Chinese Science Bulletin

REVIEW

Neuroeconomics: Opening the "black box" behind the economic behavior

YU RongJun[1] & ZHOU XiaoLin[1,2†]

[1] Department of Psychology, Peking University, Beijing 100871, China;
[2] Center for Brain and Cognitive Sciences, Peking University, Beijing 100871, China;

This paper introduces an emerging interdisciplinary research field, namely neuroeconomics, which uses the neuroscientific methods to investigate the neural systems supporting economically relevant behaviors. Traditional economic research is restricted to the level of describing decision behaviors, leaving the cognitive mechanisms behind them unknown. It also fails to predict many decision behaviors in real life. The combination of neuroscience and economics makes it possible to uncover the underlying mental and neural processes of economic decision making. This paper reviews the findings from the neuroeconomic literature on encoding of utility in the brain, showing that neuroeconomic research can test the validity of economic concepts and theories and provide new explanations to economic phenomenon. It discusses the important role the emotion plays in economic decision making and the associated neural evidence, suggesting the possibility of understanding the impact of emotion upon decision making by measuring the neural activity of emotion-related brain regions. This paper also summarizes neuroscientific studies on cooperation and trust in monetary games, pointing out that the trend of neuroeconomic research is to model the real life decision making in the laboratory with solid ecological validity. Neuroeconomics provides not only neuroscientific evidence for economic theories, such as the prospect theory, the regret theory and the game theory, but also foundations for more comprehensive and powerful economic models.

neuroeconomics, neuroimaging, economic behavior, utility, regret, cooperation

PSYCHOLOGY

Why do we gamble on lottery in which the chance of winning is slim? Why cannot we resist the temptation of immediate satisfaction and fail on long-term finance plans? Why do we like to punish others at the expense of self interest? From the perspective of traditional economics, these are all "irrational behaviors", contradicting the predictions of traditional economic models. Such discrepancies between the economic behaviors in real life and predictions of economic models make the limitation of traditional economic research methods apparent. Due to the complexity of human mind, economists traditionally treat the brain as a "black box" that cannot be opened or fully understood. They believe that economic research should focus on the observable external behaviors. By measuring input and output information, economics has gained great achievements, including development of economic models. However, this approach leads to an obvious problem: the theoretically predicted behaviors sometimes deviate from the real behaviors in humans.

Recently, thanks to the development of neuroscience, it is possible to measure the brain activity in normal people using brain imaging technologies. With advanced neuroscience methods, it is now the time to open the "black box" by exploring the neural and psychological mechanisms underlying economic behaviors. Neuroeconomics, an interdisciplinary research approach,

Received August 6, 2006; accepted March 29, 2007
doi: 10.1007/s11434-007-0193-1
†Corresponding author (email: xz104@pku.edu.cn)
Supported by the National Pandeng Project (Grant No. 95-special-09), the Natural Science Foundation of China (Grant Nos. 30070260, 30470569 and 60435010), and the Ministry of Education of China (Grant Nos. 01002 and 02170)

aims to analyze economically relevant brain processes using neuroscience methods like single-cell measurement, brain damaged individuals studies, and functional brain imaging. The most popular methods used in neuroeconomics studies is functional imaging, including position emission computerized tomography (PET), functional magnetic resonance imaging (fMRI), magnetoencephalography (MEG), and electroencephalography (EEG). The PET and fMRI relies on the assumption that any mental activity increases demand for oxygen at active regions in the brain, which is met by increased blood flow to the region. The indirect measure of blood flow thus reflects neural activity in a particular region. The EEG and MEG, on the other hand, measure products of brain activity, i.e., the electric (EEG) or magnetic (MEG) signals. The fMRI, offering high spatial resolutions, and the event-related potential (ERP), offering high temporal resolutions, are the two most popular neuroscience techniques in cognitive neuroscience.

Although neuroeconomics as a field of study is relatively new, it has made some interesting and important contributions to economic theories[1 − 10]. This paper summarizes the neuroeconomic research findings in three areas: utility computation, the role of emotion in decision making, and decision in social context. We discuss how these findings can inform us about some major economic theories such as the prospect theory, the regret theory, and the game theory. We demonstrate that neuroscience can help economics by generating conceptualization at the neural level and by providing methodologies for testing new as well as existing theories. Some challenges for carrying out research in this field are also discussed.

1 Major research topics

1.1 Utility computation in decision making

Utility is a key concept in economics. Economists assume that people assign a utility for each option and then make choices by comparing these utilities. However, since these options might involve a wide range of rewarding stimuli, how our brain computes the utility for these diverse stimuli remains unknown. Recent fMRI studies suggest that different types of rewarding stimuli consistently increase activity in a common set of neural structures, including the orbitofrontal cortex (OFC), amygdale, and nucleus accumben (NAc). Studies have shown that primary rewards such as fruit juice and water[11,12], appetitive smells[13,14], and social rewards such as attractive faces[15,16], romantic love[17,18], aesthetic paintings[19], humor[20,21], music[22,23], cultural objects (sports cars)[24], and cooperation and revenge (discussed in detail later) would activate the same coterie of neural structures. Commonly used rewards such as money also activate these structures[25−29]. This pattern of activation, responding to these diverse stimuli, suggests that the brain may process rewards along a single common pathway. This network allows widely different rewards to be directly compared for the purpose of choosing between possible courses of action[30,31].

