional to the magnitude of anticipated gains but not losses (Knutson et al., 2001). Together, the results of these studies suggested that anticipation of increasing magnitudes of financial reward activated the ventral striatum, a finding replicated in subsequent studies using both gambling and cued reaction time tasks (O'Doherty, 2004; Knutson and Cooper, 2005).

Investigators then examined the contribution of probability to the expected reward signal, typically by varying both the magnitude and probability of cued incentives. A cued reaction time study and two gambling studies replicated the finding that ventral striatal activation increased during anticipation of rewards of increasing magnitude, but this signal either did not differ as a function of increasing probability (Knutson et al., 2005) or peaked at an intermediate probability value (Dreher et al., 2006; Preuschoff et al., 2006). However, other gambling studies found that ventral striatal activation increased as a function of both increasing reward magnitude and increasing probability (Abler et al., 2006; Yacubian et al., 2006). In some of these studies, a region of the medial prefrontal cortex (MPFC) also showed increasing activation during anticipation of rewards of increasing probability (Knutson et al., 2005; Yacubian et al., 2006).

The reason for the discrepancies between these findings in the ventral striatum remains to be elucidated, but a few possibilities exist. First, a phasic signal may pass through the ventral striatum that encodes both magnitude and probability, followed by a tonic signal responsive to magnitude (and possibly uncertainty) but not probability. Second, even during anticipation, nonreward outcomes might suppress ventral striatal activation as a result of signals of decreased reward probability emanating from the MPFC (Knutson et al., 2003). Future studies with enhanced temporal resolution will undoubtedly help to resolve these issues. It is worth noting that simultaneous inclusion of both rewarding and punishing incentives has enabled investigators to equate and rule out potential anticipatory confounds related to attention, motor preparation, arousal, salience, and learning (Knutson et al., 2005; Yacubian et al., 2006). Interestingly, one study additionally found evidence suggesting that amygdalar activation correlated with anticipated punishment (Yacubian et al., 2006).

Neural correlates of expected risk

Although the role of expected value in decision-making has been widely recognized, financial theory additionally and separately considers the role of risk (Markowitz, 1952). Importantly, risk influences people's investment decisions in opposition to expected reward; although people pay to maximize expected reward, they also pay to minimize expected risk. To a first-order degree, risk can be modeled as the expected deviation from the expected outcome (i.e., the mathematical variance). When the chance of a fixed reward ranges from 0 to 100% probability, risk is greatest at 50% probability and thus varies in a manner orthogonal to probability, increasing to the point of maximal uncertainty. One gambling task study found that ventral striatal activation increased during reward anticipation proportional to cued risk. Furthermore, activation in other regions including the insula, lateral orbitofrontal cortex, and midbrain also increased proportional to increasing risk (Dreher et al., 2006; Preuschoff et al., 2006). Of these regions, the insula in particular has shown activation correlated with uncertainty in other tasks involving money (Critchley et al., 2001) as well as nonmonetary stimuli (Huettel et al., 2005; Grinband et al., 2006).

To cleanly isolate anticipatory activation, most of the studies reviewed above manipulated expectations in the absence of choice. A number of these studies suggest that the anticipatory activation in the ventral striatum correlates with aspects of expected reward, whereas others point toward anticipatory activation in the insula as a potential correlate of expected risk. Recent research has begun to examine whether anticipatory activation in these regions can predict choice in opposite directions, as implied by financial theory.

Predicting financial decisions

In a reversal of the typical logic of brain imaging studies, rather than examining how stimuli influence brain activation, investigators have begun to examine whether brain activation can predict subsequent behavior. In the case of financial decisions, these choices have included whether to invest in a risky or safe option and whether to purchase products or not. However, financial decisions also extend to the social realm, such as deciding to financially reward a friend or punish an enemy.

