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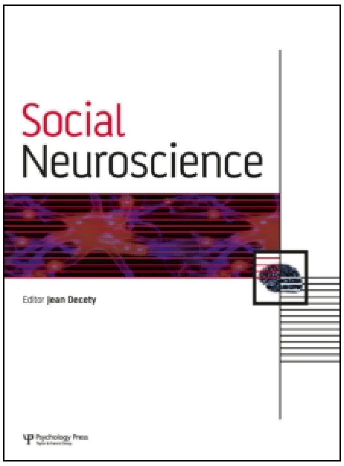
How to cite

BROSCH, Tobias et al. Generating value(s): Psychological value hierarchies reflect context-dependent sensitivity of the reward system. In: Social neuroscience, 2011, vol. 6, n° 2, p. 198–208. doi: 10.1080/17470919.2010.506754

This publication URL: https://archive-ouverte.unige.ch//unige:25822

Publication DOI: 10.1080/17470919.2010.506754



Social Neuroscience
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t741771143

Generating value(s): Psychological value hierarchies reflect context-dependent sensitivity of the reward system

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To cite this Article Brosch, Tobias , Coppin, Géraldine , Scherer, Klaus R. , Schwartz, Sophie and Sander, David(2011) 'Generating value(s): Psychological value hierarchies reflect context-dependent sensitivity of the reward system', Social Neuroscience, 6: 2, 198 — 208, First published on: 13 August 2010 (iFirst)

To link to this Article: DOI: 10.1080/17470919.2010.506754

URL: http://dx.doi.org/10.1080/17470919.2010.506754

SOCIAL NEUROSCIENCE, 2011, 6 (2), 198–208
Psychology Press
Taylor & Francis Group

Generating value(s): Psychological value hierarchies reflect context-dependent sensitivity of the reward system

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Values are motivational constructs that determine what is important to us and which goals we choose to pursue. Cross-cultural research suggests that the structure of the human value system is universal, but people and cultures differ in terms of relative value priorities. Differences in psychological value hierarchies can be parsimoniously described using the orthogonal dimensions *self-interest* and *openness to change*. Using fMRI, we investigated whether individual differences in these universal dimensions are reflected in basic neural reward mechanisms during a donation task and a GO/NOGO-task. Individuals with high self-interest value sacrificed less money for charitable donations and showed higher activation of the ventral striatum when receiving monetary rewards. Furthermore, individuals with high openness to change value showed a greater sensitivity of the dorsal striatum when trying to inhibit habitual prepotent responses. Our findings suggest that context-dependent neural reward sensitivity biases reflect (and may even determine) differences in individual value hierarchies and underlie the effects of values on decisions and behaviors.

Keywords: Values; Value hierarchy; Decision-making; Reward system; fMRI.

INTRODUCTION

People often refer to their *values* when asked to explain their preferences, decisions, and behaviors, and use the notion of *value differences* to explain fundamental differences between themselves and other people or social groups. Values are broad motivational constructs that determine what we consider important and which goals we choose to pursue (Rohan, 2000). Each individual possesses a hierarchy of numerous values with varying degrees of importance. Cross-cultural research has shown that the overall structure of human values is universal and that people in many different cultures use and recognize the same set of values, including, for example, honoring tradition, enjoying life, protecting the environment, or being honest (Schwartz, 1992). However, people and cultures differ in terms of their relative value priorities. A particular value, such as “honoring tradition,” may be very important to Jack, but rather unimportant to Joe. Jack will frequently behave accordingly—for example, by showing respect for the elderly and observing traditional customs on holidays—whereas Joe will not show these behaviors, as they are less important to him (Bardi & Schwartz, 2003). Similar value differences are

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This work was supported by the National Centre of Competence in Research (NCCR) Affective Sciences, financed by the Swiss National Science Foundation (SNSF, no. 51NF40-104897), and hosted by the University of Geneva, and by a SNSF fellowship for prospective researchers to TB (PBGEP1-125836).

www.psypress.com/socialneuroscience
DOI: 10.1080/17470919.2010.506754

observed between cultures: Particular values may be very important for one cultural group, but ignored in another (Inglehart & Baker, 2000). Interindividual and intercultural differences in value hierarchies can be parsimoniously described using a value space spanned by two broad orthogonal value dimensions, with one dimension delineating the range between “the pursuit of self-interest and survival” and “the pursuit of altruistic goals” (*self-interest dimension*), and a second one covering the range from “openness to change” to “conservation of traditions” (*openness to change dimension*). These dimensions are thus culturally universal (Inglehart & Baker, 2000; Schwartz, 1992), but individual people emphasize them to different degrees as guiding principles for their lives.