One important area where neuroeconomics can contribute is in identifying neural substrates associated with economic concepts and in understanding their psychological functions. Kahneman et al. distinguish between “decision utility,” which refers to the weight of an outcome in a decision, and “experience utility,” which refers to its hedonic quality[32,33]. Although decision utility may be derived from predictions of the experience utility of different options, anticipated, experienced, and decision utilities often diverge in dramatic ways[33]. Yu and Zhou[34] found that the predictive monetary loss cue elicited feedback related negativity (FRN) in brain potentials of smaller magnitude compared with that elicited by experienced loss, suggesting that expected outcomes and experienced outcomes are processed differently in the brain. Knutson et al.[35] observed that anticipation of reward activated foci in the ventral striatum, and reward outcomes activated foci in the ventromedial frontal cortex. In another study, Breiter et al.[36] visually presented several gain and loss prospects and outcomes using different roulette wheel “spinners”. With fMRI, these authors found that responses to prospects and outcomes were generally, but not always, seen in the same regions. Using a gambling task in which the gamble would not be resolved immediately, Tom et al. further show that potential losses (decision utility) are represented by decreasing activity in gain-responsive regions rather than by increasing activity in regions associated with expected and experienced negative outcomes[37]. These studies reinforce the importance of distinguishing among different utilities in economic theories of choice.

Neuroeconomic studies also support previously discovered economic rules concerning utility computation. The expected utility theory proposes that the expected utility of a choice is the sum of probability-weighted utilities for each possible outcome[38]. Neuroscience methods now offer researchers an opportunity to identify neural substrates that support the computation of these financial parameters and then to predict financial choices from brain activation. Preuschoff et al.[39] reported that during reward anticipation, initial activation in ventral striatum and other subcortical dopaminoceptive structures varied with expected reward, whereas subsequent activation in ventral striatum varied with risk. Activation correlating with expected reward and risk were thus differentiated both spatially and temporally. Knutson et al.[29] found that the subcortical nucleus accumbens (NAcc) was activated proportional to anticipated gain magnitude, whereas the cortical mesial prefrontal cortex (MPFC) was additionally activated according to anticipated gain probability. More importantly, Knutson et al.[40] provided evidence that specific patterns of brain activation predict purchasing decisions.

A core idea of prospect theory is that utility is computed by comparing the absolute value to some reference point[41]. Both ERP and fMRI studies have found neural evidence supporting this reference dependent utility computation hypothesis. In an ERP study, Holroyd et al. found that the amplitude of the FRN, an ERP component which is sensitive to the valence of outcomes, is determined by the value of the eliciting outcome relative to the range of possible outcomes rather than by the objective value of the outcome[42]. In an fMRI study, Nieuwenhuis et al.[43] observed that activity in a number of reward-sensitive areas in the brain was highly sensitive to the range of possible outcomes from which an outcome was selected. Neural response within human reward systems is also modulated by cumulative winnings or losses that participants experienced[26,44].

Another important phenomenon concerning utility computation in economic decision is the time discounting of utility. Time discounting refers to the fact that people compute the utility at a future point according to a unified discount rate. For example, if one prefers \$100 now over \$110 in a month, this indicates that one is discounting the value of the offer by at least \$10 for the delay of a month. Economic models assume that people discount future utility by a discount rate[45]. McClure et al.[46] used fMRI to examine the neural correlates of time discounting while subjects made a series of choices between monetary reward options that varied by delay to delivery. They found that the limbic system, known as an emotion-related area, was preferentially activated by decisions involving immediately available rewards. In contrast, regions of the lateral prefrontal cortex and posterior parietal cortex were engaged uniformly by intertemporal choices irrespectively of delay. Importantly, the relative engagement of the two systems was directly associated with subjects' choices, with greater relative fronto-parietal activity when subjects chose longer term options. This study suggests that the brain houses at least two discounting mechanisms, one of which is sensitive to the value of immediate rewards and another is more sensitive to the value of future rewards.

