Activity in the amygdala elicited by unfair divisions predicts social value orientation

Masahiko Haruno^{1,2} & Christopher D Frith^{3,4}

'Social value orientation' characterizes individual differences in anchoring attitudes toward the division of resources. Here, by contrasting people with prosocial and individualistic orientations using functional magnetic resonance imaging, we demonstrate that degree of inequity aversion in prosocials is predictable from amygdala activity and unaffected by cognitive load. This result suggests that automatic emotional processing in the amygdala lies at the core of prosocial value orientation.

Individual social value orientation¹ determines behavior in economic games and many real-life situations². Prosocials are defined as those who like to maximize the sum of resources for the self and the other, while simultaneously minimizing the difference between the two. By contrast, individualists like to maximize resources for the self, while competitors like to maximize the difference between the two. The question we address here is whether prosocial attitudes depend upon deliberate top-down control of selfish impulses³ or on automatic inequity aversion⁴, and what their neural substrates are. In the former case, we would expect prosocial attitudes to be associated with greater prefrontal activity³, whereas the insula^{5,6} or amygdala^{7,8} would be involved in the latter case.

We used a behavioral task to identify people with different social value orientations. Subjects were paired and had to choose for themselves and their partner an option among three different patterns of money distribution (Fig. 1a), each designated as prosocial, individualistic or competitive¹. (See Appendix 1 in **Supplementary Methods**.) We assigned subjects to a category if they made at least six consistent decisions out of eight. Informed consent was obtained from all the subjects, and the protocol was approved by the ethics committees of the Advanced Telecommunications Research Institute and Tamagawa University.

Twenty-five prosocials and fourteen individualists proceeded to the imaging experiment (Fig. 1b and **Supplementary**

Methods). In the magnetic resonance imaging (MRI) scanner, the subjects were presented with a pair of rewards for the self and the other. They were asked to evaluate the desirability of the reward pair on four different levels (least preferable (1) to most preferable (4)) by a button press.

Each subject's evaluation was linearly regressed with the reward for the subject (R_s), the reward for the other (R_o) and the absolute value of their difference (D_a) as implicated in the theory of social value orientation¹, yielding coefficients W_{R_s} , W_{R_o} and W_{D_a} , respectively (**Supplementary Fig. 1**). The two groups differed markedly in their response to the absolute reward difference, W_{D_a} ($t_{34} = 6.68$, $P < 0.00001$; Fig. 1c). The prosocials disliked large absolute differences in distributions (inequity aversion), whereas the individualists were unaffected by such differences. In contrast, individualists preferred higher self rewards (W_{R_s} ; $t_{34} = 6.54$, $P < 0.00001$; Fig. 1c), but were indifferent to other rewards (W_{R_o} ; Fig. 1c).

To identify the neural substrates corresponding to these behavioral differences, we conducted a regression analysis of functional MRI (fMRI) data at the time of reward pair presentation with three explanatory variables: the reward for the subject (R_s), the reward for the other (R_o) and the absolute value of their difference (D_a) using statistical parameter mapping⁹ (**Supplementary Methods**) and looked for brain structures whose activity distinguished between prosocials and individualists (see **Supplementary Tables 1** (D_a) and **2** (R_s and R_o)).

Figure 1 Task design and behavior. **(a)** Triple-dominance measure task. Subjects chose one of three alternatives: prosocial (1), individualistic (2) and competitive (3) distributions of money between the self and the unknown other. 90 yen $\approx$ \$1. **(b)** Reward pair evaluation task. **(c)** Comparison of model's three regression coefficients (W_{D_a} , W_{R_s} and W_{R_o} for the absolute value or difference, the self reward and the other reward, respectively) between prosocials and individualists. Error bars, s.d. over subjects.

¹Advanced Telecommunication Research Institute Computational Neuroscience Laboratories, Kyoto, Japan. ²Tamagawa University Brain Science Institute, Tokyo, Japan. ³Wellcome Trust Centre for Neuroimaging, University College London, London, UK. ⁴Center for Functionally Integrative Neuroscience, University of Aarhus, Aarhus, Denmark. Correspondence should be addressed to M.H. (mharuno@lab.tamagawa.ac.jp).