Which mechanisms might underlie the fact that for some people self-interest is an important value, but for others not, or the fact that some people are open to changing their habitual, well-established behaviors whereas others are not? From a biological perspective, human and animal behavior is strongly driven by the search for rewards. Rewards organize behavior, elicit approach, and induce subjective feelings of pleasure. Rewards are operationalized as those stimuli that positively reinforce behavior, i.e., increase the probability of a behavior. When one experiences a reward, one becomes more likely to repeat in the future the behavior that led to the reward (Schultz, 2000). Animal research has shown that the motivational aspect of reward-driven behavior is implemented by dopaminergic neurons projecting from the ventral tegmental area (VTA) to the ventral and dorsal striatum and the prefrontal cortex (Haber & Knutson, 2010). Studies in humans using functional magnetic resonance imaging (fMRI) have shown that rewarding stimuli consistently activate a common set of subcortical neural structures including the ventral and dorsal striatum and the amygdala, and cortical prefrontal regions such as the orbitofrontal cortex/ventromedial prefrontal cortex (Montague, King-Casas, & Cohen, 2006; Rangel, Camerer, & Montague, 2008). This network has been demonstrated using a wide range of rewarding stimuli, such as food (O’Doherty, 2004), money (Knutson, Fong, Bennett, Adams, & Hommer, 2003), attractiveness (Kawabata & Zeki, 2004), or trust (King-Casas et al., 2005). Within the reward network, different brain regions perform different functions. The contribution of the striatum to reward processing has been described using a critic–actor model (Kahnt et al., 2009; O’Doherty et al., 2004). The ventral striatum (*critic*) predicts the reward value associated with a certain stimulus, the magnitude of its activation increasing with subjective reward magnitude (Delgado, 2007). The dorsal striatum (*actor*) similarly shows activation when participants are presented with rewarding stimuli (Zald et al., 2004), but is moreover implicated in motivational and learning processes that underlie the preparation of actions directed toward rewarding stimuli. It maintains information about the rewarding properties of action outcomes, so that actions associated with greater long-term reward value can be chosen more frequently (O’Doherty et al., 2004). The amygdala, whose activity is tightly synchronized with striatal activity during reward processing (Popescu, Popa, & Pare, 2009), determines the relevance of a stimulus for the needs and goals of an organism (Sander, Grafman, & Zalla, 2003; Sergerie, Chochol, & Armony, 2008), and shows stronger responses to stimuli that are perceived as having a subjective “impact” on the individual (Ewbank, Barnard, Croucher, Ramponi, & Calder, 2009).

In an attempt to bridge psychological value research and neurobiological research on reward processing, we hypothesized that individual differences in activity in reward regions during situations that reflect the dimensions self-interest and openness to change may relate to (and even determine) the individual psychological value hierarchy.

The two principal value dimensions, self-interest and openness to change, reflect different response strategies to fundamental adaptive challenges. Self-interest is related to the distribution of resources within a social group and will impact on the amount that is allocated to the individual or to others. People who emphasize the self-interest value will tend to pursue selfish goals and keep resources for themselves, whereas people low on this value tend to share and to favor altruistic goals. In the present study, we investigated neural and behavioral correlates of self-interest value in a resource distribution paradigm where participants were asked to distribute a monetary amount between themselves and a charitable organization (see Figure 1a).

Openness to change reflects the tendency to embrace new things, events, and behaviors instead of conserving traditional ones. People open to change show higher cognitive flexibility and tolerate novelty, ambiguity, and complexity, whereas conservative people show more structured and persistent cognitive styles (Jost, Glaser, Kruglanski, & Sulloway, 2003). Due to their higher cognitive flexibility, people scoring high on openness to change value may be more willing to flexibly replace erroneous or inadequate established behaviors with more adaptive ones, and may consequently be more sensitive to opportunities for altering their response patterns in the service of behavior optimization. In the GO/NOGO task, participants are

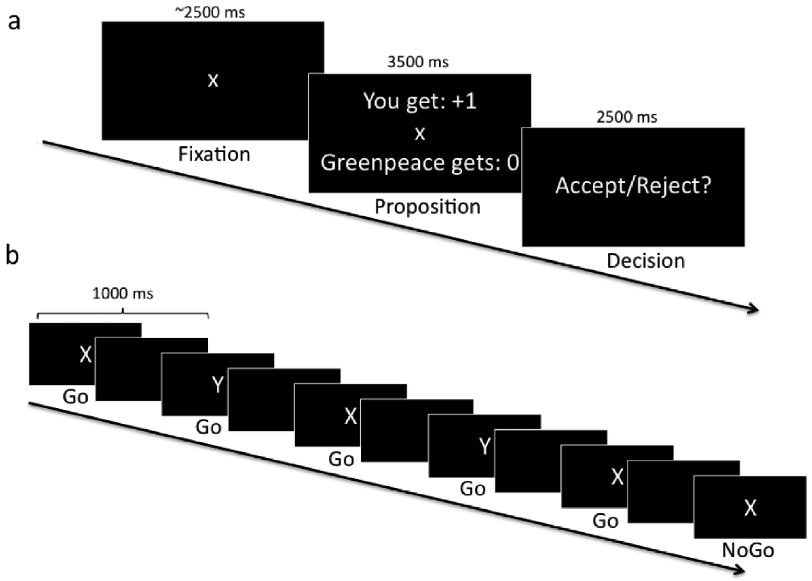

Figure 1. Illustration of the paradigms used in the current study. (a) Resource distribution paradigm. (b) GO/NOGO task (see text for details).