1.2 The role of emotions in decision making

Emotions influence our decisions. However, since it is not easy to measure emotions quantitatively, traditional economic studies usually ignore such influence and leave emotion outside the scope of decision making research. Behavioral economics begins to pay attention to the role that emotions play in decisions. The regret theory proposes that decision-makers can predict the regret they would experience when they realize that the chosen outcome is disadvantageous compared with alternative outcomes available if they choose alternative choices. The regret theory also states that people would choose options that would minimize future regret[47,48]. Neuroeconomic studies on regret support these assumptions. Camille et al.[49] tested the prediction that advantageous choice behavior depends on the ability to anticipate and hence minimize regret. In a gambling task, normal subjects chose to minimize future regret and learned from their emotional experience. Patients with orbitofrontal cortical lesions, however, did not report regret or anticipate negative consequences of their choices. With a similar gambling paradigm, Coricelli et al.[50] used fMRI to measure brain activity as subjects selected between two bets. They found that increasing regret enhanced activity in the medial orbitofrontal region, the anterior cingulate cortex (ACC), and the hippocampus. Also, subject became increasingly regret-aversive, a cumulative effect reflected in enhanced activity within medial orbitofrontal cortex and amygdale. Since the same neural substrates mediate direct experience of regret and its anticipation, these results support the hypothesis that people anticipate regret and choose to minimize the anticipated regret. Regret is mediated by a cognitive process known as counterfactual thinking. Counterfactually thinking is the mechanism by which we compare "what is" with "what might have been". Ursu et al.[51] showed that counterfactual effects are manifested in the human orbitofrontal cortex during expectation of outcomes. Taken together, these studies suggest that the orbitofrontal cortex has a fundamental role in mediating the experience of regret. They also confirm that the ability to experience and anticipate emotions is crucial to advantageous decision making[52].

Of course, emotions are not always beneficial to decisions. Extreme emotions can lead to irrational behaviors such as crime of passion. The influence of emotions on decision making can be both positive and negative, depending on the situation in which the decision is made. Shiv et al.[53,54] found that dysfunction in neural systems subserving emotions lead to more advantageous decisions. These investigators utilized a simple investment task to examine the role of losses versus gains in individuals with substance use disorder (ISD)[53]. At the beginning of the task, all subjects were endowed with $20 of play money. Subjects had to decide between two options: invest $1 or not to invest. If the subject decided not to invest, he or she would keep the dollar, and the task would advance to the next round. If the subject decided to invest, he or she would hand over a dollar bill to the experimenter. The subject would either lose the $1 that was invested or win $2.5 depending on the outcome of the coin toss by the experimenter. Individuals with substance use disorder were more likely to invest than healthy subjects even when they faced the possibility of a loss. Moreover, it appeared that these subjects responded differently to monetary feedback. Whereas normal subjects were more likely to withdraw from selecting a risky option, particularly after a loss, individuals with substance use disorder were minimally affected by the outcomes of decisions made in previous rounds. Another study also showed that patients with stable focal lesion in brain regions related to emotion also made more advantageous decisions and ultimately earned more money from their investments than normal participants and control patients[54]. These studies support the hypothesis that emotions play a central role in decision making under risk and demonstrate that the failure to process emotions can lead people to make more advantageous decisions when faced with the types of positive-expected-value gambles that most people routinely shun[55].

The role of emotions is also highlighted in the framing effect. The framing effect refers to the phenomenon that human choices are remarkably susceptible to the manner in which options are presented[32,41]. This effect represents a striking violation of standard economic accounts of human rationality, although its psychological and neural mechanisms are not well understood. Martino et al.[56] found that the framing effect was specifically associated with amygdale activity, suggesting a key role for the emotional system in mediating decision biases. Importantly, orbital and medial prefrontal cortex activity predicted a reduced susceptibility to the framing effect, reflecting the role of cognitive control in modulating the framing effect. Kahneman and Frederick[57] interpreted these results with a dual system framework, in which different frames evoke distinct emotional responses that different individuals can suppress to various degrees. They emphasized that the ability to control emotions is important to make optimal decisions in some circumstances. Lo and Repin[58] found that less experienced traders showed significant physiological reactions to about half of the market events (e.g. trend reversals). More experienced traders reacted much less to the same events, suggesting that years of experience enabled these traders to react less emotionally to dramatic events and thus to work efficiently.

Moral decisions, the evaluation of actions of other people or of our own actions made with respect to social norms and values, are not the main topic in economics. However, moral does play an important role in our daily economic decisions. Psychological research on moral decision making has long been dominated by cognitive models that emphasize the role that reasoning and "higher cognition" plays in the moral judgment[59]. However, neuroscience studies on moral decisions emphasize the role that emotions play in making moral judgment[60]. Greene et al.[61] found that brain areas associated with emotional processing were much more activated in moral-personal condition rather than moral-impersonal and non-moral conditions. These authors argued that moral dilemmas vary systematically in the extent to which they engage emotional processing and that these variations in emotional engagement influence moral judgment. Emotion might lead us to irrational decisions such as not to push a stranger onto the railway tracks to save five others. Further study has shown that brain regions associated with abstract reasoning and cognitive control are recruited to resolve difficult personal moral dilemmas in which utilitarian values require personal moral violations[62]. It has been proposed that the controversy surrounding utilitarian moral philosophy reflects an underlying tension between competing subsystems in the brain: cognition and emotion[63,64].