Financial risk can be framed as potential gains balanced against potential losses. All else equal, increasing reward expectation should cause people to weigh gains more heavily and thus to seek risk. However, increasing risk expectation should cause people to weight losses more heavily and thus to avoid risk (Slovic et al., 2002). In one task involving risky versus safe financial decisions, ventral striatal activation was more prominent during trials when subjects made risky decisions, although these trials also carried greater expected value than the safe trials (Matthews et al., 2004). In a similar task (for points rather than money), subjects showed greater insula activation during trials involving punished risky decisions, which predicted safe choices on the next trial, and this was especially the case for individuals prone to worrying (Paulus et al., 2003). In a study designed to mimic aspects of financial investing, investigators examined anticipatory activation before making a risky investment (i.e., choosing a stock) or a safe investment (i.e., choosing a bond). In addition, the risky and safe investments could optimally match the choices of a rational agent or not. Controlling for econometric variables (e.g., previous absolute earnings, previous counterfactual earnings, overall wealth, and uncertainty), the investigators found that ventral striatal activation predicted both optimal and suboptimal risky investments, whereas insula activation predicted both optimal and suboptimal safe investments. These effects were most prominent when subjects switched from one investment strategy to another (Fig. 1). Furthermore, individuals with greater average anticipatory insula activation made more safe investments overall (Kuhnen and Knutson, 2005).

The relationship of anticipatory activation to other types of financial decisions has also been investigated. For instance, in the case of purchasing, increased expected reward should enhance people's willingness to buy a product, whereas increased expected risk might decrease their willingness to buy a product. Indeed, when people are deciding whether to purchase a product or not, increased ventral striatal activation while viewing the product predicts eventual purchasing, whereas increased insula activation while viewing the associated price predicts eventual refusal to purchase (Knutson et al., 2007).

The relationship between anticipatory activation and financial decisions also extends to the social realm. In social exchange games involving financial incentives, ventral striatal activation precedes the decision to invest in a cooperating partner (Rilling et al., 2002; King-Casas et al., 2005), whereas insula activation precedes defection against an unfair partner (Sanfey et al., 2003). Some evidence also suggests that social contexts (e.g., playing

with a human rather than a computer partner) may accentuate these anticipatory activations (Rilling et al., 2002).

Implications

In summary, recent and rapid advances in functional brain imaging suggest that individuals use some of the same subcortical circuits to process money that they use to process more tangible goods. In the absence of choice, converging evidence implicates ventral striatal activation in the representation of expected reward, and possibly insula activation in the representation of expected risk. Furthermore, research suggests that activation in these circuits does not simply correlate with expectations but also precedes and may promote decisions, possibly in opposing directions. These preliminary but promising findings at minimum provide an existence proof of the feasibility of exploring financial formulations with neuroscience tools. Presently, the findings also raise more questions than they answer.

Some outstanding questions involve methodology. Improvements in temporal resolution originally enabled investigators to hone in on anticipatory signals. If this resolution could improve further, localization could be augmented, as well as tools for tracking dynamic changes in functional connectivity. Also relevant to

timing, little is known about the physiological origin of the blood oxygen level-dependent (BOLD) signal revealed by event-related FMRI, although exciting progress is occurring in the field of pharmacological MRI. For instance, current evidence suggests that postsynaptic agonism of D1 receptors partially drives BOLD signal in the ventral striatum (Knutson and Gibbs, 2007). Triangulation with other methods such as lesion studies, which can address causality (Fellows, 2004; Bechara and Van Der Linden, 2005), and positron emission tomography, which can address chemistry (Zald et al., 2004), will continue to play a critical role.