instructed to press a key whenever a frequent GO stimulus occurs, and to withhold the key press response whenever a less frequent NOGO stimulus occurs. Participants thus establish a habitual, prepotent response pattern (respond to the GO stimulus), which sometimes needs to be adjusted to accommodate changing task demands (do not respond to the NOGO stimulus). This task is appropriate to measure individual differences in the flexible adjustment of prepotent response patterns, and has been applied to compare the neural correlates of error processing in politically liberal and conservative participants (Amodio, Jost, Master, & Yee, 2007). In the present study, we investigated neural correlates of openness to change value using a GO/NOGO paradigm where participants had to inhibit a habitual prepotent manual response to a stimulus (see Figure 1b).

Using fMRI, we investigated the hypothesis that individual differences in the responsivity of neural reward regions during decisions and behaviors that tap mechanisms of resource distribution and behavior optimization reflect the structure of individual value hierarchies. The link between context-dependent reward system sensitivity and psychological value dimensions was studied in two separate experiments with the same group of 19 subjects, whose individual scores for self-interest and openness to change values (Schwartz, Sagiv, & Boehnke, 2000) did not correlate ($p > .20$); individual value profiles spanned all four quadrants of the value space (as defined by high/low self-interest × high/low openness to change). We focused our analyses on the striatum and the amygdala, two brain regions critically involved in reward processing (Lieberman & Eisenberger, 2009). We tested two specific hypotheses: (A) When participants are asked to share money during a financial resource distribution task, neural reward activity when receiving money reflects self-interest value. As the ventral striatum has been shown to encode the subjective value of rewards associated with a stimulus (Delgado, 2007), it should reflect differences in the valuation of the monetary rewards, which may drive more self-interested vs. altruistic decisions. Similar predictions may be made about the amygdala, which reflects the individual relevance or impact of a stimulus (Ewbank et al., 2009; Sander et al., 2003). (B) When participants are trying to overcome a habitual response during a GO/NOGO task, neural activity to the NOGO stimuli reflects openness to change value. In a GO/NOGO task different types of available behavioral responses, one of them a habitual prepotent response, must be chosen depending on the situational contingencies. The dorsal striatum maintains information about the motivational properties of behaviors and behavioral outcomes (O'Doherty et al., 2004) and has been linked to mechanisms of behavioral error correction (Lawrence, 2000). Differences in dorsal striatal activation may thus reflect differences in the motivational value or effort of overcoming habitual response patterns, which may be stronger in individuals scoring high on openness to chance value.

In addition to our main hypotheses, we explored activation of the dorsomedial prefrontal cortex (DMPFC) during the resource distribution task. This was motivated by the fact that the resource distribution task gives subjects the opportunity to act either selfishly or altruistically. Whereas self-interested behavior was hypothesized to be related to the reward system, altruistic behavior may predominantly be related to a consideration of the needs of others. DMPFC is involved in forming impressions of others (Mitchell, Macrae, & Banaji, 2006) as well as in making inferences about others' thoughts, needs, and goals (Frith & Frith, 1999; Van Overwalle & Baetens, 2009).

METHOD

Subjects

Nineteen participants (8 males, 11 females, mean age = 28.9 years, *SD* = 4.59) participated in the experiment after giving informed consent according to the ethics regulation of the Geneva University Hospitals. All participants were right-handed, had normal or corrected-to-normal vision, and had no history of psychiatric or neurological diseases.

Functional MRI procedure

Resource distribution paradigm

Before the scan, the procedures were carefully explained to the participants, making sure that they understood that their decisions would directly affect the amount of money they would receive for their participation in the experiment. Before entering the scanner, participants chose one out of three charitable organizations (Red Cross, Amnesty International, or Greenpeace, chosen by 11, 6, and 2 participants, respectively) that they wanted to support. A choice between different charities was given to increase the personal relevance of the charities and the resulting commitment of the participants. In the scanner, visual stimuli were back-projected on a screen that the participants viewed through a mirror system attached to the head coil. At the beginning of each trial, a fixation cross with a variable duration (between 500 and 8000 ms, mean 2565 ms) was presented. Then, a proposition of how a part of the money could be distributed was presented (3500 ms). Afterwards, a question mark appeared on the screen (2500 ms) and participants had to make a YES/NO choice by pressing a key with their right index or middle finger using an MRI-compatible response box.