1.3 Economic decisions in social context

Human always make decisions in social situations. We care about others' decisions and outcomes and learn from others' behaviors. The game theory proposes that people make decisions based on the prediction of others' possible actions and the associated outcomes. Neuroeconomic studies have found evidence to support this view. Recently, a number of studies showed that decisions in social context are closely related to theory of mind, which is the ability to attribute various mental states to self and others in order to explain and predict behavior[65]. These studies implicated generally a network of brain areas for theory of mind, including posterior superior temporal sulcus, medial prefrontal regions, and temporo-parietal junction[66,67]. Rilling et al.[68] examined whether playing interactive economic games with social partners similarly engaged the putative theory of mind neural network. They observed stronger activations in these regions for human-human interaction than for human-computer interaction. Fukui et al.[69] also found that the counterpart effect (human minus computer) exclusively activated mentalizing related areas (medial frontal area and superior temporal sulcus). Yu and Zhou[70] found that observing someone else losing money in a gambling task elicits an FRN-like effect in brain potentials, mirroring the brain responses to the outcomes of one's own performance. Importantly, the observed outcomes are completely irrelevant to the subjects' own outcomes, suggesting that people care about others' outcomes even though these outcomes are not related to their own interests. Other studies also showed that it is not easy to resist the influence of the other's behavior and the outcome. Asch et al. showed that people tend to conform to others[71,72]. Using a similar paradigm as Asch, Berns et al.[73] found in an fMRI study that independent judgment was associated with increased activation in amygdale, which was the marker of the emotional load. The authors suggested that it is painful to stand alone and stick to one's belief.

Cooperation behaviors, especially those that happen among strangers are common but still not well-understood by economists. Take the ultimatum game for an example. In this game, two players are given the opportunity to split a sum of money. One player is deemed the proposer and the other, the responser. The proposer makes an offer as to how this money should be split between the two. The responder can either accept or reject this offer. If it is accepted, the money is split as proposed. But if the responder rejects the offer, then neither player receives anything. Under the standard game theory, the proposer would offer smallest sum of money possible and the responder would accept this offer. From a purely economic point of view, a rejection of any money is "irrational" because some money is better than none. However, considerable behavioral research showed that offers are typically around 50% of the total amount and offers smaller than 20% of the total have about a 50% chance of being rejected[74,75]. The neuroeconomics studies of cooperation are now helping to shed light on these interesting controversies in behavioral and game theory. Decety et al.[76] observed that cooperation was associated with left medial orbitofrontal cortex involvement, suggesting that cooperation is a socially rewarding process. Rilling et al.[77] used fMRI to scan women as they played the iterated Prisoner's Dilemma Game, a famous game used by economists to model cooperation. Mutual cooperation was found to be associated with consistent activation in brain areas that have been linked with reward processing: nucleus accumbens, the caudate nucleus, ventromedial frontal/orbitofrontal cortex, and rostral anterior cingulated cortex. These authors proposed that activation of this neural network positively reinforces reciprocal altruism, thereby motivating subjects to resist the temptation to selfishly accept but not to reciprocate favors. An fMRI study about charitable donation revealed that the mesolimbic reward system is engaged by donations in the same way as when monetary rewards are obtained. The anterior sectors of the prefrontal cortex are distinctively recruited when altruistic choices prevail over selfish material interests[78]. Since cooperation is rewarding, there should be a competition between this non-material reward and the immediate material reward. Overall, these studies consistently suggest that prosocial behaviors such as cooperation, trust, and donation are rewarding in themselves.

Although individuals cooperate more often than the game theory would predict, there is also a substantial percentage of the population which do not trust and cooperate. Given this heterogeneity, an important question for neuroeconomic study is to examine the neural differences underlying the observed heterogeneity. McCabe et al.[79] divided subjects into two groups based on their behavior data in a standard two-person "trust and reciprocity" game: cooperators and non-cooperators. For cooperators, they found that prefrontal regions are more active when these subjects are playing with a human than when they are playing with a computer. For non-cooperators, however, there are no significant differences in prefrontal activation between the computer and human conditions. The authors argued that prefrontal regions are part of the neural architecture that allows gratification delay in order to obtain larger rewards through cooperation. Sanfey et al.[80] scanned players as they responded to fair and unfair proposals in the Ultimatum Game. Unfair offers differentially activated the emotion (anterior insula) and cognition (dorsolateral prefrontal cortex) related brain areas. Those with the strongest activation of the anterior insula rejected a higher proportion of the unfair offers. Because the anterior insula is often implicated in negative emotional responses (more specifically in disgust) and the DLPFC is often implicated in executive function and goal maintenance, Sanfey et al.[80] concluded that low offers in the ultimatum game are rejected because of a sense of disgust, while DLPFC activation may signal the importance of acquiring money. The explanation for the fact that the DLPFC is more strongly activated for unfair offers compared with fair offers, however, is controversial. Another plausible hypothesis states that the DLPFC is involved in overriding selfish impulses and maintain and to implement culture-dependent fairness goals. Knoch et al.[81] showed that disruption of the right, but not the left, DLPFC by low-frequency rTMS substantially reduces subjects' willingness to reject their partners' intentionally unfair offers in the Ultimatum game, which suggests that subjects are less able to resist the economic temptation to accept these offers.