Other questions involve theory. Computationally, the expected reward/expected risk framework might complement existing theoretical frameworks (Montague and Berns, 2002). Psychologically, anticipatory activations may index anticipatory feeling states. For instance, investigators have repeatedly demonstrated that ventral striatal activation during anticipation of monetary reward correlates with individual differences in cueelicited positive arousal (Knutson et al., 2005), but additional research must determine whether insula activation correlates with negative arousal, undifferentiated arousal, or any subjective experience. Functionally, it is unclear whether expected reward and risk have separate influences on decisions or whether their output combines in some other common circuit. Contextually, the limits of the influence of these value-based components on decisions have yet to be specified. For instance, some evidence suggests that they may play particularly prominent roles when uncertainty is high or when decision strategies change.

Surprisingly, this new work suggests that humans may use the same neural machinery to surf the stock exchange that they once used to scavenge the savannah (Olds and Fobes, 1981; Schultz et

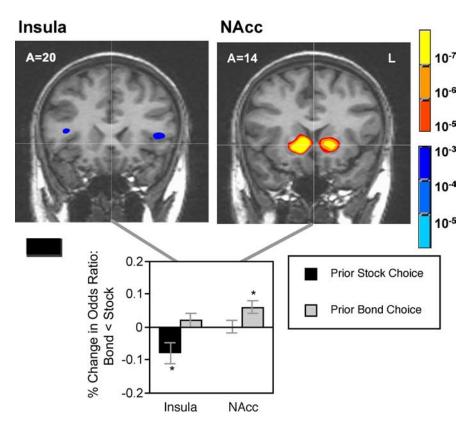


Figure 1. Insular and NAcc activation precede shifts in financial risk taking. Top, Insular deactivation (left) and NAcc activation (right) associated with gain versus loss outcomes after stock (high-risk) choices. Bottom, Insular activation predicts bond (low-risk) choice conditional on previous stock choice, whereas NAcc activation predicts stock (high-risk) choice conditional on previous bond choice. *p < 0.05. Adapted from Kuhnen and Knutson (2005).

al., 1997). Although ancient, that machinery continues to provide fast, flexible, finely tuned, and fundamental input to our daily decisions.

References

Abler B, Walter H, Erk S, Kammerer P, Spitzer M (2006) Prediction error as a linear function of reward probability is coded in the human nucleus accumbens. NeuroImage 31:790–795.

Bechara A, Van Der Linden M (2005) Decision-making and impulse control after frontal lobe injuries. Curr Opin Neurol 18:734–739.

Breiter HC, Aharon I, Kahneman D, Dale A, Shizgal P (2001) Functional imaging of neural responses to expectancy and experience of monetary gains and losses. Neuron 30:619–639.

Critchley HD, Mathias CJ, Dolan RJ (2001) Neural activity in the human brain relating to uncertainty and arousal during anticipation. Neuron 29:537–545.

Delgado MR, Nystrom LE, Fissell C, Noll DC, Fiez JA (2000) Tracking the hemodynamic response to reward and punishment in the striatum. J Neurophysiol 84:3072–3077.

Dreher JC, Kohn P, Berman KF (2006) Neural coding of distinct statistical properties of reward information. Cereb Cortex 16:561–573.

Elliott R, Friston KJ, Dolan RJ (2000) Dissociable neural responses in human reward systems. J Neurosci 20:6159–6165.

Fellows LK (2004) The cognitive neuroscience of human decision making: a review and conceptual framework. J Cogn Neurosci 3:159–172.

Grinband J, Hirsch J, Ferrerra VP (2006) A neural representation of categorization uncertainty in the human brain. Neuron 49:757–763.

Huettel SA, Song AW, McCarthy G (2005) Decisions under uncertainty: probabilistic context influences activation of prefrontal and parietal cortices. J Neurosci 25:3304–3311.

King-Casas B, Tomlin D, Anen C, Camerer CF, Quartz SR, Montague PR (2005) Getting to know you: reptutation and trust in a two-person economic exchange. Science 308:78–83.

Knutson B, Cooper JC (2005) Functional magnetic resonance imaging of reward prediction. Curr Opin Neurol 18:411–417.

