In Focus

Featured Articles in This Month’s Animal Behaviour

A Fair Deal

The concept of what is fair seems to be deeply imbedded in the human psyche. Equal pay for equal work has been a rallying call for some since the industrial revolution. To see others get a better reward for the same job is aggravating as is ‘bait and switch’ when a better prize is first offered and a lesser one given. The question is, how far back in evolutionary history do these sentiments go?

To examine this question, experiments have been set up with primates and quite a few other nonhuman species whereby one individual sees another get a better reward for completing the same task. Sometimes this lesser reward is rejected but responses to this inequity are variable within and across species. Responses can be influenced by rank, sex, age and social group. In this issue (pp. 75–87) Sarah Brosnan of Georgia State University and her associates asked whether personality attributes also explain some of the differences in the behavioural response to inequity. They also asked whether personality traits affected responses similarly when individuals had been shown a better reward than what they ultimately received.

Twenty-four chimpanzees from four social groups were allowed to choose to participate with a particular partner. Pairs alternated trading a token to receive a food reward (Fig. 1) that was the same or of less value than what they saw their partner receive (inequity condition) or the reward was of less value than what they had been previously shown (contrast condition in which the outcome is compared to a nonsocial referent such as past experience). In the control condition, both subjects were offered and received the same, less preferred reward. Brosnan et al. predicted that both personality and the quality and duration of the pair’s relationship would influence the chimpanzees’ reaction to these ‘unfair’ conditions.

After establishing that all chimpanzees preferred a grape to a piece of raw carrot and after they had been trained to exchange a length of PVC pipe for the reward, each pair was tested in the inequity, contrast and equity control conditions with partners alternating as subject. Personality ratings were collected from questionnaires from staff members. The 41 traits were reduced to six dimensions: methodical, extraversion, agreeableness, openness, reactivity/undependability and dominance. Information on the quality of the relationship was collected through scan samples of interactions scoring contact, proximity and grooming. The length of time that the subjects had lived in the same social group was also considered.

Subjects refused to accept the less desirable reward between about 20 and 40% of the time, which varied significantly depending on the condition, personality traits and the length and quality of the relationship of the two partners. Personality played a role in the reactions to both the inequity (when the partner had a better reward) and the contrast (when the subjects were first shown the better reward than the one they received) conditions. Individuals that were rated higher in ‘extraversion’ and lower in ‘agreeableness’ were more likely to respond to inequity whereas those that were rated lower in ‘reactivity’ were more likely to refuse in the contrast situation. Those that were rated higher in ‘openness’ and lower in ‘methodical’ reacted strongly in both the inequity and contrast conditions. Contrary to the researchers’ expectations, the quality of the relationship did not influence the strength of the individuals’ response to either the inequity or contrast conditions whereas the longer that the two partners had lived together, the less likely they were to refuse the less desirable reward in the contrast condition. When paired with a partner that they were comfortable with, they were more accepting of lower than anticipated rewards and less bothered by their partner’s better outcome. As had been shown

Figure 1. ‘Joey’ about to enjoy a grape, the preferred reward. Photo: Jenny Bridges, courtesy of The Keeling Center of MD Anderson Cancer Center.
in other studies, males, dominant chimpanzees and younger ones were more likely to refuse.

Thus different personality dimensions correlated differently with the inequity and the contrast conditions indicating that the chimpanzees viewed these unfair outcomes differently. This is particularly intriguing as it implies that whether or not a task is social may influence how it is perceived. Although both tasks involve a violation of the subject’s expectations, the inequity condition has a social comparison, based on what the partner received, and the contrast condition involves a nonsocial comparison, based on a past experience. Although both comparisons are presumably underpinned by the same cognitive mechanisms, small differences in brain functions must account for these differences in perception. Presumably this means that the circuitry of the brain that processes social information in chimpanzees is somewhat distinct from that dealing with nonsocial issues, as seems to be the case with humans. Dunbar (1998) and others have argued that selective pressure from increasingly complex social systems has led to the enhancement of neural circuits that specifically support social cognition in the primates (i.e. the social brain hypothesis). As one example, there seems to have been strong selection on how organisms perceive social stimuli, as both humans and other animals (including nonprimates) have sensory areas specifically devoted to social stimuli. Following from this, perhaps the subjects in this study perceived the better rewards given to conspecifics differently from better rewards that were merely shown to them. One (very) speculative possibility is that the personality differences that were seen in this study reflect differences in the strength of connection between higher-level cognitive areas (where comparisons of expected to received outcomes would occur) and lower-level social-motivational systems.

