32. It is not crucial for our purposes that identical actions lead to high payoffs. Instead, the necessity of coordinated choices for a high payoff is important. Thus, if the choice combination A for player 1 and B for player 2 led to a high payoff, then the players would simply need to coordinate on (A, B). Almost every bargaining problem or economic exchange involves some necessity for coordinating expectations and actions.
33. J. G. Jorgensen, Western Indians (Freeman, New York, 1980).
37. Materials and methods are available as supporting material on Science Online.
45. This research was supported by the Swiss National Science Foundation (105312-114017) and is part of the Research Priority Program “Foundations of Human Social Behavior—Altruism versus Egocism” at the University of Zurich. We thank S. Bowles for valuable comments on an earlier version of this article and R. McElreath for helpful insights during the initial stages of the project.

Supporting Online Material
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Understanding Overbidding: Using the Neural Circuitry of Reward to Design Economic Auctions

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We take advantage of our knowledge of the neural circuitry of reward to investigate a puzzling economic phenomenon: Why do people overbid in auctions? Using functional magnetic resonance imaging (fMRI), we observed that the social competition inherent in an auction results in a more pronounced blood oxygen level–dependent (BOLD) response to loss in the striatum, with greater overbidding correlated with the magnitude of this response. Leveraging these neuroimaging results, we design a behavioral experiment that demonstrates that framing an experimental auction to emphasize loss increases overbidding. These results highlight a role for the contemplation of loss in understanding the tendency to bid “too high.” Current economic theories suggest overbidding may result from either “joy of winning” or risk aversion. By combining neuroeconomic and behavioral economic techniques, we find that another factor, namely loss contemplation in a social context, may mediate overbidding in auctions.

An unresolved question in the emerging field of neuroeconomics is whether data from neuroscience can inform economic theory such that it motivates behavioral economic institutional design (1–4). In this report, we address this question by taking advantage of our knowledge of the neural circuitry of reward to investigate a puzzling economic phenomenon. Specifically, why do people overbid in auctions? (5, 6).

Auctions are an old and widely used method in allocating goods (7). Mention of them dates back to Roman times, when spoils of war were sold on the block. Although there are many different types of auctions, they all share the feature that bidders must determine a bidding strategy (or bid function) to be used in submitting their bid. A bid function for a buyer in an auction is a mapping from the value that the bidder places on the good for sale to the bid chosen. A set of bidding functions is considered to be an equilibrium (Nash equilibrium) if, given the strategy used by one’s opponents, no bidder has any incentive to change his or her bidding strategy. One robust finding in experimental auctions is that bidders tend to bid above their Nash equilibrium risk-neutral bid function (5); this behavior has been labeled “overbidding” in the economics literature. In other words, given the value of the good for sale they submit bids that are “too high.” Two competing explanations for this phenomenon exist. Many scholars have assumed that risk aversion is responsible for this increase in bids, because bidding above one’s risk-neutral Nash equilibrium bid function is exactly what risk aversion prescribes (5, 6, 8). Another explanation stems from the ideas that bidders enjoy a “joy of winning” the social competition inherent in an auction (5, 6).

The goal of this study is to provide insight into the neural circuitry of experimental auctions and to use this insight to generate and test a behavioral economic approach to understand overbidding. First, we used functional magnetic resonance imaging (fMRI) to examine the neural correlates of winning and losing an experimental auction, while modulating potentially important variables such as type of social competition (auction versus lottery) and type of incentive (money versus points with no monetary value). On the basis of these brain imaging results and our understanding of the neural circuitry of reward, we generated a hypothesis concerning the mechanisms underlying overbidding in experimental auctions. We then tested this hypothesis in a behavioral economic experiment.