Reputation is an important factor that determines our intention to cooperate. Singer et al.[82] asked subjects to play sequential Prisoner's Dilemma game and then scanned subjects as they made gender judgments on faces of people they had played against. The moral status of partners had been introduced as fair or unfair and the moral responsibility was introduced as either intentional or non-intentional. They reported that faces of the intentional cooperators activated insula, amygdale, and ventral striatal areas. Since the striatum is an all-purpose reward area, activation in that region means that simply seeing the face of a person who has intentionally cooperated with you is rewarding. The results suggest that a good reputation may be neurally encoded in a way similar to other rewarding stimuli. King-Casas et al.[83] used event-related hypoerscan-fMRI to monitor homologous regions of two subjects' brains simultaneously as they played the multi-round trust game. They reported that reciprocity expressed by one player strongly predicted future trust expressed by his partner and the head of caudate nucleus responded more greatly to benevolent reciprocity than to malevolent reciprocity. The authors proposed that the caudate nucleus processes information about the fairness of a social partner's decision and the intention to repay with trust. Delgado et al.[84] investigated whether prior social and moral information about potential trading partners affects reward learning. They found that activation of the caudate nucleus differentiated between positive and negative feedback, but only for the "neutral" partner. Notably, it did not do so for the "good" partner and did so only weakly for the "bad" partner, suggesting that prior moral perception can diminish reliance on feedback mechanisms in the neural circuitry of trial-and-error reward learning.

Cooperation can also be influenced by physiological factors. Recent studies also showed that hormones played an important role in trust games. Zak et al.[85] examined whether oxytocin is associated with the receipt of a signal of trust that motivates individuals to be trustworthy, that is, to reciprocate trust. In a canonical trust game, one player can invest up to $10 which is tripled. A second "trustee" player can keep or repay as much of the tripled investment as they want. Zak and colleagues[85] found that oxytocin rose in the trustee if the first player trusted her by investing a lot and higher oxytocin levels were strongly associated with trustworthy behaviors. Recently, Kosfeld et al.[86] analyzed the effect of exogenously administered oxytocin on individuals' decisions in a trust game. The study shows that intranasal administration of oxytocin specifically caused a substantial increase in trust behaviour but not reciprocity behaviour and risk preference, suggesting an essential role for oxytocin as a biological basis of prosocial approach behaviour.

Another type of cooperation is to punish those non-cooperators. People sometimes voluntarily incur costs to punish violations of social norms, known as altruistic punishment[87]. de Quervain et al.[88] used PET to examine the neural basis of altruistic punishment of defectors in an economic exchange. Subjects could punish defection either symbolically (without reduction in payoff) or effectively (with reduction in payoff). They found that both symbolical and effective punishment activated the dorsal striatum and subjects with stronger activations in this region were willing to incur greater costs in order to punish. The authors argued that people derive satisfaction from punishing norm violations and the activation in the dorsal striatum reflects the anticipated satisfaction from punishing defectors. Recently, Singer et al.[89] showed that the brain empathic responses are modulated by the affective bond between individuals. They engaged male and female subjects in an economic game, in which two confederates played fairly or unfairly, and then measured brain activity with fMRI while the same subjects observed the confederates receiving painful stimuli. Both sexes exhibited empathy-related activation in pain-related brain areas towards fair players. However, these empathy-related responses were significantly reduced in males when they observed an unfair person receiving pain. Moreover, increased activation in reward-related areas was correlated with an expressed desire for revenge. The authors concluded that men empathic responses are shaped by evaluation of other people's social behavior, such that they empathize with fair opponents while favoring the physical punishment of unfair opponents.

2 Conclusion

This article reviews three research fields in which the neuroeconomic endeavor can make important contributions to economic theories. Neuroscientific methods offer the promise of identifying neural substrates that support the emotional and high level cognitive process. Thereby neuroeconomics has the advantage of providing direct tests of existing as well as new economic theories. To facilitate the build up of more revealing models of decision making, it should be taken into account the underlying neural mechanisms that drive economic behaviors. Neuroeconomic studies can deepen our understating of various decision making phenomena and the clinic symptoms such as addictive gambling, compulsive shopping, and so on. It also has great applicable implications in areas such as making more effective advertising, building cooperative relationship in economics trade, and designing more reasonable payment protocol to enhance the work efficacy and happiness of workers.

