Sensitivity of the brain to loss aversion during risky gambles

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Little is known about the neural systems that subserve human loss aversion. A recent neuroimaging study by Tom, Poldrack and colleagues reports that this pattern of behaviour is directly tied to the greater sensitivity of the brain to potential losses compared with potential gains and uncovers a brain network whose activity increases with potential gains and decreases with potential losses. These results challenge the common view that loss aversion engages a distinct emotion-related brain network (e.g. amygdala and insula).

Introduction

When deciding between risky options, humans are about twice as sensitive to the possibility of losing goods or money than to the possibility of winning them. Prospect theory, the leading behavioural model of decision making under risk, uses the concept of loss aversion (as measured by the willingness to reject gambles) to explain risk aversion during monetary mixed (gain or loss) gambles (Box 1) [1]. Several recent brain imaging studies have suggested that higher sensitivity to loss entails emotional processes recruiting structures such as the amygdala and the anterior insula [2–5]. However, the recent study by Tom *et al.* reported that neither of these two brain regions showed increasing activity with the size of potential losses [6]. In fact, the same neural substrates (e.g. striatum and ventromedial prefrontal cortex) exhibited both decreased activity with potential losses and increased activity with potential gains (Figure 1). Moreover, there was a diminished neural sensitivity to losses among individuals who were less loss averse (i.e. more risk seeking), which might shed light on several neuropsychiatric and behavioural disorders, such as impulsive and risky behaviour, pathological gambling as well as substance abuse. This study elegantly illustrates how the integration of theoretical models and brain imaging approaches provides a better understanding of decision making in risky situations.

The study: deciding between risky options

Tom *et al.* [6] scanned subjects while they had to accept or reject gambles offering a 50/50 chance of winning an amount of money (range = $10–$40 in $2 increments) or losing another amount ($5–$20 in $1 increments) (Figure 1). All possible combinations of gains and losses were presented. Subjects had to bring $60 on the scanning day and were told that they could actually lose this money in the scanner. Participants pressed one of four buttons to indicate their willingness to play each gamble (strongly or weakly accept, or strongly or weakly reject). Importantly, gambles were not immediately resolved during scanning. Instead, one trial from each run was selected at random and played for real at the end of the scanning session.

After computing, for each subject, a behavioural measure of loss aversion defined as the ratio of loss to gain responses, the authors confirmed that subjects were, on average, indifferent to gambles in which the potential gain was about twice the amount of the potential loss.

The brain imaging results showed that a unique set of brain regions, including the ventral striatum and ventromedial prefrontal cortex, exhibited both increased activity for gains and decreased activity for losses (Figure 1). Importantly, these brain regions also exhibited a pattern of neural loss aversion, that is, the negative slope reflecting the decreasing activity for increasing losses was greater than the slope reflecting the increasing activity for increasing gains. Thus, this study confirms that the function that maps money onto subjective value is steeper for losses than for gains, as predicted by prospect theory, and directly links loss aversion behaviour to the greater sensitivity of the brain to potential losses compared with potential gains.

Single or different neural substrates for potential gains and loss?

On the one hand, brain regions showing increased activity with potential gains included a 'gain-brain network' (striatum, ventromedial prefrontal cortex, anterior cingulate cortex and midbrain) previously observed during anticipation and receipt of monetary gain [7–9] or rewarding juice [10]. Thus, correlation with the size of potential gains when evaluating gambles without expectation of immediate reinforcement elicits neural responses similar to those observed during anticipation and receipt of monetary gains.

On the other hand, one might have expected that loss aversion would increase activity in distinct brain regions traditionally involved in negative affect processing as the size of potential losses increased. In fact, potential losses were associated with decreased activity in several areas of the 'gain-brain network'. These results are particularly interesting in light of recent reports suggesting that loss aversion entails emotional processes recruiting the amygdala and anterior insula. For example, during a guessing task with possible gain and loss outcomes, loss-related expected value (probability of loss × its magnitude) during reward anticipation and the associated prediction error (discrepancy between actual and expected outcome) at the

Box 1. Expected utility and prospect theories

Loss aversion as explained by prospect theory. To decide optimally between multiple options in uncertain situations, it is important to evaluate expectations about the magnitude and probability of valued outcomes. In classical decision theories, decision makers choose the option that offers the highest expected value (product of gain magnitude by probability) or the highest expected utility (concave function over states of wealth). However, behavioural evidence suggests that humans do not always act to maximize the expected value when offered to decide between different alternatives [1]. In fact, people are not the rational actors described by expected utility theory but often make decisions that this theory is unable to explain.

