THE BIOLOGY OF FAIRNESS REVEALED

By Stephen M. Fleming

Parents of quarrelsome siblings will know that the best rule for dividing up a cake is 'whoever cuts chooses last'. This rule uses a child's natural self-interest to engineer a fair outcome for all. As we grow up, such cunning strategies are no longer needed: generally, we seem to see virtue in fairness for its own sake, and share the cake accordingly. But when do we develop these desirable qualities? What is it about our biology or culture that leads us to be fair? Do other animals also tend towards selfless egalitarianism? In the past few years, compelling new evidence from the fields of economics, ethology and neurobiology has begun to provide us with answers to these questions.

Researchers are fond of using a version of this cake-cutting dilemma to ask just how fair we are. In the ultimatum game, one player is given a pot of money, and asked to share it with a second player. If the recipient refuses to accept the offer, both players get nothing. The most rational thing for the recipient to do is to accept anything, even very small offers; after all, beggars cannot be choosers. Knowing this, the player cutting the cake should offer as little as possible, keeping most of the spoils. However, a reliable finding across culture, gender and economic status is that people do not behave rationally – unfair offers are punished, especially when they amount to less than around 20% of the total pot. People forgo personal gain to ensure that the unfairness of others is appropriately punished. Similarly (possibly because fear of rejection is high) proposals are usually around half of the money available. Economists have argued that this inclination to be fair is uniquely human.

To test this assumption, a team of researchers led by Keith Jensen in Leipzig, Germany, trained pairs of chimpanzees to play a version of the ultimatum game. The game proceeds as follows: one chimpanzee chooses between two ways of dividing up a dish of raisins; a second chimp then either accepts the offer by pulling a rod connected to the dish, or rejects it. If the proposal is rejected, the researchers remove the dish of raisins, so both animals get nothing. In the experiment, the crucial result was that the chimpanzees tended to accept any offer, fair or unfair, in stark contrast to human players (Jensen et al 2007, 108). It is possible that the animals simply found it difficult to say no, despite feeling cheated, but this does not seem likely to Dr. Jensen: 'If the raisins were highly valued, it should be more upsetting, leading to more rejections, not less'. This was not the case, just as a cold, rational theory of behaviour would predict. Chimpanzees, our closest living relatives, seem not to share our sensitivity to fairness. It remains to be tested whether this difference extends to social interaction in the wild.

So why are we more likely to be fair in comparison to chimps? Daria Knoch and her colleagues at the University of Zurich may have the beginnings of an answer to this question. They also used the ultimatum game, this time with human volunteers, asking people to accept or reject a proportion of Swiss francs doled out by another player. Just before the task began, the researchers applied a harmless magnetic field to the front of the volunteers' heads (a technique known as transcranial magnetic stimulation, or TMS), momentarily interfering with brain activity in a small region of the prefrontal cortex. This disruption led to a sharp increase in the tendency to accept unfair offers in the game, similar to the behaviour of the chimpanzees – but only when the pulses were applied to the right, not the left, prefrontal cortex (Knoch et al 2006, 830). This finding elegantly shows that the tendency to accept unfair treatment is not just due to a general effect on brain function caused by the magnetic field; instead, it appears that the right prefrontal cortex is playing a causal role in our penchant for fairness.

Exactly what this region of the brain is doing to make us behave more fairly is unclear (apes have similar brain areas, though possibly with fewer connections to other regions). The prefrontal cortex has long been thought to play a role in controlling our immediate urges and desires, and some theorists believe it forms a separate brain system designed to keep our ancient emotional impulses in check. Being fair requires us to suppress self-interest for the sake of harmony with our peers, which may have evolved as a good way of ensuring we are treated fairly in the future. As Dr. Knoch notes, this theory has a Freudian flavour, suggesting that a daily battle between moral and selfish behaviour is played out in the firing of our nerve cells.

Intriguingly, the prefrontal regions of the brain are also some of the last parts to fully develop. In a paper published recently in *Nature* (Fehr et al 2008, 1079-84), again by the Zurich group, it was found that 7-8 year olds will naturally play fair, but that 3-4 year olds prefer to keep the spoils (in this case, sweets) for themselves. Such data do indeed suggest that the maturation of certain brain regions such as the prefrontal cortex is required to exert 'top-down' control over our more automatic selfish urges. This developmental process is controlled by gene complexes that are responsible for assembling the myriad of connections between brain cells. Hence it is not surprising to learn that the tendency towards egalitarianism has a genetic component, at least in the context of the ultimatum game (Wallace et al 2007, 15631-634). Indeed, genes that contribute to fair behaviour may have been selected in tightly-knit societies where the sharing of hunted game was vital for survival.

Whether these mechanisms are enough to engender a full-fledged understanding of fairness is an open question. It is unclear, for example, whether improved cognitive control in chimpanzees would ever lead to the same selflessness we (sometimes) admire in ourselves. Cultural factors are likely to play a part: it would be of interest if the developmental transition seen in the Zurich study were linked to the period when children begin to acquire the language needed to talk about fairness, or if the transition were connected with the effects of schooling. Still, next time you are refereeing an argument about who gets the biggest piece of cake, reassure yourself that soon your little monkeys (or chimpanzees) will have graduated into fair adults, regardless of exactly how they got there.

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