In the fMRI study, 17 participants were instructed that they would each be playing two types of games: a two-person auction and a lottery (52 events for each treatment) (9). Before participants were scanned, they briefly met their competitor for the auction and were informed that they would be playing an unknown but fixed strategy. In the auction game, participants were assigned a value (\( V \)) at the beginning of each trial. These values were drawn from a finite set with equal probability. Participants were asked to choose a bid (\( b \)) (the decision phase) and were then informed if they won or lost the auction (the outcome phase). There were four possible \( V \)’s assigned for the good sold (6, 8, 10, 12) and four options for \( b \) (2, 5, 7, 8). The competitor bid according to the Nash equilibrium strategy (\( Vb \) equals 6,2, 8,5; 10,7; 12,8). In the money condition, \( V \) and \( b \) represented dollars, and the participants were informed they would receive a payoff of \( V \) minus \( b \) if they won that trial and zero if they lost. They would be paid their total winnings from one randomly selected block out of the four
money blocks presented (each encompassing 13 trials) at the end of the study. In the points condition, $V$ and $b$ represented points. Participants were told that the accumulation of points from a random points block (the sum of $V$ minus $b$ for win trials) would be a measure of how well they did relative to other participants, with final anonymous results disseminated at the conclusion of the study. The auction game used the first-price sealed-bid rule in which the participant did not know the $V$ assigned to the competitor on each trial and the higher bid won. In case of identical bids, ties were broken at random. Because losses yielded zero payoffs, a loss did not signify a monetary or points loss per se, but merely that the participant did not win that particular auction (10).

In the lottery game, subjects played against a computer that used the same fixed Nash equilibrium bid strategy as the auction game confederate. Unlike the auction, participants were not required to submit a bid for the random value assigned to them. Rather, they were assigned both $V$ and $b$ at the beginning of each trial and were simply asked to indicate if they wanted to play the lottery for that trial (decision phase). If their assigned $b$ was greater than the $b$ generated by the computer’s Nash equilibrium bid, they won the lottery, if not, they lost (outcome phase). As in the auction game, participants played the lottery for either money or points. Behavioral measures of reaction time and choice were collected throughout the experiment, along with postexperimental Likert-scale ratings (9).

As in previous auction studies (5, 6), participants overbid with respect to the risk-neutral Nash equilibrium ($[@(16) = 3.04, P < 0.008$]. Overbidding compared with choosing the equilibrium bid was greatest when the incentive was monetary ($[@(16) = 3.30 P < 0.005$]. Overall, participants’ chosen $b$ was greater than the equilibrium $b$ on 65% of the money trials and 57% of the points trials (11).

The goal of the fMRI study was to examine the effects of type of social competition (auction versus lottery) and type of incentive (money versus points) on blood oxygen level-dependent (BOLD) responses to winning or losing. Given this, the focus of the analysis was the outcome phase. Statistical maps contrasting wins and losses across all conditions were generated ($P < 0.001$, cluster threshold of 3 mm$^3$ contiguous voxels). Mean beta weights (19) from each region of interest (ROI) defined by this contrast were extracted and input into two separate analyses of variance (ANOVA) to examine main effects of social competition and incentive during win or loss outcomes separately. Regions identified during the outcome phase included both left and right striatum, specifically the ventral caudate nucleus, previously implicated in monetary outcome processing and learning from feedback (12–18), along with ROIs in the occipital lobe (table S4). An examination of the BOLD response in these ROIs revealed differential responses for type of social competition or for type of incentive, only in the right and left striatum (Fig. 1A). Activation in this region has previously been shown to be graded according to the magnitude of monetary gain and loss during probabilistic games (12–15), with an increase in BOLD signal relative to resting baseline for positive outcomes (wins) and a decrease for negative outcomes (losses) (14–16) that resemble learning signals (17, 18). Within the right striatum ROI (20), results differed across win and loss trials. A main effect of incentive ($[@(16) = 9.67, P < 0.01$) was observed during win trials, driven primarily by a larger response to monetary reward compared with points reward ($[@(16) = 3.11, P < 0.01$), but no main effect of social competition was observed. Instead, differences between auction and lottery trials were apparent only in the context of losses ($[@(16) = 5.29, P < 0.05$). Of particular interest, post hoc $t$ tests showed that mean beta weights for win trials during the auction game (irrespective of incentive) were not significantly different from the lottery game ($[@(16) = -0.60, P = 0.55$). In contrast, mean beta weights for losses led to a more pronounced decrease from baseline

![Fig. 1. Striatal response to loss is enhanced by social competition in the auction game. (A) Win versus loss outcome contrast: right striatum, including the ventral caudate nucleus was identified as a region of interest (peak at $x, y, z = 10, 2, 1$). (B) Parameter estimates, or mean beta weights, for win and loss trials from the right ventral caudate ROI for auction and lottery games show differential responses between auction and lottery only during losses. Error bars are SEM. (C) Across participants, the general tendency to overbid during auction trials correlated with BOLD signals in the right striatum ROI (depicted by parameter estimates) when an auction outcome was a loss ($r = -0.493, P < 0.05$), but not when the outcome was a win ($r = -0.059, P = 0.82$).](image)

**Table 1.** Results of two separate regressions on the auction data (cluster analysis by subjects) (±SEM). First regression analysis: Overbids are regressed on BOLD signals from the right striatal ROI for individual win-and-loss trials (outcome phase) during the auction game. Second regression analysis: Overbids are regressed on BOLD signals from the rights striatum ROI and on values ($V$). The number of observations ($N$) for each trial is given.