The prospect theory solves apparent anomalies and contradictions in human behaviour (e.g. subjects might be risk-averse when offered a choice formulated in one way but might be risk-seeking when offered the same choice formulated in a different way). This theory describes how individuals make decisions between alternatives under risk and explains risk aversion for mixed (gain or loss) gambles using the concept of loss aversion [1]. An asymmetric s-shaped function, called the value function, passes through a reference point (usually the *status quo*) (Figure I). Given the same variation in absolute value, there is a bigger impact of losses compared with gains (loss aversion), simply because of the asymmetry of the value function. Thus, loss aversion can be defined as a bias in individual decision-making captured by the shape of the value function in prospect theory. An important implication of prospect theory is that choices are influenced by how prospects are represented in terms of losses versus gains and their associated probabilities, whereas expected utility theory assumes that people act as if they were assessing the impact of options on final states of wealth.
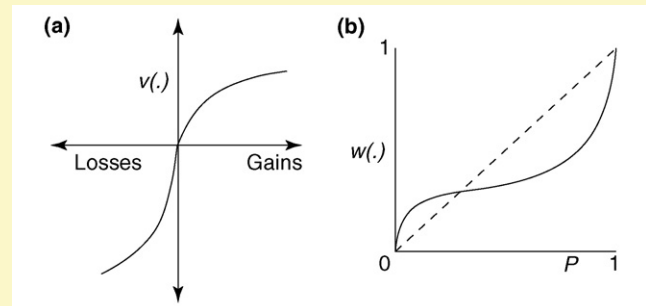

Figure I. Value and probability weighting functions from prospect theory. (a) Value function v (power function) as a function of gains and losses. (b) Probability weighting function w for gains as a function of the probability P of an event, expressing that people tend to overreact to small probability events but under react to medium and large probabilities. According to prospect theory, value is assigned to gains and losses and probabilities are replaced by decision weights. The value V of a prospect that pays \$x with probability P (and nothing otherwise) is simply the product $v(x) \times w(P)$, where v measures the subjective value of the consequence x and w is the impact of probability P on the attractiveness of the prospect. The value function is defined on deviations from a reference point and is normally concave for gains (implying risk aversion), convex for losses (risk seeking) and is steeper for losses than for gains (loss aversion). Decision weights are generally lower than the corresponding probabilities, except in the low probabilities range. Reproduced, with permission, from Ref. [15].
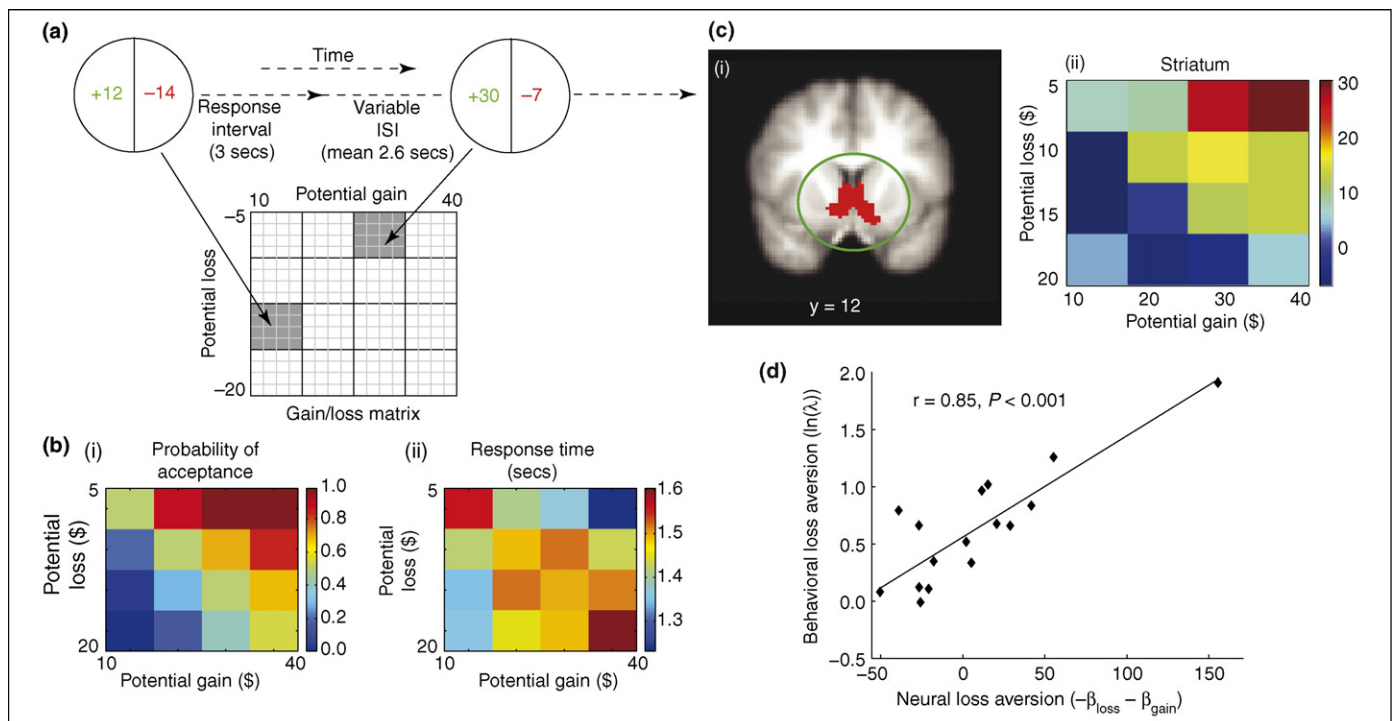