- Knutson B, Gibbs SE (2007) Linking nucleus accumbens dopamine and blood oxygenation. Psychopharmacology (Berl) 191:813–822.
- Knutson B, Westdorp A, Kaiser E, Hommer D (2000) FMRI visualization of brain activity during a monetary incentive delay task. NeuroImage 12:20–27.
- Knutson B, Adams CM, Fong GW, Hommer D (2001) Anticipation of increasing monetary reward selectively recruits nucleus accumbens. J Neurosci 21:RC159(1–5).
- Knutson B, Fong GW, Bennett SM, Adams CM, Hommer D (2003) A region of mesial prefrontal cortex tracks monetarily rewarding outcomes: characterization with rapid event-related FMRI. NeuroImage 18:263–272.
- Knutson B, Taylor J, Kaufman M, Peterson R, Glover G (2005) Distributed neural representation of expected value. J Neurosci 25:4806–4812.
- Knutson B, Rick S, Wimmer GE, Prelec D, Loewenstein G (2007) Neural predictors of purchases. Neuron 53:147–156.
- Koepp MJ, Gunn RN, Lawrence AD, Cunningham VJ, Dagher A, Jones T, Brooks DJ, Bench CJ, Grasby PM (1998) Evidence for striatal dopamine release during a video game. Nature 393:266–268.
- Kuhnen CM, Knutson B (2005) The neural basis of financial risk-taking. Neuron 47:763–770.
- Markowitz H (1952) Portfolio selection. J Finance 7:77-91.
- Matthews SC, Simmons AN, Lane SD, Paulus MP (2004) Selective activation of the nucleus accumbens during risk-taking decision making. NeuroReport 15:2123–2127.
- Montague PR, Berns GS (2002) Neural economics and the biological substrates of valuation. Neuron 36:265–284.
- O'Doherty JP (2004) Reward representations and reward-related learning in the human brain: insights from neuroimaging. Curr Opin Neurobiol 14:769–776.

- Olds ME, Fobes JL (1981) The central basis of motivation: Intracranial selfstimulation studies. Annu Rev Psychol 32:523–574.
- Paulus MP, Rogalsky C, Simmons A (2003) Increased activation in the right insula during risk-taking decision making is related to harm avoidance and neuroticism. NeuroImage 19:1439–1448.
- Preuschoff K, Bossaerts P, Quartz SR (2006) Neural differentiation of expected reward and risk in human subcortical structures. Neuron 51:381–390.
- Rilling J, Gutman D, Zeh T, Pagnoni G, Berns G, Kilts C (2002) A neural basis for social cooperation. Neuron 35:395–405.
- Sanfey AG, Rilling JK, Aronson JA, Nystrom LE, Cohen JD (2003) The neural basis of economic decision-making in the Ultimatum Game. Science 300:1755–1758.
- Schultz W, Dayan P, Montague PR (1997) A neural substrate of prediction and reward. Science 275:1593–1599.
- Slovic P, Finucane M, Peters E, MacGregor D (2002) The affect heuristic. In: Heuristics and biases: the psychology of intuitive judgment (Gilovich T, Griffin D, Kahneman D, eds), pp 397–420. New York: Cambridge UP.
- Thut G, Schultz W, Roelcke U, Nienhusmeier M, Missimer J, Maguire RP, Leenders KL (1997) Activation of the human brain by monetary reward. NeuroReport 8:1225–1228.
- von Neumann J, Morgenstern O (1944) Theory of games and economic behavior. Princeton, NJ: Princeton UP.
- Yacubian J, Glascher J, Schroeder K, Sommer T, Braus DF, Buchel C (2006) Dissociable systems for gain-and loss-related value predictions and errors of prediction in the human brain. J Neurosci 26:9530–9537.
- Zald DH, Boileau I, El-Dearedy W, Gunn RN, McGlone F, Dichter GS, Dagher A (2004) Dopamine transmission in the human striatum during monetary reward tasks. J Neurosci 24:4105–4112.