<table>
<thead>
<tr>
<th>Type of trial</th>
<th>$N$</th>
<th>Regression coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><strong>Values</strong></td>
</tr>
<tr>
<td><strong>First regression analysis</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Win trials</td>
<td>397</td>
<td>-0.016 ± 0.1342</td>
</tr>
<tr>
<td>Loss trials</td>
<td>372</td>
<td>-0.316 ± 0.2384*</td>
</tr>
<tr>
<td><strong>Second regression analysis</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Win trials</td>
<td>397</td>
<td>0.024 ± 0.0208*</td>
</tr>
<tr>
<td>Loss trials</td>
<td>372</td>
<td>0.072 ± 0.0816</td>
</tr>
</tbody>
</table>

*P < 0.05
during auction compared with lottery trials \(t(16) = -2.30, P < 0.05\) (Fig. 1B). Finally, a correlation between mean beta weights in the right striatal ROI and a participant’s tendency to overbid in general (i.e., the total number of times a participant chose to overbid during auction trials) was observed for loss \((r = -0.493, P < 0.05)\), but not win \((r = -0.059, P = 0.82)\) outcomes (Fig. 1C).

Given that there was no actual loss of money or points in either game, it is somewhat surprising that the response to losses during the auction game yielded a significant decrease in BOLD signal relative to the resting baseline and the lottery game. One possibility is that the social competition inherent in the auction game resulted in a loss signal in the right striatum, mirroring that observed with actual monetary loss. The importance of social competition in driving responses in the auction game is further supported by the data from the points condition. Notably, the points incentive could be interpreted as a more relative reward (with respect to other competitors), whereas the monetary incentive is a more abstract reward. A two-way repeated measures ANOVA, including only the data from the points condition with type of social competition and type of feedback (win and loss) as factors, revealed a main effect of competition \((F_{1,16} = 4.44, P < 0.05)\). This was driven by right striatal responses to winning versus losing during the auction \([t(16) = 2.01, P = 0.06]\), rather than the lottery game \([t(16) = 0.50, P = 0.63]\) (see fig. S1). The finding that social factors can modulate responses in the striatum to monetary incentives has been previously demonstrated with other economic games \((21–25)\). For experimental auctions, it appears that the social interaction specifically alters the response to losses in the striatum, in addition to enhancing overall responses to a nonmonetary reinforcer.

Although the inference of psychological states from BOLD responses should generally be viewed with caution \((26)\), our imaging results provide some initial hypotheses as to the nature of overbidding in experimental auctions. The lack of an enhanced BOLD response in the striatum to wins (in the auction compared with the lottery) suggests that the “joy of winning” may not be mediating overbidding in experimental auctions. In contrast, the stronger BOLD response to losses in the auction game suggests that a fear of losing a social competition may be linked to overbidding. The fear of losing the social competition of an auction may lead to a striatal response similar to that observed in loss aversion \((27)\). However, because no actual losses occurred in this experiment, it would appear that the “fear of losing” the social competition was a factor independent of pure loss aversion.

To further explore these hypotheses a post hoc analysis was conducted. For each subject, we extracted beta weights from the right striatal ROI for wins and losses (outcome phase) for each auction trial. With these beta values, we ran two separate regressions, with a cluster analysis by subjects, examining the relation between the overbids (the difference between the actual bids and the Nash equilibrium), the value assigned \((V)\), and the BOLD response during the outcome phase to a win or loss. Our results indicate that the BOLD response coefficient is not significantly different than 0 for the win trials \([t = -0.25, P > 0.05]\), but significant responses are observed for loss trials \([t = -2.81, P < 0.05]\) (Table 1, first regression analysis). The BOLD response regression coefficient of loss trials is significant even when value \((V)\) is included as a controlling factor \((t = -2.74, P < 0.05)\) (Table 1, second regression analysis). These results, combined with our cross-subject correlation (see Fig. 1C), lead to the intriguing conjecture that perhaps it is the anticipation of a possible loss in experimental auctions that is, at least in part, driving the tendency to bid “too high.”