The different trial types were REWARD (participant: +1, charity: 0), NONCOSTLY DONATION (participant: 0, charity: +1), COSTLY DONATION (participant: −1, charity: +2), and CONTROL (participant: −1, charity: −1) (Moll et al., 2006). The critical trials for our hypotheses were the REWARD trials, where participants could actually increase their personal financial outcome (thus reflecting self-interested behavior), and the COSTLY DONATION trials, where participants could sacrifice a part of their financial outcome in order to donate it to charity (thus reflecting altruistic behavior). CONTROL trials gave us a further option to make sure that participants understood the task and paid attention to the individual trials (as these trials should be rejected each time). In total, participants performed 100 trials. In these trials, they could achieve a maximum of 25 points for themselves (when always refusing the COSTLY DONATION trials) and a maximum of 75 points for the charitable organization (when always accepting both NONCOSTLY and COSTLY DONATION trials). These points were converted into CHF (1 CHF is approximately 1 USD) with a conversion rate of 0.6 CHF/point. Participants started with an endowment of CHF 25 for their participation; additionally, they received the money they allocated to themselves during the experiment and thus could receive between CHF 10 (when accepting all COSTLY DONATION trials) and CHF 40. Depending on the participants' choices, the charity could receive between CHF 0 and CHF 45. Participants accepted on average 97% (*SD* 4) of the REWARD trials, 77% (*SD* 36) of the NONCOSTLY trials, 41% (*SD* 40) of the COSTLY trials, and 1% of the CONTROL trials (*SD* 3). On average, participants received CHF 33.18 (*SD* 6.4) and allocated CHF 23.65 (*SD* 15.9) to charity. The actual behavioral decisions were implemented and the charities received the money donated by the participants.

GO/NOGO paradigm

Participants then completed a GO/NOGO task (Garavan, Ross, Murphy, Roche, & Stein, 2002). The letters X and Y were presented serially in an alternating pattern at 1 Hz; participants were required to make a button-press response to each letter, unless a NOGO stimulus occurred. NOGO trials were defined by the interruption of the letter alternation (such as X–Y–X–Y–X–Y–X–X). NOGO trials were distributed unpredictably throughout the stimulus stream. In order to produce an equal number of correct NOGO nonresponses and NOGO errors (key presses), stimulus timing was adapted to the performance level of the individual participants. Within the constraint of maintaining the stimulus presentation frequency at 1 Hz (to ensure that session duration and total number of trials were equal for all subjects and to facilitate time-locking stimuli presentation to fMRI image acquisitions), stimulus duration within the 1-s window was manipulated. Stimulus presentation durations varied from 800 to 450 ms, followed by a blank screen of 200 to 550 ms, respectively, so that trial duration added up to 1000 ms. Subjects were instructed to try to respond while the stimulus was still on the screen. A moving average window tracked participants' error rates and adaptively changed the stimulus presentation and blank durations in steps of 50 ms to achieve a correct NOGO response rate of about 50%. When participants made too many errors on NOGO trials, stimulus presentation time was increased; when participants made too few errors, stimulus presentation time was decreased. Mean error rate was 47%. During fMRI scanning, participants were presented with 540 GO stimuli and 60 NOGO stimuli.

Behavioral assessment of individual value hierarchies

The Schwartz Value Scale (Schwartz et al., 2000) is based on theoretical considerations as well as cross-cultural validation work on the universality of the factors that describe differences between individual value hierarchies. The basic value structure comprises 10 motivationally distinct types of values promoting the attainment of central goals: power, achievement, hedonism, stimulation, self-direction, universalism, benevolence, tradition, conformity, and security. These 10 values yield an integrated circumplex structure of values that can be summarized with two orthogonal dimensions: (1) self-enhancement vs. self-transcendence, opposing the pursuit of self-interests and the concern for the welfare and interests of others; and (2) openness to change vs. conservatism, opposing independent thought and self-restriction.

After undergoing the fMRI experiments, participants completed a 58-item inventory of their values, covering the 10 different types of values from the theory. Each of the single value items was followed in parentheses by a short explanatory phrase, e.g., SOCIAL ORDER (stability of society). Respondents rated the importance of each value as a guiding principle in their life on a 9-point scale from *opposed to my principles* (–1) through *not important* (0) to *of supreme importance* (7). Indices of the importance of each value type were computed by averaging the importance ratings of the specific values representative of that type. Indices of the two orthogonal dimensions were then formed by averaging across the respective value types. Individual scores for self-interest and openness to change did not correlate ($p > .20$, *ns*), and individual value profiles spanned all four quadrants of the value space (high/low self-interest × high/low openness to change).

MRI data acquisition and analysis

Data acquisition

MRI data were acquired on a 3-T whole-body TIM system (Siemens, Munich, Germany) using an 8-channel head coil. For each participant, functional images were acquired with a gradient-echo EPI sequence, repetition time (TR)/echo time (TE)/flip angle = 2150 ms/30 ms/80°, field of view (FOV) = 192 mm, matrix = 64 × 64 × 36, voxel size: 3 × 3 × 3 mm. Each functional image was composed of 36 contiguous axial slices oriented parallel to the AC–PC line. A total of 383 functional images during the resource distribution task and 291 functional images during the GO/NOGO task were acquired. Structural images were acquired with a T1-weighted sequence (192 contiguous sagittal slices, TR/TE/flip angle = 1900 ms/2.32 ms/9°, FOV = 230 mm, matrix = 246 × 256 × 192, voxel-size = 0.9 × 0.9 × 0.9 mm).