But there are several challenges ahead for neuroeconomic research. First of all, each of cognitive neuroscience methods has it own inherent disadvantages[90]. The limitation of the fMRI technique is its poor temporal resolution (2—8 s), which is far cruder than the most detailed features of brain organization and function. The ERP technique provides higher temporal resolution than the fMRI but lower spatial resolution. More importantly, cognitive neuroscience studies usually cannot establish the causal relationship between a pattern of brain activity and a particular psychological function. Cognitive neuroscience methods, such as fMRI, reveal only a correlation between brain activity and a task manipulation or behavioral response. Such correlations should be taken with caution and must not be misunderstood as a proof of causality. Furthermore, high level cognitive processes such as cooperation are challenging to emulate and control in the psychology or neuroscience laboratories. For example, in the fMRI scanning environment, the freedom of movement for subjects is limited to reduce artifact of head movement. In an ERP study, it is important to pay attention to the subject's fatigue that occurs because of the so many trials required for this technique. Researchers have to be cautious when they extend conclusions from neuroeconomic studies in the laboratory to the real social life. Nevertheless, it is clear that although neuroeconomics is still far from opening the "black box" of the brain completely, it offers tremendous potentials to shed new and important insights on the mental and neural processes underlying economic behaviors.

1 Trepel C, Fox C R, Poldrack R A. Prospect theory on the brain? Toward a cognitive neuroscience of decision under risk. Cogn Brain Res, 2005, 23: 34—50

2 Kenning P, Plassmann. Neuroeconomics: An overview from an economic perspective. Brain Res Bull, 2005, 67: 343—354

3 Glimcher P W, Rustichini A. Neuroeconomics: The consilience of brain and decision. Science, 2004, 306: 447—452

4 Braeutigam S. Neuroeconomics —— From neural systems to economics behaviour. Brain Res Bull, 2005, 67: 355—360

5 Zak P J. Neuroeconomics. Philos Trans R Soc Lond B Biol Sci, 2004, 359: 1737—1748

6 Sanfey A G, Loewenstein G, McClure S M, et al. Neuroeconomics: Cross-currents in research on decision-making. Trends Cogn Sci, 2006, 10(3): 108—116

7 Camerer C F, Loewenstein G, Prelec D. Neuroeconomics: How neuroscience can inform economics. J Econ Lit, 2005, 43(1): 9—64