If this conjecture is correct, we should be able to take advantage of this fear of losing to design an experimental auction that will result in an even stronger tendency to overbid. More precisely, if the anticipation of the unpleasant state associated with a loss led participants to increase their bids to avoid that state, then manipulating the parameters of a first-price auction to highlight the potential for loss, as opposed to gain, should increase bid values, even if the equilibrium bid function was left unaltered. Hence, we would expect that the loss-frame auction would not only increase bids conditional on value, but also raise more revenue than either a control auction or one where gains or “wins” are emphasized.

In order to test these assumptions, we ran a behavioral economic experiment with three conditions. In all conditions, participants played 30 rounds of an auction game with a randomly assigned single competitor (another participant) on each trial. The range of \(V\) was 0 to 100 experimental dollars. In each round, participants knew their own assigned \(V\) and the distribution \((28)\) of their competitor’s assigned values and were asked to submit a bid \(b\). The participant submitting the highest \(b\) won the good. The payoff was equal to \(V\) minus \(b\) for the winner and zero for the loser.

There were three experimental groups: baseline, loss-frame, and bonus-frame. The baseline condition was a typical first-price auction as described above. The loss-frame auction was identical to the baseline except that participants were given a sum of 15 experimental dollars at the beginning of each round and were told it was theirs to keep if they won the auction, but that they would have to give it back if they lost. As previously discussed, the purpose of the loss-frame was to prime or enhance the possibility of a loss while hypothesizing, based on the observed striatum BOLD responses, that such priming would increase bidding behavior. The bonus-frame auction was again identical to the baseline, except that participants were told that, in addition to receiving the payoff \((V - b)\) if they won the auction, they would also be given a bonus.

**Fig. 2.** Estimations of bid functions for the loss-frame, bonus-frame, and baseline control conditions with reference equilibrium functions. Relative to reference equilibrium bids (light blue and purple lines), participants overbid in all three treatment conditions. Consistent with increased overbidding in the loss-frame condition (pink line), bids were higher overall in this condition and the slope of the bidding function was significantly steeper in the loss treatment than in either the bonus-frame (light blue line) \((t = 3.023, P < 0.005)\) or the baseline control (yellow line) \((t = 11.743, P < 0.005)\) conditions. In addition, the slope of the bidding function for the bonus-frame condition was significantly steeper than the baseline control condition \((t = 8.283, P < 0.005)\). See Table 2 for bid functions.

**Table 2.** Reference equilibrium and estimation of bid strategies for baseline, bonus- and loss-frame conditions. Regressions were conducted with random effects. For estimation of bid strategies, we used a linear specification. Bid functions were estimated using higher-order polynomials, but the coefficients associated with those higher order terms were insignificant.
Table 3. Mean revenue by treatment and statistical comparisons (one-tailed t test) of revenues across treatments in the behavioral study. Revenue generated in the loss-frame is significantly greater than both the bonus-frame and baseline conditions. In addition, the bonus-frame condition resulted in greater revenue than the baseline condition.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Revenue (USD)</th>
<th>Analysis</th>
</tr>
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<tbody>
<tr>
<td><strong>Loss treatment</strong></td>
<td></td>
<td>t(1108) = 3.534</td>
</tr>
<tr>
<td>Bonus treatment</td>
<td></td>
<td>t(1468) = 2.943</td>
</tr>
<tr>
<td>Baseline</td>
<td>40.88 ± 1.857</td>
<td></td>
</tr>
</tbody>
</table>

of 15 experimental dollars. Note that in both the loss- and bonus-frame conditions, only the winners get an additional 15 experimental dollars, so the auctions are strategically identical. The difference is simply the way it is framed (9). Given this, equilibrium bid functions are the same in the loss-frame and bonus-frame treatments for any given form of the utility function. In the risk-neutral Nash equilibrium for the two nonbaseline treatments, participants’ bids should be the same as the baseline condition plus 15 experimental dollars. However, if the hypothesis derived from our fMRI results is correct and the fear of losing is prompting overbidding, we should observe higher overall bids in the loss-frame condition than either the bonus-frame or baseline conditions.