Data analysis

The GO/NOGO data for two subjects (one female) had to be excluded due to failure to comply with the task instructions. Functional images were analyzed using the general linear model (GLM) for event-related designs in SPM8 (Wellcome Department of Imaging Neuroscience, London; http://www.fil.ion.ucl.ac.uk/spm). All images were realigned, corrected for slice timing, normalized to an EPI template (resampled voxel size of 3 mm), spatially smoothed (8 mm full width, half maximum (FWHM) Gaussian kernel), and high pass-filtered (cutoff 120 s). Statistical analyses were performed on a voxel-wise basis across the whole brain. Individual events were modeled by a standard synthetic hemodynamic response function (HRF). *Resource distribution task*: Four event types were defined, including each of the experimental trial types (REWARD, NONCOSTLY DONATION, COSTLY DONATION, and CONTROL). Individual predictors began at the presentation of the distribution proposition. *GO/NOGO task*: Two event types were defined, including each of the experimental trial types (NOGO correct, NOGO error). Individual predictors began at the presentation of the NOGO stimulus. To account for residual movement artifacts after realignment, movement parameters derived from realignment corrections (three translations, three rotations) were entered as covariates of no interest. The GLM was then used to generate parameter estimates of activity at each voxel, for each condition, and each participant. Statistical parametric maps were generated from linear contrasts between the HRF parameter estimates for the different conditions.

We performed random-effect group analyses on the contrast images from the individual analyses, using one-sample *t*-tests. To identify regions responsive to rewards during the resource distribution task, we contrasted the REWARD condition to all other conditions [REWARD > (NONCOSTLY DONATION + COSTLY DONATION + CONTROL)]. We then performed regression analyses to test for a linear relationship between the strength of the regional activations of interest in the REWARD and the COSTLY DONATION conditions with individual self-interest value ratings and individual number of accepted costly donations. To investigate regions associated with altruistic behavior, we contrasted the donations conditions to the reward condition [NONCOSTLY DONATION + COSTLY DONATION > REWARD] and performed regression analysis to test for a linear relationship with the individual number of accepted costly donations. For the GO/NOGO task, we compared correct and incorrect responses to the NOGO stimulus [NOGO correct > NOGO error]. We then performed regression analyses to test for a linear relationship between the strength of regional activation with individual openness to change value ratings.

We expected regions classically involved in reward processing to be modulated by the different conditions in the two tasks, in particular striatum and amygdala (Delgado, 2007; Delgado, Nearing, LeDoux, & Phelps, 2008; Lieberman & Eisenberger, 2009). Additionally, we explored activation in the DMPFC, a region involved in impression formation and mentalizing (Frith & Frith, 1999; Mitchell et al., 2006). Activation results are reported at uncorrected $p < .001$, $k = 5$ for peak voxels in a priori regions of interest (striatum, amygdala, DMPFC) unless reported otherwise. For non-a priori whole brain analyses, family-wise error (FWE) correction at $p < .05$ was applied. No regions outside the a priori regions showed differential activations as a function of the experimental conditions.

RESULTS

Self-interest value

We investigated the neural and behavioral correlates of self-interest value in a task where participants were given an amount of investment money that they were to distribute between themselves and a charitable organization of their choice (Moll et al., 2006). High self-interest value was associated with more selfish decisions, as it was negatively correlated with the number of accepted COSTLY trials, $r(17) = -.51$, $p = .026$. However, it was not correlated with the number of accepted REWARD or NONCOSTLY trials (both p values > 0.2). Due to their reluctance to accept costly donations, participants high in self-interest value received more money for participation in the experiment, $r(17) = .54$, $p = .018$, and donated less to charity, $r(17) = -.48$, $p = .039$. These behavioral results confirm that reported high self-interest values are actually reflected in more selfish decisions.

Examining the neural mechanisms involved in self-interest-related decisions, we found that REWARD trials led to increased activation of the ventral and dorsal striatum for all participants (Figure 2a, 2b, left ventral striatum, peak coordinates $x = -18$, $y = 14$, $z = -11$, z-score $= 3.91$, $p < .001$; left caudate head, peak coordinates $x = -9$, $y = 14$, $z = 10$, z-score $= 2.82$, $p = .002$). However, regression analysis revealed that the activation was modulated by self-interest, as the strength of activation in the ventral striatum in the REWARD condition increased with the importance of self-interest value (Figure 2c, 2d, peak coordinates $x = -24$, $y = 11$, $z = -8$, z-score $= 2.99$, $p = .001$). Furthermore, selfish participants showed stronger right amygdala activation than nonselfish participants during REWARD trials (Figure 2e, 2f, peak coordinates $x = 30$, $y = -1$, $z = -11$, z-score $= 2.99$, $p = .001$). Importantly, these differences in activation during the REWARD trials were not directly driven by the amount of money received in those trials, as self-interest value was not associated with the number of accepted REWARD trials ($p > .39$, *ns*).

