The Neural Basis of Economic Decision-Making in the Ultimatum Game
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Science 300, 1755 (2003);
DOI: 10.1126/science.1082976

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ide–sensitive factor) (33–35) or AP2 (36) may be required for export of functional heteromeric receptor complexes and/or stabilization of these complexes at the cell surface.

Our results suggest that phosphorylation of GluR2 Ser830 is necessary for LTD induction. In hippocampal cells transfected with GluR2 K882A, which presumably contain at least some GluR2 K882A/GluR3 and/or GluR2 K882A/GluR4c heteromeric receptor complexes, the presence of a PKC consensus site on subunits other than GluR2 appears to be insufficient to enable LTD. It is unknown whether the corresponding serines on GluR3 and GluR4c are indeed phosphorylated by PKC or if upstream sequence differences and differential protein binding render these subunits incapable of supporting LTD.

Previous attempts to test the involvement of cerebellar LTD in motor learning paradigms have relied on drugs or genetic manipulations that act early in the LTD induction signaling cascade, either at receptors or second messengers (1). These studies have been limited owing to the nonspecific nature of the manipulations (e.g., disruption of mGluR1 or PKC function). A GluR2 K882A knock-in mouse could provide the first strong test of the hypothesis that cerebellar LTD is required for certain forms of motor learning.

References and Notes

23. Single-letter abbreviations for the amino acid residues are as follows: A: Ala; C: Cys; D: Asp; E: Glu; F: Phe; G: Gly; H: His; I: Ile; K: Lys; L: Leu; M: Met; N: Asn; P: Pro; Q: Gln; R: Arg; S: Ser; T: Thr; V: Val; W: Trp; X: any amino acid; and Y: Tyr.
25. We obtained polyclonal antisera directed against a GluR2 carboxy-terminal peptide phosphorylated at Ser830 as previously described (78). To account for the possibility that mutation of LynSer interferes with the recognition of phosphorylated Ser830 by this antibody, we purified polyclonal antisera on an affinity column consisting of a bovine serum albumin (BSA)-conjugated GluR2 carboxy-terminal peptide containing the K882A mutation (KVGGEPS*VAI; p58 = phosphoSer830).
27. Z. Jia et al., Neuron 17, 945 (1996).
32. See supporting data on Science Online.
37. Thanks to R. Bock for skillful technical assistance, K. Takamori for advice on PCR genotyping, and members of the Huganir and Linden labs for helpful comments. This work was supported by HHMI and USPHS NS36715 (R.L.H.), USPHS MH51106 and MH01590 (D.J.L.) and the Devensky Fund (D.J.L.).

Supporting Online Material

www.sciencemag.org/cgi/content/full/300/5626/1751/DC1
Materials and Methods
Fig. S1
References

29 January 2003; accepted 6 May 2003

The Neural Basis of Economic Decision-Making in the Ultimatum Game

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The nascent field of neuroeconomics seeks to ground economic decision-making in the biological substrate of the brain. We used functional magnetic resonance imaging of Ultimatum Game players to investigate neural substrates of cognitive and emotional processes involved in economic decision-making. In this game, two players split a sum of money; one player proposes a division and the other can accept or reject this. We scanned players as they responded to fair and unfair proposals. Unfair offers elicited activity in brain areas related to both emotion (anterior insula) and cognition (dorsolateral prefrontal cortex).

Further, significantly heightened activity in anterior insula for rejected unfair offers suggests an important role for emotions in decision-making.

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Why do people do this? The game is so simple that it is improbable that these rejection are due to a failure to understand the rules of the game, or an inability to conceptualize a single-shot interaction with a partner (9). On the basis of participant reports, it appears that low offers are often rejected after an angry reaction to an offer perceived as unfair (10). Objecting to unfairness has been proposed as a fundamental adaptive mechanism by which we assert and maintain a social reputation (11), and the negative emotions provoked by unfair treatment in the Ultimatum Game can lead people to sacrifice sometimes considerable financial gain in order to punish their partner for the slight. Unfair offers in the Ultimatum Game induce conflict in the responder between cognitive (“accept”) and emotional (“reject”) motives, motives that we might expect to see represented in brain areas implicated in cognitive and emotional modes of thought, with additional regions possibly mediating these competing goals (12).

To shed light on the neural and psychological processes mediating such behaviors, we scanned 19 participants using functional magnetic resonance imaging (fMRI), each in the role of the responder in the Ultimatum Game. We were interested in neural and behavioral reactions to offers which were fair (the money is split 50:50) or unfair (the proposer offered an unequal split to his or her advantage). In particular, we hypothesized that unfair offers would engage neural structures involved in both emotional and cognitive processing, and that the magnitude of activation in these structures might explain variance in the subsequent decision to accept or reject these offers.

