For goodness' sake

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Humans engage in complex social interactions, including altruism. A study in this issue finds that watching a computer perform an altruistic act, earning money for charity, is sufficient to activate a brain region that has been implicated in the evaluation of others' motives and goals, suggesting that this area may be involved in detecting agency in other creatures.

Thoreau wrote that "Goodness is the only investment that never fails." Among the bits of wisdom imparted to us when we are young, the separate charges to be fair and good typically make the top-ten list. Despite the simplicity and intuitiveness of these gentle nudges, this childhood advice raises important issues about social cognition. One cannot be fair and good simultaneously, and there's the rub.

Fairness implies an equitable exchange, and it further implies the existence of an understood norm for what is equitable. For social creatures, getting the fairness computation correct is crucial for one's ongoing existence in a group. In stark contrast, goodness is exactly not fairness. Goodness is a positive deviation from what is considered fair. A behavioral act is not good if it merely represents a reasonably reciprocal gesture. Instead, goodness requires a full measure of sacrifice, and consequently goodness implies a loss to the giver of the good act. This is precisely what humans mean by altruism—delivering a good act to someone at a cost to oneself. However, fairness and altruism also share features in common. They apply to living creatures and they are expressed during social interactions with other like-minded agents. Thus, fairness and altruism both depend on brains that can decide whether an agent is present and then decide on the meaning of the agent's actions. Might we have neural tissue dedicated to identifying these agents? In this issue, Tankersley, Stowe and Huettel tackle this question[1].

Humans can sense deviations in fairness as readily as they can smell burning food, so it is reasonable to compare our fairness-sensing capacities to our refined abilities to recognize extraordinarily subtle changes in facial structure and expression. Fairness is easy to understand as a kind of economic computation that all socially interacting nervous systems must carry out. Individuals who depend on one another must share if the group is to be valuable to them. Fairness games have been paired with neuroimaging experiments to identify dynamic neural responses associated with the detection and response to fairness[2–6]. Altruism (goodness) causes a lot more head-scratching. There is no debate about whether humans display altruism—they do[7]. Humans are deeply altruistic across a variety of settings; however, at this point, the explanations of altruism bifurcate. Although both explanations follow Thoreau's prescription—that goodness is an investment—the open question is "An investment in what?" One camp holds that altruism is really self-interest in disguise, and that altruistic acts are merely reward-harvesting behavioral ploys where the altruist consciously or unconsciously expects to get some real return back for the investment[8]. The other camp holds that human altruism is about injecting good behavioral acts that help only the group while not necessarily favoring the individual good guy[7]. These differences are important, but cannot be settled here.

Under either hypothesis, the first step toward altruism is the perception of agency. (As much as one may appreciate a pet rock, there is little sense in which altruism toward that rock could or should be considered.) Tankersley and colleagues[1] used a simple monetary choice task and functional magnetic resonance imaging (fMRI) to probe this important precursor to altruism. They describe two experiments that test the neural correlates of detecting agency and asked whether these brain regions are involved in how altruistic a person tends to be. The authors used a reaction-time game and

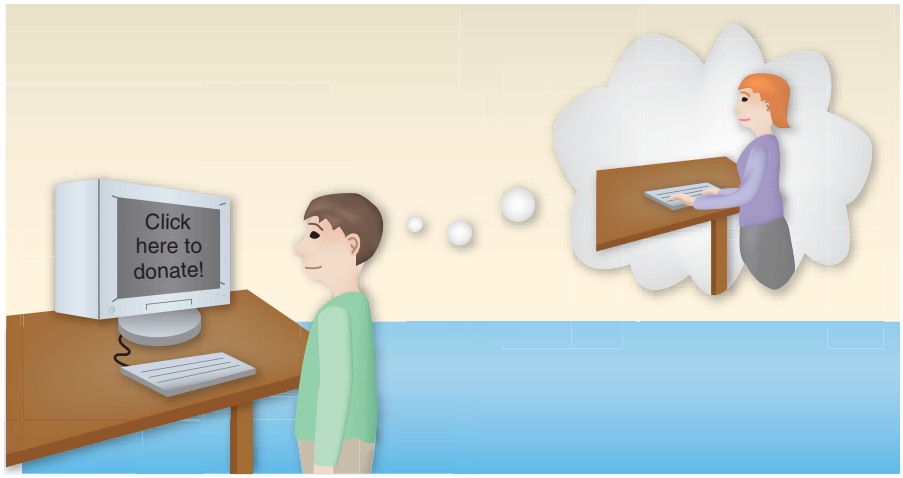

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Figure 1 Subjects in the experiment watched the computer play a game after they were told that the computer's performance would earn money for a charity that they had chosen. This observation of 'agency' was sufficient to cause activation in the pSTS, a brain region involved in considering the intentions of other beings.