When investigating reward-related activation during the COSTLY DONATION trials, we observed that the more money participants donated to charity during these trials, the less activation was observed in the striatum (Figure 3a, 3b, peak coordinates $x = -24$, $y = -1$, $z = 4$, z-score $= 3.39$, $p < .001$), which is consistent with striatal deactivations observed during financial loss (Delgado, 2001). Participants who frequently agreed to donate money during these trials showed stronger relative activation during donation trials in the dorsomedial prefrontal cortex (DMPFC;

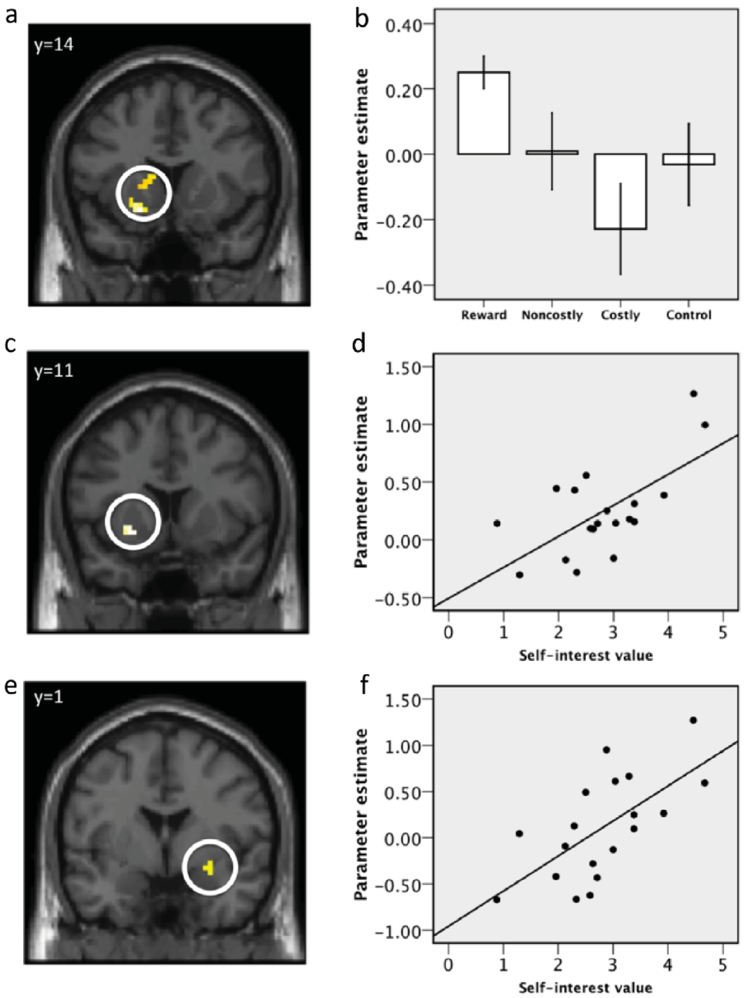

Figure 2. Brain regions showing differential sensitivity to financial rewards as a function of individual self-interest value. (a) Activation of the dorsal and ventral striatum during reward trials. (b) Parameter (contrast) estimates for left ventral striatum (peak coordinates $x = -18$, $y = 14$, $z = -11$) showing activity increase during reward trials and decrease during costly donation trials. (c) Regression analysis between regional brain activity during reward trials and individual self-interest value revealing that individuals scoring high on the self-interest value dimension had a stronger response of the ventral striatum (peak coordinates $x = -24$, $y = 11$, $z = -8$) to reward trials. (d) Parameter estimates of reward response for left ventral striatum and individual self-interest value scores. (e) Regression analysis showing that individuals scoring high on the self-interest value dimension had a stronger response to reward trials in the right amygdala (peak coordinates $x = 30$, $y = -1$, $z = -11$). (f) Parameter estimates of reward response for the right amygdala and self-interest value scores. Statistical maps overlaid on T1-weighted anatomical single-subject template, threshold at $P < 0.005$, uncorrected.

Figure 3c, 3d, peak coordinates $x = 9$, $y = 47$, $z = 34$, z-score = 3.47, $p < .001$).

Openness to change value

To investigate the neural correlates of openness to change value during the inhibition of habitual prepotent responses, the same participants then performed a GO/NOGO task where the letters X and Y were presented serially in an alternating pattern, and participants were required to make a button-press response to each letter, unless a NOGO stimulus occurred (Garavan et al., 2002). Stimulus timing was continuously adapted to the performance level of the individual participants to achieve a NOGO error rate of about 50%.