Figure 2 Difference between prosocials and individualists in the correlation of brain activity with the absolute value of reward difference D_a . (a) Coronal section of the right amygdala, where the two groups showed a significant difference in correlation with the absolute value of reward difference D_a (Montreal Neurological Institute coordinates 20, -2, -12). (b) BOLD signal increase at the amygdala peak during 12 trials with the largest D_a values (solid line) and 12 trials with the smallest D_a values (dotted line) for prosocials and individualists. Time 0 specifies the presentation of reward pair. Error bars, s.e. over subjects. (c) Left: beta values of each prosocial (gray) and individualist (black) in correlation with D_a . Right: correlation of each subject's beta value and W_D (the subject's dislike of D_a) (gray, prosocials; black, individualists). t -test for a regression coefficient significantly different from 0.

Twenty-four prosocials and eight individualists were instructed to evaluate the reward pair and press a corresponding button as soon as possible. They were also required to memorize a five-digit number sequence before the presentation of each reward pair, and their memory was probed after each evaluation. A high-load, random number sequence was contrasted with a low-load, fixed number sequence (01234). There were no differences between the groups in their performance of the memory tasks (Supplementary Fig. 9). As in the imaging study, the prosocials showed inequity aversion, whereas the individualists did not ($F_{1,30} = 12.98$, $P = 0.0006$). However, there was no effect of cognitive load on inequity aversion for the prosocials ($t_{23} = 0.08$; $P = 0.94$). In contrast, the individualists became slightly more competitive under cognitive load, showing greater dislike of higher reward to the other (paired t -test; $t_7 = 1.94$, $P < 0.05$; Supplementary Fig. 10). Evaluation times were also unaffected by cognitive load (Supplementary Fig. 10).

These results suggest that prosocial value orientation is driven by an intuitive aversion for the inequitable division of resources. Our findings highlight an important role for automatic intuitive processing in social interaction, in addition to the slow strategic processes that were the focus of previous studies^{5–7,15} using interactive games.

Note: Supplementary information is available on the Nature Neuroscience website.

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The dorsal amygdala¹⁰ was the only area where the groups differed in the correlation of activity with the absolute value of reward difference D_a (Fig. 2a, $P < 0.001$; uncorrected). This activity was positively correlated with D_a in prosocials but slightly negatively correlated in individualists. The amygdala activity increased only in prosocials when the absolute value of reward difference D_a was large (Fig. 2b, significantly positive 5 s after the reward pair onset ($P < 0.01$); and Fig. 2c). The same effect was seen in the left amygdala with weaker significance ($P < 0.005$, uncorrected; Supplementary Fig. 2). In addition, the activity in the amygdala predicted individual differences in how much each person disliked the imbalance of reward (D_a). We found a negative correlation in prosocials ($P = 0.029$) but not in individualists ($P = 0.69$; Fig. 2c).

Several other brain structures, including the insula, anterior cingulate cortex, striatum and dorsolateral prefrontal cortex, also showed activity correlated with the absolute value of reward difference D_a , but this effect was largely driven by trials on which the reward for the other R_o was larger than the reward for the subject R_s and did not distinguish between prosocials and individualists (Supplementary Table 1 and Supplementary Figs. 3–7). Previous studies have implicated these regions in various aspects of decision making^{11–13} and, more particularly, as responsive to offers that the subject considers to be unfair^{5,6}. It is possible that the lack of impact of social value orientation on activity in these regions arises because they are involved with more deliberate, top-down appraisals of outcomes that are unfair to the self³.

Because inequity aversion in the prosocials was associated with activity in amygdala and not prefrontal cortex, we hypothesized that this reflected a rapid intuitive response rather than deliberation. To test this hypothesis, we conducted a further behavioral experiment of the reward pair evaluation task in which we measured speed of response and applied a cognitive load to prevent the use of deliberative processes¹⁴ (Supplementary Fig. 8 and Supplementary Methods).

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