Figure 1. (a) Event-related design of the mixed-gambles task. Participants were presented with a mixed gamble showing the size of the potential gain (green) and loss (red). After accepting or rejecting the gamble, there was a variable inter-stimulus interval (ISI). Gambles were not resolved during scanning. The values of gain and loss for each trial were sampled from the gain/loss matrix, as shown here for two example gambles: a gamble from each cell in this 16 × 16 matrix was presented during scanning, but the data were collapsed into a 4 × 4 matrix for analysis. All combinations of gains and losses were presented. (b) Colour-coded heatmap of gamble acceptance (i) and response times (ii) at each level of gain or loss. Red indicates high willingness to accept the gamble (i) and indicates slower response times (ii). (c) (i) Map showing striatal activation from a conjunction analysis with conjointly significant positive gain response and negative loss response ($P < 0.05$, whole-brain corrected). (ii) The heatmap was created by averaging parameter estimates versus baseline in the conjunction map for each of the 16 cells (of 16 gambles each) in the gain/loss matrix. Colour coding reflects strength of neural response for each condition, such that dark red represents the strongest activation and dark blue represents the strongest deactivation. (d) Tight coupling between neural loss aversion and behavioural loss aversion in the ventral striatum. β_{loss} and β_{gain} are the unstandardized regression coefficients for the loss and gain variables, respectively. Reproduced, with permission, from Ref. [6].

time of the outcome were both represented in the amygdala [2]. Amygdala activity was also shown to correlate with choices of risky gambles framed as losses and sure outcomes framed as gains [3]. Moreover, the anterior insula, involved in the affective recognition of noxious stimuli [11], has been linked to anticipation of monetary loss, pain and emotionally aversive pictures [12], and to anticipation of riskless choices as well as risk-aversion mistakes (in which people do not take risks when they should) [4]. This brain region is also more responsive when unfair offers are rejected during the ultimatum game in which two players split a sum of money, one player proposing a division and the other accepting or rejecting it [5].

Concluding remarks

This study provides important new insights into the functional properties of decision making in humans. The reduced neural sensitivity to losses among individuals who were less loss averse is particularly relevant for several neuropsychiatric and behavioural disorders, such as substance abuse and pathological gambling, associated with increased risk taking and impulsive behaviour. These individual differences in behavioural and neural loss aversion might be related to naturally occurring differences in dopamine function. Future studies could test how hormonal and genetic individual variations influence brain response to loss aversion, as recently investigated during anticipation and receipt of monetary rewards [13]. Multivoxel pattern analysis should also test whether the activation of common brain regions for gain and loss reflect engagement of a common neural population or whether these overlapping brain regions reflect functionally independent neural populations engaging the same brain regions [14]. Finally, this study should open up new lines of research in neuroeconomics that could help uncover further the nature of processes involved in social cognition, for example, by comparing financial loss and the perception of sanctions in the context of social interaction (social exclusion).

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Letters

Teachers in the wild: some clarification

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In a Research Focus article published in the March 2007 issue of *Trends in Cognitive Sciences*, Csibra [1] highlights recent work on teaching in non-human animals [2,3] and examines its role in the transfer of cultural information. We welcome a greater integration between human and non-human research and feel that more open discussion between the two fields would be highly productive. However, we would like to clarify three issues. First, Csibra begins by reviewing work on pied babblers, *Turdoides bicolor*, by Radford and Ridley [4], noting that Rapaport [5] has interpreted it as providing evidence for teaching. The babbler study is mentioned before the two established examples of animal teaching (tandem running ants, *Temnothorax albipennis* [2], and meerkats, *Suricata suricatta* [3]) and in place of other studies that have explicitly exam-

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Available online 4 June 2007.