Comparing the neural activations associated with correct and incorrect NOGO responses, we found that NOGO correct trials led to a stronger activation in dorsal and ventral striatum compared to NOGO error trials across all participants (Figure 4a, 4b, peak coordinates right striatum $x = 24$, $y = 5$, $z = 7$, z-score = 4.06, $p < .001$). Regression analysis revealed that the differential response in the dorsal striatum (caudate) increased with the individual importance of openness

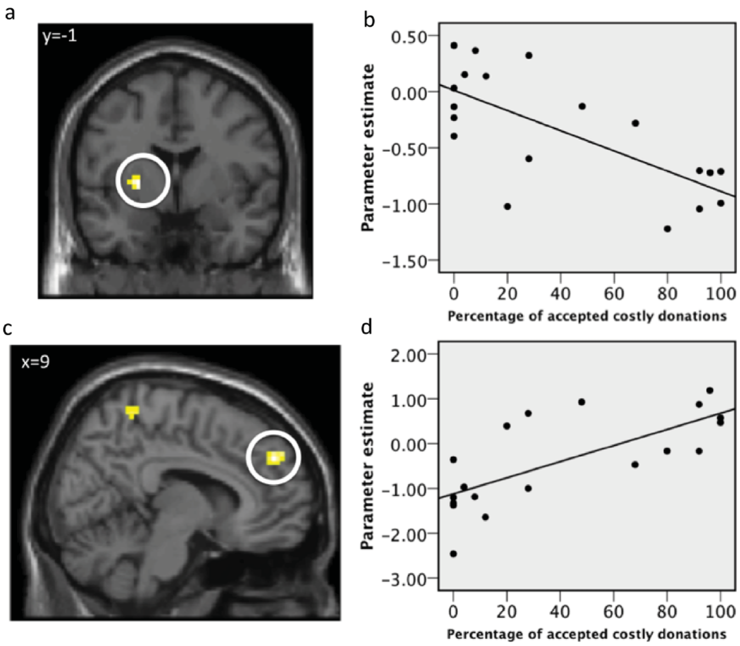

Figure 3. Brain regions involved in individual differences in altruistic behavior. (a) Regression analysis showing that individuals with a high percentage of accepted costly donations showed less activation in the left ventral striatum (peak coordinates $x = -24$, $y = -1$, $z = 4$) during COSTLY trials. (b) Parameter estimates for the left ventral striatum response to COSTLY trials and individual percentage of accepted costly donations. (c) Positive correlation of individual percentage of accepted costly donations and activation in DMPFC (peak coordinates $x = 9$, $y = 47$, $z = 34$) during donation trials. (d) Parameter estimates for the DMPFC and individual propensity to accept costly donations.

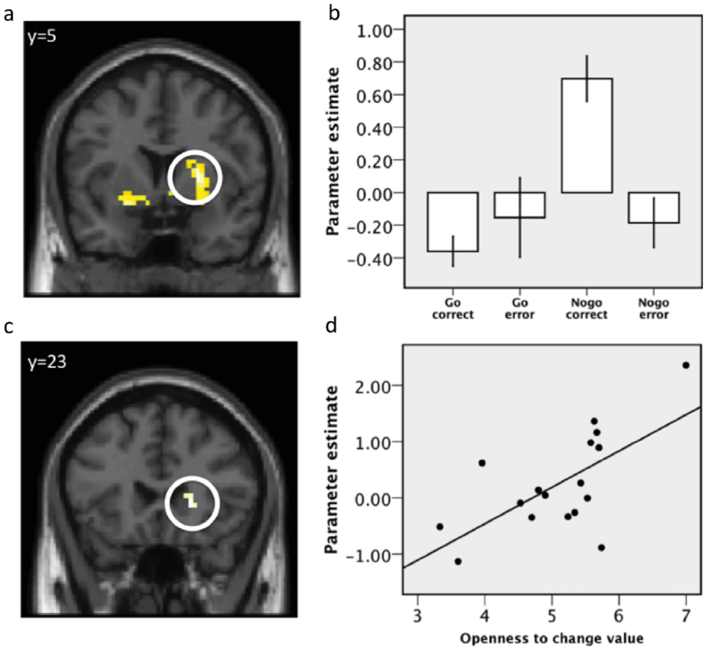

Figure 4. Striatal sensitivity to avoided behavioral errors is modulated by openness to change value. (a) Higher activation of the ventral and dorsal striatum during NOGO correct trials than during NOGO error trials (peak coordinates right striatum $x = 24$, $y = 5$, $z = 7$, z-score = 4.06, $p < .001$). (b) Parameter estimates for the right striatum. (c) Dorsal striatal sensitivity to avoided behavioral errors is modulated by openness to change value: Correlation between individual openness to change value and successful response inhibition in the right caudate (peak coordinates $x = 24$, $y = 23$, $z = 1$). (d) Parameter estimates for the right caudate and individual scores on the openness to change value.

to change value (Figure 4c, 4d, peak coordinates $x = 24$, $y = 23$, $z = 1$, z-score = 2.89, $p = .002$).