8 Camerer C F, George L, Drazen *P. Neuroeconomics*: Why economics needs brains. J Econ, 2004, 106(3): 555－579
9 Lee N, Broderick A, Chamberlain L. What is 'neuromarketing'? A discussion and agenda for future research. Int J Psychophysiol, 2006, 63(2): 199－204
10 Lee D. Neuroeconomics: Making risky choices in the brain. Nat Neurosci, 2005, 8(9): 1129－1130
11 McClure S M, Berns G S, Montague P R. Temporal prediction errors in passive learning task activation human striatum. Neuron, 2003, 38: 339－346
12 O'Doherty J, Dayan P, Friston K J, et al. Temporal difference models and reward-related learning in the human brain. Neuron, 2003, 38: 329－337
13 Gottfried J A, O'Doherty J, Dolan R J. Appetitive and aversive olfactory learning in humans studied using event-related functional magnetic resonance imaging. J Neurosci, 2002, 22: 10829－10837
14 Anderson A K, Christoff K, Stappen I, et al. Dissociated neural representations of intensity and valence in human olfaction. Nat Neurosci, 2003, 6: 196－202
15 Aharon I, Etcoff N, Ariely D, et al. Beautiful faces have variable reward value: fMRI and behavioral evidence. Neuron, 2001, 32: 527－551
16 Kawabata H, Zeki S. Neural correlates of beauty. J Neurophysiol, 2004, 91: 1699－1705
17 Bartels A, Zeki S. The neural correlates of maternal and romantic love. Neuroimage, 2004, 21: 1155－1166
18 Aron A, Fisher H, Mashek D J, et al. Reward, motivation, and emotion systems associated with early-stage intense romantic love. J Neurophysiol, 2005, 94: 327－337
19 Vartanian O, Goel V. Neuroanatomical correlates of aesthetic preference for paintings. Neuroreport, 2004, 15: 893－897
20 Azim E, Mobbs D, Jo B, et al. Sex differences in brain activation elicited by humor. Proc Natl Acad Sci USA, 2005, 102: 16496－16501
21 Mobbs D, Hagan C C, Azim E, et al. Personality predicts activity in reward and emotional regions associated with humor. Proc Natl Acad Sci USA, 2005, 102: 16502－16506
22 Menon V, Levitin D J. The rewards of music listening: Response and physiological connectivity of the mesolimbic system. Neuroimage, 2005, 28: 175－184
23 Steven B, Michael M, Lawrence P. Passive music listening spontaneously engages limblic and paralimbic systems. Neuroreport, 2004, 15(13): 2033－2037
24 Erk S, Spitzer M, Wunderlich A P, et al. Cultural objects modulate reward circuitry. Neuroreport, 2002, 13: 2499－2503
25 Delgado M R, Nystron L E, Fissell C, et al. Tracking the hemodynamic responses to reward and punishment in the stratum. J Neurophysiol, 2001, 84: 3072－3077
26 Elliott R, Friston K J, Dolan R J. Dissociable neural responses in human reward systems. J Neurosci, 2000, 20: 6159－6165
27 O'Doherty J P, Kringelbach M L, Rolls E T, et al. Abstract reward and punishment representations in the human orbitofrontal cortex. Nat Neurosci, 2001, 4: 95－102
28 Knutson B, Adams C M, Fong G W, et al. Anticipation of increasing monetary reward selectively recruits nucleus accumbens. J Neurosci, 2001, 21: RC159(1－5)
29 Knutson B, Taylor J, Kaufman M, et al. Distributed neural representation of expected value. J Neurosci, 2005, 25: 4806－4812
30 Shizgal P. Neural basis of utility estimation. Curr Opin Neurobiol, 1997, 7: 198－208
31 Montague P R, Berns G S. Neural economics and the biological substrates of valuation. Neuron, 2002, 36: 265－84.
32 Kahneman D, Tversky A. Prospect theory: An analysis of decision under risk. Econometrica, 1979, 47: 263－291
33 Kahneman D, Wakker P P, Sarin R. Back to Bentham? Explorations of experienced utility. Q J Econ, 1997, 112: 375－405
34 Yu R J, Zhou X L. Brain potentials associated with outcome expectation and outcome evaluation. Neuroreport, 2006, 17(15): 1649－1653
35 Knutson B, Fong G W, Adams C M, et al. Dissociation of reward anticipation and outcome with event-related fMRI. Neuroreport, 2001, 12: 3683－3687
36 Breiter H C, Aharon I, Kahneman D, et al. Functional imaging of neural responses to expectancy and experience of monetary gains and losses. Neuron, 2001, 30(2): 619－639
37 Tom S M, Fox C R, Trepel C, et al. The neural basis of loss aversion in decision-making under risk. Science, 2007, 315(26): 515－518
38 von Neumann J, Morgenstern O. Theory of Games and Economic Behavior. Princeton: Princeton University Press, 1944
39 Preuschoff K, Bossaerts P, Quartz S R. Neural differentiation of expected reward and risk in human subcortical structures. Neuron, 2006, 51: 381－390
40 Knutson B, Rick S, Wimmer E, et al. Neural predictors of purchases. Neuron, 2007, 53: 147－156
41 Tversky A, Kahneman D. The framing of decisions and the psychology of choice. Science, 1981, 211: 453－458
42 Holroyd C B, Larsen J T, Cohen J D. Context dependence of the event-related brain potential to reward and punishment. Psychophysics, 2004, 41: 245－253
43 Nieuwenhuis S, Heslenfeld D J, von Geusau N J A, et al. Activity in human reward-sensitive brain areas is strongly context dependent. Neuroimage, 2005, 25: 1302－1309
44 Akitsuki Y, Sugiura M, Watanabe J, et al. Context-dependent cortical activation in response to financial reward and penalty: An event-related fMRI study. Neuroimage, 2003, 19: 1674－1683
45 Frederick S, Loewenstein G, O'Donoghue T. Time discounting and time preference: A critical review. J Econ Lit, 2002, 40: 351－401
46 McClure S M, Laibson D I, Loewenstein G, et al. Separate neural systems value immediate and delayed monetary rewards. Science, 2004, 306: 503－507
47 Loomes G, Sugden R. Regret theory: An alternative of rational choice under uncertainty. Econ J, 1982, 92: 805－824
48 Bell D E. Regret in decision making under uncertainty. Oper Res, 1982, 30: 961－981
49 Camille N, Coricelli G, Sallet J, et al. The involvement of the orbitofrontal cortex in the experienced of regret. Science, 2004, 304: 1167－1170
50 Coricelli G, Critchley H D, Joffily M, et al. Regret and its avoidance: A neuroimaging study of choice behavior. Nat Neurosci, 2005, 8: 1255－1262

