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Altruism is associated with an increased neural response to agency

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Although the neural mechanisms underlying altruism remain unknown, empathy and its component abilities, such as the perception of the actions and intentions of others, have been proposed as key contributors. Tasks requiring the perception of agency activate the posterior superior temporal cortex (pSTC), particularly in the right hemisphere. Here, we demonstrate that differential activation of the human pSTC during action perception versus action performance predicts self-reported altruism.

Altruistic acts are those that intentionally benefit another organism, incur no direct personal benefit and sometimes bear a personal cost[1]. The propensity for altruism influences how humans interact and modulates health and well-being[2]. Yet the mechanisms underlying altruistic behavior remain unknown. Perceptual models suggest that an early-developing and rudimentary capacity to perceive another agent's action as self-generated and goal-oriented may form the basis of empathic perception and, in turn, altruism[3–7]. Neuroimaging studies indicate that brain regions in the pSTC contribute to the perception of agency. Both low-level perceptual tasks, such as target detection and prediction of complex movements[8], and more complex tasks, such as consideration of other agents' beliefs or (inter)actions in the environment[9–11], evoke activation in the pSTC. For example, right pSTC activation increases when people watch geometrical shapes performing seemingly purposeful acts, but not when the shapes move at random[12]. The pSTC may support rudimentary computations about the meaning of perceived actions, which might in turn subserve more complex social capacities, including empathy and theory of mind[3,13]. Thus, the functional integrity of the pSTC may be a prerequisite for prosocial traits such as empathy and altruism[13].

We hypothesized that if the perception of agency is a precursor to altruism, then activity in supporting brain regions, such as the right pSTC, should predict subjects' propensity for altruistic behavior. To address this hypothesis, we conducted two functional magnetic resonance imaging (fMRI) experiments in which young adults played or watched a simple reaction-time game[14], to earn money for themselves and for a selected charity (**Supplementary Methods** online). Informed written consent was obtained from all subjects and no deception was used. In both experiments (E1, $n = 27$; E2, $n = 18$), we observed greater activation in the right pSTC (**Fig. 1** and **Supplementary Fig. 1** online) when subjects watched a computer play the game ('Watching' trials) than when they played the game themselves ('Playing' trials). The loci of activation in the pSTC were similar to those of previous neuroimaging studies, in which subjects viewed intentional actions, read about others' intentions or performed target detection or oddball tasks (**Supplementary Fig. 2** online).

In our first experiment, subjects performed an event-related version of the reaction-time game in the MRI scanner and, after the session, provided a self-assessment of altruistic tendency (**Supplementary Note** online). Beside the right pSTC, we also observed activation in bilateral posterior cingulate cortex, bilateral hippocampus, left temporal pole, left pSTC and orbital and lateral prefrontal cortex (**Supplementary Tables 1** and **2** online).We found a significant relation between altruism and right pSTC activation, such that individuals who expressed a greater tendency toward altruism also showed increased pSTC activation on Watching trials and decreased activation on Playing trials ($r = 0.57$, $P = 0.002$; **Fig. 2a**,**b**; **Supplementary Table 3** online). Forward and backward stepwise regression analyses revealed that, of the activated regions, only the right pSTC made an independent contribution

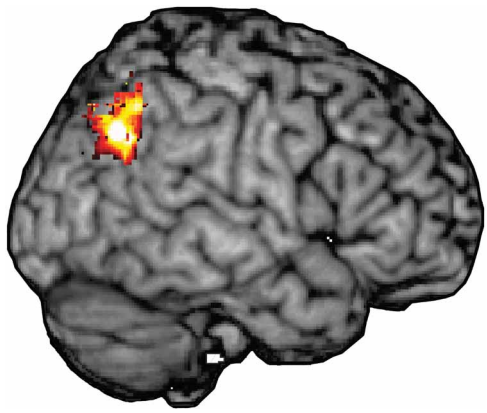

Figure 1 Increased right pSTC activation to action perception compared with action performance. We used fMRI to identify brain regions that show greater activation in response to action perception (watching a computer play) than to action performance (playing) in a game to earn money for oneself or for charity. In two experiments, increased activation in Watching compared with Playing trials was observed in the cortex surrounding the pSTC. Shown on the red and yellow color map are voxels with significantly greater activation ($P < 0.05$, controlling for false discovery rate) for this contrast in E2 (centroid: $x = 41$, $y = -48$, $z = 45$). We found similar pSTC activation in E1 (centroid: $x = 46$, $y = -64$, $z = 23$). This brain region has been associated with the extraction of meaning from visual stimuli in both biological and nonbiological contexts (**Supplementary Fig. 1**).