The bid function for each condition is summarized in Table 2. As expected from previous research, there was overbidding in all three conditions relative to the risk-neutral Nash equilibrium. In addition, there was a constant relative increase in overall bid amount in the two nonbaseline conditions due to the additional potential profit of 15 experimental dollars. Consistent with our hypothesis, there was also a significant difference in the slope of the bid functions across conditions. As can be seen in Fig. 2, the bid function for the loss-frame condition is higher overall than the bid function in all other conditions. This is true despite the fact that both the bonus- and loss-frame conditions have identical equilibrium bid functions. If we calculate the actual revenue to a hypothetical auctioneer generated in the experiment, the revenue generated by the loss-frame (45.62) was significantly higher than either the bonus-frame (42.41) or baseline (40.88) conditions (Table 3). By taking advantage of our knowledge of the brain’s reward circuitry, we were able to design a novel auction paradigm that led to greater overbidding.

Previous economic investigations of experimental auctions have led to two opposing views as to the nature of overbidding (5, 6). The combination of neuroscience and behavioral techniques provides an interesting perspective on this age-old question. Both our brain imaging and behavioral results are inconsistent with the suggestion that the “joy of winning” mediates overbidding. Although our findings are not inconsistent with a role for risk aversion in the tendency to bid too high, they suggest we should more specifically consider the fear of losing or social loss aversion. If sensitivity to risk alone is mediating overbidding, then the simple framing manipulation in our behavioral study would not have been effective, because risk was equivalent in both the loss- and bonus-frame conditions. By emphasizing the potential loss in the loss-frame auction, we were able to increase overbidding. Our results suggest that contemplated loss is an important factor in experimental auctions. The fear of losing the social competition inherent in an auction may lead people to pay too high a price for the good for sale. The results of this report, therefore, highlight an extra component in subject’s behavior, chiefly the social component of competition, which is not captured by models limited to typical economic variables like profits and probabilities.

Recently, there has been significant debate about whether neuroscience techniques can provide novel insights to economic questions (1–4). Although there have been a number of neuroeconomics studies that have utilized economic games to further our understanding of brain function, the benefits to traditional behavioral economics as a result is unclear. As was observed in the progression of cognitive neuroscience, using neuroscience models to inform behavioral or psychological questions requires an initial basic understanding of the neural mechanisms underlying the behavior in question (3, 4, 29). Because of recent advances in neuroeconomics and our knowledge of the neural circuitry of reward, we were able to leverage our neuroimaging results to develop an auction design that highlights the importance of framing and, specifically, the contemplated loss, as an explanation for overbidding during experimental auctions. Our results provide evidence of how an understanding of the neural systems of economic behavior might inform economic theory.

References and Notes

8. In auctions, for any given value received, the bidder chooses his optimal bid by trading off the probability of winning (increasing with higher bids) with lower profits if a win occurs. In the trade-off, risk-averse bidders are willing to receive less profit in order to be more certain of a win, hence, overbidding.
9. See supporting online material, available on Science Online, for further methodological details including procedures and additional analyses. Each trial was 30 s long, with decisions lasting 4 s, followed by 12 s of fixation and outcomes lasting 2 s, followed by 32 s of intertrial interval.
10. A “loss” refers to losing the bidding phase and not the actual v minus b payoff. There were a few trials where participants’ b exceeded the presented v, which resulted in an auction “win” but with an associated cost to this excess overbidding (negative final profit). These trials (six overall, across the experiment) were excluded from neuroimaging analysis.
11. See table S3 and supporting online material (SOM) for further analysis. Overbidding was also significant when the incentive was points (P = 0.05).
19. Mean beta weights are parameter estimates derived from the general linear model that indicate how much each factor (i.e., individual condition) contributes to the overall data. For detailed explanation see (10).
20. Similar results for the left ventral caudate ROI are reported in the SOM.
28. The distribution of values for all bidders was uniform over the four values available (i.e., each value had an equal probability of being chosen).
31. The authors would like to acknowledge support from the James S. McDonnell Foundation and National Institute of Mental Health, NIH (MH62104) to A.E.P. and the support of the Seaver Foundation to NYU’s Center for Brain Imaging. We also thank the Center for Experimental Social Science for its support. We are grateful to D. Schwarz for his efforts in the initial stages of collection and analysis of neuroimaging data. We thank J. Zakrzewski and K. Nearing for their assistance during data collection, M. Niniznik for assistance during data analysis, and R. Advani for his programming help on the behavioral experiment.

Supporting Online Material

www.sciencemag.org/cgi/content/full/321/5897/1849/DC1

Materials and Methods

SOM Text

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