Before scanning, each participant was introduced to 10 people they were told would partner with them in the games to follow. They were told that they would play a single iteration of the game with each partner and that their decisions with each partner would not be revealed to the other partners and, therefore, could not affect subsequent offers. The participants were then placed inside the MRI scanner and began playing the Ultimatum Game with their partners via a computer interface (Fig. 1A) (13). They completed 30 rounds in all, 10 playing the game with a human partner (once with each of the 10 partners), 10 with a computer partner, and a further 10 control rounds in which they simply received money for a button press. The rounds were presented randomly, and all involved splitting $10. Offers made by human partners in fact adhered to a predetermined algorithm, which ensured that all participants saw the same set (and a full range) of offers (14, 15). Half of these offers were fair, that is, a proposal to split the $10 evenly ($5:$5), with the remaining half proposing unequal splits (two offers of $9:$1, two offers of $8:$2, and one offer of $7:$3). The 10 offers from the computer partner were identical to those from the human partners (half fair, half unfair). The 10 control trials were designed to control for the response to monetary reinforcement, independent of the social interaction. The distribution of offers generally mimics the range of offers typically made in uncontrolled versions of the game (i.e., involving freely acting human partners).

Behavioral results were very similar to those typically found in Ultimatum Game experiments (Fig. 1B) (16). Participants accepted all fair offers, with decreasing acceptance rates as the offers became less fair. Unfair offers of $2 and $1 made by human partners were rejected at a significantly higher rate than those offers made by a computer ($9:$1 offer: $x^2 = 5.28, df = 1, P = 0.02; $8:$2 offer: $x^2 = 8.77, df = 1, P = 0.003$), suggesting that participants had a stronger emotional reaction to unfair offers from humans than to the same offers from a computer (17).

Among the areas showing greater activation for unfair offers compared with fair offers from human partners (Fig. 2, A and B; table S1) were bilateral anterior insula, dorsolateral prefrontal cortex (DLPFC), and anterior cingulate cortex (ACC). The magnitude of activation was also significantly greater for unfair offers from human partners as compared to both unfair offers from computer partners (left insula: $t = 2.52, P < 0.02$; right insula: $t = 2.2, P < 0.03$) and low control offers (left insula: $t = 3.46, P < 0.001$; right insula: $t = 2.83, P < 0.05$). This suggests that these activations were not solely a function of the amount of money offered to the participant but rather were also uniquely sensitive to the context, namely perceived unfair treatment from another human (Fig. 2C and D). Further, regions of bilateral anterior insula demonstrated sensitivity to the degree of unfairness of an offer, exhibiting significantly greater activation for a $9:$1 offer than an $8:$2 offer from a human partner (Fig. 2E) (left insula, $P < 0.001$; right insula, $P < 0.01$), in addition to the aforementioned greater activation for unfair offers than fair ($5:$5) offers.

Activation of bilateral anterior insula to unfair offers from human partners is particularly interesting in light of this region’s oft-noted association with negative emotional states. Anterior insula activation is consistently seen in neuroimaging studies of pain and distress (18–20), hunger and thirst (21, 22), and autonomic arousal (23). This region has also been implicated in studies of emotion, in particular involvement in the evaluation and representation of specific negative emotional states (24). Chief amongst these are anger and disgust, both of which have been found to engage a distinct region of the anterior insula activated by an unfair offer in the present study (25, 26). Though studies of disgust have largely focused on physical sensations of taste and odor (27), it has been suggested that emotion-based disgust (as perhaps induced by an insultingly unfair offer) may be conceptually similar. The recruitment of similar neural structures, namely the anterior insula, in both physical and moral disgust gives some credence to this notion.

If the activation in the anterior insula is a reflection of the responders’ negative emotional response to an unfair offer, we might expect activity in this region to correlate with the subsequent decision to accept or reject the offer. Because all fair offers and the vast majority of $7:$3 offers were accepted, we focused on the $8:$2 and $9:$1 offers from a human partner for the analysis of whether neural activity was related to the decision made in the game. Indeed, looking at the participant level, those partici-
In contrast to the insula, DLPFC usually has been linked to cognitive processes such as goal maintenance and executive control (28, 29). Thus, the DLPFC activation we observed in response to unfair offers may relate to the representation and active maintenance of the cognitive demands of the task, namely the goal of accumulating as much money as possible. An unfair offer is more difficult to accept, as indicated by the higher rejection rates of these offers, and hence higher cognitive demands may be placed on the participant in order to overcome the strong emotional tendency to reject the offer. Although DLPFC activated to unfair offers, this activation did not correlate with acceptance rates ($r = 0.04, P > 0.05$), suggesting that activation of this region alone is not sufficient to predict behavior. However, motivated by the hypothesis that this region may be competing with emotional areas in influencing the decision, we examined the balance between activation in anterior insula and DLPFC for unfair offers. Unfair offers that are subsequently rejected have greater anterior insula than DLPFC activation, whereas accepted offers exhibit greater DLPFC than anterior insula (Fig. 3B). The contrast in activation between these two areas is significantly different for accepted and rejected offers ($P = 0.033$, one-tailed), consistent with the hypothesis that competition between these two regions influences behavior. DLPFC activity remains relatively constant across unfair offers, perhaps reflecting the steady task representation of money maximization, with anterior insula scaling monotonically to the degree of unfairness, reflecting the emotional response to the offer. Caution is needed when comparing the magnitude of the fMRI signal across brain regions. However, it is interesting to note that the outcome of the decision may reflect the relative engagement of these regions, with greater anterior insula activation biasing toward rejection and greater DLPFC biasing toward acceptance. Finally, unfair offers were also associated with increased activity in ACC. ACC has been implicated in detection of cognitive conflict (30, 31), and activation here may reflect the conflict between cognitive and emotional motivations in the Ultimatum Game.