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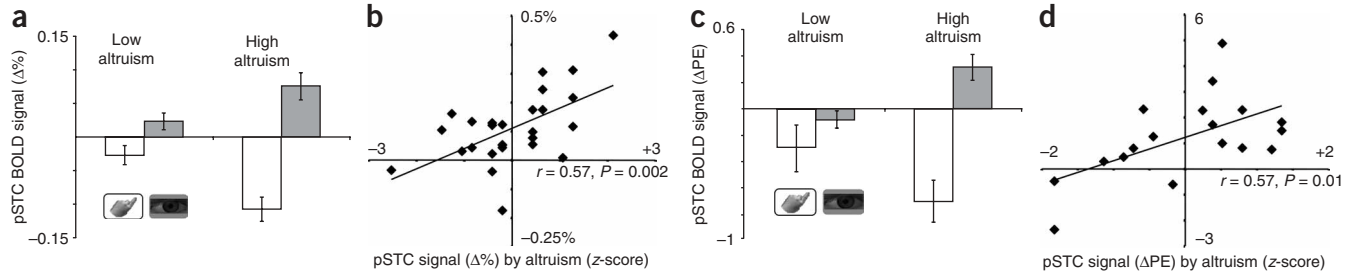

Figure 2 Altruism is predicted by pSTC activation. In each of our two fMRI experiments (E1 and E2), we examined the relation between the subjects' self-reported altruism and the magnitude of activation in pSTC. (**a**,**b**) E1. (**c**,**d**) E2. All data are drawn from pSTC regions of interest whose centroids are reported in **Figure 1**. Low-altruism subjects showed no difference in pSTC activation between Watching trials (gray bars, indicated by eye) and Playing trials (white bars, indicated by hand) in either E1 (**a**) or in E2 (**c**). All bars indicate group mean ± s.e.m. High-altruism subjects exhibited significantly greater pSTC activation for Watching than for Playing trials. Across subjects, there was a significant correlation between altruism scores and pSTC activation for both E1 (**b**) and E2 (**d**). *Y*-axes for **a** and **b** represent the difference in percent blood-oxygenation signal between Watching and Playing, and *y*-axes in **c** and **d** represent the difference in the Watching and Playing parameter estimates, which provides an estimate of relative blood-oxygenation signal, normalized to arbitrary units.

to intersubject differences in altruism (all values of $P = 0.002$). These results provide strong, albeit initial, evidence that activation of the right pSTC predicts intersubject differences in altruism.

To determine the extent to which this finding was specific to altruism, and not attributable to other personality measures, we then replicated the basic result in another experiment. In this second experiment we used a blocked design for increased detection power, incorporated a revised altruism scale designed specifically for our young adult subject population and collected data on a range of other measures, including empathy, personality and impulsiveness (**Supplementary Note** and **Supplementary Data** online). Only the right pSTC (**Fig. 1**) and bilateral orbitofrontal cortex (OFC) showed significant activation increases in the Watching condition compared with the Playing condition. Replication of the fMRI analysis using our altruism measure as a correlate in the second-level (that is, across-subjects) contrast confirmed that the right pSTC activation predicted altruism scores. We next examined correlations across subjects between the parameter estimates for the Watching > Playing contrast and each of our psychometric measures (**Supplementary Table 4** online). Only the correlation between right pSTC activation and altruism was significant ($r = 0.57$, $P < 0.01$; **Fig. 2c**,**d**). No psychometric measure significantly correlated with the activation of OFC. As in our first experiment, both forward and backward regressions indicated that altruism was the only significant positive predictor of right pSTC activation ($P < 0.01$; **Supplementary Note**).

These two experiments provide converging evidence for the relation between pSTC and altruism. The first demonstrates that increased activation in the right pSTC during action perception, compared with action performance, was predictive of higher self-reported altruism. The second experiment replicated this result, and also indicates that pSTC activity makes a specific and independent contribution to altruism, but not to the other traits tested. We interpret the activation of the right pSTC to reflect the attribution of agency to a change in the stimulus display, namely the appearance and disappearance of a target, which signals that the computer has responded for that trial. The occurrence of pSTC activation is consistent with the idea that simple, non-biological stimuli are capable of creating inferences of agency, at least in high-altruism subjects. The further result that pSTC activity predicts helping behavior (but not other psychometric measures like empathy) supports recent models of pSTC function that suggest that this region supports low-level encoding of actions[13], including the kinematics of movement[8], which feeds into systems that produce different types of empathic responses[8]. Our results indicate that the functioning of brain regions associated with relatively low-level perceptual processing can predict sophisticated behaviors such as altruism.

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

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AUTHOR CONTRIBUTIONS

D.T. and S.A.H. designed the fMRI task; D.T. and C.J.S. designed the altruism scale and selected the psychometric measures; and D.T. conducted the data analyses, under the supervision of S.A.H. D.T and S.A.H wrote the manuscript.

COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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