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simply asked participants to either play the game themselves or watch the game being played by a computer. The earnings in the game were either paid to the player or to a charity chosen by the player before the game started. The game is uncomplicated—respond to the cue on time, and money is earned. Each participant played the game and watched the computer play the game. With just these simple manipulations by the experimenters, a machine was transformed from merely a stimulus display box to one that performed a purposeful act. That is, the authors created an intentional agent in the computer. By asking participants to watch the computer play the game, they called upon the players' brains to decide whether an agent was indeed present (**Fig. 1**). How did these brains respond?

When the human players watched the computer earn monetary points, in contrast with playing the game themselves, a distinct brain region was activated, the posterior superior temporal sulcus (pSTS). This brain region is important for considering the goals and intentions of other beings and specifically for understanding the behavior of social agents as they relate to the goals of a social interaction[9–12]. An important point differentiates the work of Tankersley and colleagues from these other studies: in the new study, the computer is an agent only in that the human player has been instructed that it is generating a purposeful act (earning money for a cause). Without these instructions, the human participant is simply viewing a series of flashing symbols, and the experiment might as well assess questions about visual perception. The pSTS may thus be implicated in generic computations about agency, regardless of whether a social interaction is involved.

To relate the perception of agency to altruism, Tankersley and colleagues asked participants in a separate setting to indicate how strongly they agreed with such statements as "I would help a stranger carry a heavy object" and "I would let my friend borrow my car for a day." The authors then correlated altruism scores with the pSTS activation described above and demonstrated that neural activity in this brain region was indeed related to altruism: greater activation in pSTS to the perception of agency was found in people with greater altruistic tendencies. Those subjects who reported that they were more altruistic also showed greater neural responses when their brains were evaluating the responses of the computer agent. pSTS activation was strikingly related to altruism specifically, not to measures of impulsivity, personality or empathy.

The data reported in this issue by Tankersley and colleagues[1] highlight the idea that neural tissue dedicated to the perception of agency may be a requirement for the generation of altruistic behaviors. As discussed above, altruism and fairness are currencies exposed during interactions with like-minded beings. Thus, to the extent that ongoing altruism and fairness with other agents is critical to survival—and it does appear to be so—the capacity to correctly detect the eligible agents is crucial. The report by Tankersley *et al.* provides evidence that the pSTS is essential in the generic assessment of agency. However, these data also pose the intriguing question for follow-up studies: is the same brain region used to call upon these agency assignments once an interaction has occurred?

COMPETING INTERESTS STATEMENT
The authors declare that they have no competing financial interests.

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Olfactory identity kicked up a NOTCH

Stefan Fuss, Arzu Çelik & Claude Desplan

A new study shows that the identity of olfactory sensory neurons in flies is regulated by Notch signaling, which divides the neurons into two classes that express specific sets of olfactory receptors and project to distinct glomeruli.

Animals as well as humans rely on their sense of smell in everyday life to identify appropriate and palatable food, to avoid predators and sources of danger, and to make mating choices. The olfactory system is thus confronted with the complex task of detecting and discriminating a seemingly endless number of different odor cues. This remarkable ability depends on both the specificity of chemosensory receptor cells in the periphery and on their specific connections to the brain. Olfactory sensory neurons (OSNs) in both vertebrates[1] and some invertebrates[2] obtain their identity by the exclusive expression of a single member of the olfactory receptor gene superfamily. There are 1,000 olfactory receptor genes in rodents and around 60 in the fruit fly.

Olfactory receptor proteins mediate the interaction with odorants and thereby dictate the response profile of OSNs[1]. Odor signals are then transmitted to the first olfactory relay in the brain, the antennal lobe in insects[2] or its vertebrate counterpart, the olfactory bulb[3]. Axons of OSNs that share the same olfactory receptor identity converge onto a single anatomically distinct glomerulus, which thus collects sensory input from OSNs with identical response profiles before relaying the information to higher brain centers. In this issue, Endo *et al.*[4] identify asymmetric Notch signaling as an early event that sets up OSN identity, contributing an important step to our understanding of how the functional olfactory map is established in the fruit fly.

To achieve specific and exclusive olfactory receptor gene expression and axonal projection to a single glomerulus during development in the fruit fly, the expression of ~60 olfactory receptor genes has to be coordinated to achieve the necessary molecular identity and anatomical specificity. Although we have some limited understanding of the transcriptional regulation of olfactory receptor genes[5,6] and of some of the guidance molecules involved in correct axonal targeting to the antennal lobe[7], little is known about early signaling events that set up OSN identity.

In a genetic screen aimed to identify genes involved in establishing specific connections to antennal lobe glomeruli, Endo *et al.*[4] identified *mastermind* (*mam*), which encodes a

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