51 Ursu S, Carter C S. Outcome representations, counterfactual comparisons and the human orbitofrontal cortex: Implications for neuroimaging studies of decision-making. Cogn Brain Res, 2005, 23: 51－60
52 Bechara A, Damasio H, Tranel D, et al. Deciding advantageously before knowing the advantageous strategy. Science, 1997, 275: 1293－1295
53 Shiv B, Loewenstein G, Bechara A,et al. Investment behavior and the negative side of emotion. Psychol Sci, 2005, 16: 435－439
54 Shiv B, Loewenstein G F, Bechara A. The dark side of emotions in decision making: When individuals with decreased emotional reactions make more advantageous decisions. Cogn Brain Res, 2005, 23(1): 85－92
55 Mellers B, Schwartz A, Ritov I. Emotion-based choice. J Exp Psychol: General, 1999, 128: 332－345
56 de Martino B, Kumaran D, Seymour B, et al. Frames, biases, and rational decision-making in the human brain. Science, 2006, 313: 684－687
57 Kahneman D, Frederick S. Frames and brains: Elicitation and control of response tendencies. Trends Cogn Sci, 2007, 11: 45－46
58 Lo A W, Repin D V. The psychophysiology of real-time financial risk processing. J Cogn Neurosci, 2002, 14(3): 323－339
59 Kohlberg L. Stage and sequence: The cognitive-developmental approach to socialization. In: Goslin D A, ed. Handbook of Socialization Theory and Research. Chicago: Rand McNally, 1969. 347－480
60 Greene J D, Haidt J. How (and where) does moral judgment work? Trends Cogn Sci, 2002, 6(12): 517－523
61 Greene J D, Sommerville R B, Nystrom L E, et al. An fMRI investigation of emotional engagement in moral judgment. Science, 2001, 293: 2105－2108
62 Greene J D, Nystrom L E, Engell A D, et al. The neural bases of cognitive conflict and control in moral judgment. Neuron, 2004, 44: 389－400
63 Cohen J D. The vulcanization of the human brain: A neural perspective on interactions between cognition and emotion. J Econ Perspect, 2005, 19(4): 3－24
64 Montague P R, King-Casas B, Cohen J D. Imaging valuation models in human choice. Annu Rev Neurosci, 2006, 29: 417－448
65 Premack D, Woodruff G. Does the chimpanzee have a theory of mind? Behav Brain Sci, 1978, 1(4): 515－526
66 Frith C D, Frith U. Interacting minds: A biological basis. Science, 1999, 286(5445): 1692－1695
67 Gallagher H L, Frith C D. Functional imaging of 'theory of mind'. Trends Cogn Sci, 2003, 7: 77－83
68 Rilling J K, Sanfey A G, Aronson J A, et al. The neural correlates of theory of mind within interpersonal interactions. Neuroimage, 2004, 22: 1694－1703
69 Fukui H, Murai T, Shinozaki J, et al. The neural basis of social tactics: An fMRI study. Neuroimage, 2006, 32: 913－920
70 Yu R J, Zhou X L. Brain responses to outcomes of one's own and the other's performance in a gambling task. Neuroreport, 2006, 17(16): 1747－1751
71 Asch S E. Effects of group pressure upon the modification and distortion of judgments. In: Guetzkow H S, ed. Group, Leadership and Men Research in Human Relations. Pittsburgh: Carnegie Press, 1951. 177－190
72 Asch S E. Social Psychology. New York: Prentice-Hall, 1952
73 Berns G S, Chappelow J, Zink C F, et al. Neurobiological correlates of social conformity and independence during mental rotation. Biolog Psychiatry, 2005, 58: 245－253
74 Bolton G E, Zwick R. Anonymity versus punishment in ultimatum games. Games Econ Behav, 1995, 10(1): 95－121
75 Henrich J, Boyd R, Bowles S, et al. In search of homo economicus: Behavioral experiments in 15 small scale societies. Am Econ Rev, 2001, 91(2): 73－78
76 Decety J, Jackson P L, Sommerville J A, et al. The neural bases of cooperation and competition: An fMRI investigation. Neuroimage, 2004, 23: 744－751
77 Rilling J, Gutman D, Zeh T, et al. A neural basis for social cooperation. Neuron, 2002, 35(2): 395－405
78 Moll J, Krueger F, Zahn R, et al. Human fronto-mesolimbic networks guide decisions about charitable donation. Proc Natl Acad Sci USA, 2006, 103: 15623－15628
79 McCabe K, Houser D, Ryan L, et al. A funtional imaging study of cooperation in two-person reciprocal exchange. Proc Natl Acad Sci USA, 2001, 98: 11832－11835
80 Sanfey A G, Rilling J K, Aaronson J A, et al. Probing the neural basis of economic decision making: An fMRI investigation of the ultimatum game. Science, 2003, 300: 1755－1758
81 Knoch D, Pascual-Leone A, Meyer K,et al. Diminishing reciprocal fairness by disrupting the right prefrontal cortex. Science, 2006, 314: 829－832
82 Singer T, Kiebel S J, Winston J S, et al. Brain responses to the acquired moral status of faces. Neuron, 2004, 41(4): 653－662
83 King-Casas B, Tomlin D, Anen C, et al. Getting to know you: Reputation and trust in a two-person economic exchange. Science, 2005, 308: 78－83
84 Delgado M R, Frank R H, Phelps E A. Perceptions of moral character modulate the neural systems of reward during the trust game. Nat Neurosci, 2005, 8: 1611－1618
85 Zak P J, Kurzban R, Matzner W T. The neurobiology of trust. Annu N Y Acad Sci, 2004, 1032: 224－227
86 Kosfeld M, Heinrichs M, Zak P J, et al. Oxytocin increases trust in humans. Nature, 2005, 435: 673－676
87 Fehr E, Rockenbach B. Detrimental effects of sanctions on human altruism. Nature, 2003, 422: 137－140
88 de Quervain D J F, Fischbacher U, Treyer V, et al. The neural basis of autruistic punishment. Science, 2004, 305: 1254－1258
89 Singer T, Seymour B, O'Doherty J P, et al. Empathic neural responses are modulated by the perceived fairness of others. Nature, 2006, 439: 466－469
90 Shiv B, Bechara A, Levin I, et al. Decision neuroscience. Mark Lett, 2005, 16: 375－386