This study sought to identify the neural correlates of fairness and unfairness, and in particular the relative contributions of cognitive and emotional processes to human decision-making. A basic sense of fairness and unfairness is essential to many aspects of societal and personal decision-making and underlies notions as diverse as ethics, social policy, legal practice, and personal morality. Our results are consistent with...
they had been suspicious of the offers they received. Further, the behavioral results in the human partner condition replicate those found in versions of the game using no deception, with approximately half of offers of 20% or less of the total bank being rejected ($9:$1 split, 45% versus 42%; $8:$2 split, 47% versus 49%). Perhaps most importantly, if subjects suspected deception, this should have diminished emotional responses (i.e., if subjects suspected the offers to be fictitious, their emotional reactions to these offers, particularly unfair offers, should have been muted). The fact that we observed significant effects consistent with emotional responses suggests, once again, that the effects of deception were minimal and, if they were present, they likely have simply caused an under-estimate of the observed effects. Although we are sensitive to the issue of deception, we believe that the methodological constraints of fMRI justified our practice and that the findings do not appear to be tainted by subjects' possible perceptions of the deception used.

15. A common concern regarding the use of deception involves possible contamination of the participant pool. As mentioned previously, rejection rates in the current study replicate those typically reported from uncontrolled Ultimatum Game studies; therefore, we do not believe we suffered unduly from this. Furthermore, a comparison of rejection rates over the course of the experiment (i.e., independently of participants) indicates no systematic trends in these rates (mean rejection rate of offers for first six participants was 32%; mean of last six participants was 35%).

16. After the conclusion of the Ultimatum Game with all partners, subjects then played a single round of the Prisoner’s Dilemma (PD) game with each of the partners. This raises the possibility that subjects did not treat the Ultimatum Game as a true single-shot game. We do not believe playing the PD game affected their pay in the Ultimatum Game in this study for several reasons. First, our behavioral results support the notion that the Ultimatum Game was played as a single-shot game. As noted above, the proportion of rejected offers in our study matches proportions reported in the experimental economic literature when the game is strictly controlled as single-shot. We would have expected much higher rejection rates in an iterated Ultimatum Game. Second, unpublished data of ours using a single-shot Ultimatum Game (with no subsequent task) produced rejection rates of unfair offers that are virtually identical to those reported here ($58.52 split, 47% versus 49%; 59.51 split, 61% versus 60%). We believe this evidence strongly supports that subjects treated the Ultimatum Game as a single-shot game, as instructed.

17. We asked our participants as part of the debriefing process what they considered a “fair” offer to be irrespective of their decision to accept or reject, thus providing an indication of their standards of fairness. Of our participants, 58% considered any offer less than $5.55 as unfair, with the remaining 42% deeming anything less than $7.53 as an unfair division.


36. We would like to thank D. Kahneamen, A. Scheres, and three anonymous reviewers for their helpful comments. This work was supported in part by grants from the Seaver Institute and the Mind, Brain, Body, and Health Initiative.

Supporting Online Material

www.sciencemag.org/cgi/content/full/300/5626/1755/DC1

Materials and Methods

Table S1

31 January 2003; accepted 15 April 2003

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**V1 Neurons Signal Acquisition of an Internal Representation of Stimulus Location**

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A fundamental aspect of visuomotor behavior is deciding where to look or move next. Under certain conditions, the brain constructs an internal representation of stimulus location on the basis of previous knowledge and uses it to move the eyes or to make other movements. Neuronal responses in primary visual cortex were modulated when such an internal representation was acquired: Responses to a stimulus were affected progressively by sequential presentation of the stimulus at one location but not when the location was varied randomly. Responses of individual neurons were spatially tuned for gaze direction and tracked the Bayesian probability of stimulus appearance. We propose that the representation arises in a distributed cortical network and is associated with systematic changes in response selectivity and dynamics at the earliest stages of cortical visual processing.

To assess whether monkeys (Macaca mulatta) form an internal representation of stimulus location, we devised a task in which information about future stimulus locations could be acquired progressively with successful trials in one experimental condition but...