DISCUSSION

Our results provide evidence for a link between the universal psychological value hierarchy and the sensitivity of the neural reward system during basic neurocognitive processes. When receiving money, all our participants showed activation of the ventral striatum, a region that has been shown to reflect the reward value associated with a certain stimulus (Delgado, 2007). However, the activation was stronger for individuals for whom the pursuit of self-interest is especially important, and who were less prone to donate their money for a good cause. For these participants, self-enhancing behavior may be more rewarding (and thus more reinforcing) that for other participants. Furthermore, selfish people showed more amygdala activation when they encountered stimuli signaling reward. This finding is consistent with the notion that the amygdala acts as a relevance detector that is sensitive to the importance of a stimulus for the needs and goals of the organism (Sander et al., 2003), assuming that monetary gains for oneself are more relevant for a selfish person than for a nonselfish person. Accepted costly donations were associated with deactivation of the striatum, consistent with striatal deactivations observed in other studies during financial punishments (Delgado, Locke, Stenger, & Fiez, 2003). One may thus speculate that donating money was not inherently rewarding; rather, it was experienced as a financial loss. However, when altruistic subjects faced the opportunity to donate money, they showed increased activation in the DMPFC, an area implicated in forming impressions of others and in thinking about the needs, goals, and beliefs of others (Frith & Frith, 1999; Van Overwalle & Baetens, 2009). Note that the peak coordinates of our DMPFC activation ($x = 9$, $y = 47$, $z = 34$) were close to the ones observed in a study where participants mentalized about others whom they perceived as not very similar to themselves ($x = -9$, $y = 45$, $z = 42$; Mitchell et al., 2006). The decision to donate money may thus have been related to more thorough reflection of the needs of the charities and the causes that they support.

In addition to showing the interrelatedness of value priorities and the basic functioning of the reward system, these findings contribute to the debate about whether altruistic donations might be due to the inherent reward value of the act of giving itself (Andreoni, 1990; Fehr & Camerer, 2007). In our study, giving was not associated with a rewarding "warm glow of altruism" (Harbaugh, Mayr, & Burghart, 2007; Moll et al., 2006). It rather appeared that selfish participants were rewarded for their egoism and felt a "warm glow of selfishness," raising the question of whether there is a common currency for multiple reward types or whether altruism is based on different mechanisms, such as increased deliberate consideration of the needs of dissimilar others. However, it might also be possible that a potentially intrinsic reward of altruism was difficult to evoke in the current experimental setup.

During the GO/NOGO task, all participants showed increased dorsal and ventral striatal activation to correct NOGO responses. The dorsal striatum has been linked to motivational and learning processes that underlie the preparation of instrumental actions. It has furthermore been suggested to play a role in comparing motor output to an internal model or prediction, thus functioning as an internal error feedback control (Lawrence, 2000). One may thus speculate that the observed activation differences of the dorsal striatum reflect intrinsically generated feedback about correct task performance in NOGO trials, even when no external feedback is given. Individuals with high openness to change value showed a greater differential response in the dorsal striatum to correct and incorrect responses. They might thus be more sensitive to behavioral errors resulting from persisting in habitual prepotent responses, which may ultimately result in a greater motivation to change behavior in order to reduce errors and optimize one's actions. This dovetails with findings from a study using event-related potentials to demonstrate enhanced error-related negativity (ERN) in a similar task in individuals who described themselves as politically liberal (Amodio et al., 2007). The ERN reflects activation of a neural error-processing system that is activated when a negative reinforcement signal is conveyed to the anterior cingulate cortex via the mesencepalic dopamine system. This signal is then used to modify performance on the current task (Holroyd & Coles, 2002). To demonstrate the involvement of the error-processing system in our task, we performed an additional ROI analysis of cingulate cortex activation in our GO/NOGO task. This analysis revealed increased activation in the cingulate cortex during NOGO errors (peak coordinates 0, −1, 40, $P = 0.003$), a location consistent with the source localization of the error-related negativity in the EEG study by Amodio et al. (2007).

An alternative interpretation of the observed data is that the striatal activation reflects the suppression of a prepotent response, without being related to motivating internal feedback signals (Vink et al., 2005). In this case, participants scoring high on openness to change value would show a generally stronger inhibition of habitual prepotent responses. However, this interpretation is not supported by the behavioral data, which did not reveal any indication of reduced errors on NOGO trials for such participants (such as fewer total errors or shorter stimulus presentation times by the adaptive algorithm). Furthermore, the increased activation of the cingulate cortex during NOGO errors suggests an involvement of error processing mechanisms.

Our findings point to neural mechanisms that may underlie the development of differences in individual value hierarchies and the effects of such differences on decisions and behaviors. Habitually stronger activation of the reward circuits when receiving valued objects, which may be due to either genetic or epigenetic factors, may lead to an increase in self-interested behavior via positive reinforcement and to a more positive evaluation of prospective outcomes of such a behavior in related decision-making processes (Sanfey, 2007; Scherer & Brosch, 2009). This may result in an increased probability of choosing selfish alternatives and may crystallize in an accordingly adjusted value hierarchy that emphasizes self-interest related values. Similarly, habitually stronger responsiveness of the reward circuits to intrinsically generated feedback about behavioral errors may strongly reinforce the avoidance of errors, which in turn may lead to a greater willingness to give up established behaviors and adopt new behaviors in order to avoid errors.

To our knowledge, this is the first study connecting individual differences in the psychological value hierarchy to basic neural mechanisms of reward processing. These findings may promote the integration of theories in cognitive neuroscience and psychological value research, allowing researchers to tackle the question of how and why some things are more important for some people than for others by combining a neurophysiological and a psychological perspective.

Manuscript received 16 March 2010
Manuscript accepted 24 June 2010

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