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Visual Orientation and Courtship in Fiddler Crabs

The enlarged claw in male fiddler crabs is an example of a conspicuous trait selected by both female preferences and male—male competition for mates. Such traits are widespread in the animal kingdom and detailed studies of the underlying behavioural mechanisms of preference and competition are crucial for understanding how sexual selection works.

Male fiddler crabs sometimes build domes, semidomes, hoods or pillars at their burrows using sand or mud. The size and shape of these structures as well as when and how often they are built vary substantially. Their function as sexual signals has been studied extensively in *Uca terpsichores*. In this species, the period when females choose their mate and males court females vigorously coincides with the time when males build hoods at their burrows (Fig. 2). Earlier experiments have demonstrated that females are attracted to male burrows by the hoods and that the basis for such a behavioural preference is landmark orientation selected by predation. Males also use the hoods for visual orientation to return to their burrows when they stray far during their vigorous courting of females and errors are introduced to their nonvisual path integration mechanism. Hoods also allow males to return to their burrows more quickly. Therefore, a hood is likely to reduce a male’s risk of predation and increase his resource-holding ability. All these earlier results demonstrate that hood building by males is sexually selected by both female preference and male—male competition.

In the present issue (pp. 61–66), the authors of some of these earlier studies ask whether hoods affect male behaviour in other ways that are favoured by sexual selection. Tae Won Kim (Korea Institute of Ocean Science and Technology and University of Science and Technology, Daejeon, Korea) and John Christy (Smithsonian Tropical Research Institute, Balboa, Panama) set out to test whether *U. terpsichores* males move further and more freely when there is a courtship structure on their burrow. In a recent study, Kim and co-authors demonstrated that this is indeed the case for the massive semidomes built by males in another *Uca* species (Kim, Kim, & Choe, 2010). Here Kim and Christy extend this approach by also conducting experiments to determine whether any use of the courtship structure as a beacon is contingent on the male using it having built it.

The experiments were carried out on a sand beach on the east side of the Pacific Entrance to the Panama Canal. The first experiment involved 35 pairs of adjacent vigorously courting males. Each pair comprised one male with and one male without a hood at his burrow. In the second experiment, each of the 29 pairs consisted of two males with hoods but the hood of one of them, chosen at random, was removed. In the final, third experiment, both males in each of 25 pairs did not have a hood but an artificial hood of average dimensions was added at the burrow opening of one of them, chosen at random. In each of the three experiments, at 40 cm from each male, a reproductively active female was tethered to a thin wooden stake with a light string. She could move at most 5 cm and was prevented from burrow. Each female was used as a decoy for not more than three male pairs. All individuals involved were released unharmed back to their local populations immediately after the experiments. Analysis was carried out on video recordings.

Kim and Christy found that male fiddler crabs that built a hood did not move further away from it than males that did not build a hood. However, the transverse body axis deviated more from the bearing to the burrow for males that built a hood than for males that did not. Males that built hoods compared with those that did not also exhibited greater deviations from the bearing to their home when they were furthest away from it.

When one of the males in the pair had his hood removed, there was a reduction in all three of the above measurements of freedom and distance of movement from the burrow for the male with a removed hood and only after it was removed.

Finally, when one of the members of the pair had a hood added to his burrow, there was a change in one of the three
measurements. The deviation of the transverse body axis from the bearing of the burrow increased for the male with an added hood and only after this manipulation.

With these results Kim and Christy demonstrate that, similarly to the *Uca* fiddler crab species that build semidomes, males with hoods move more freely and further away from their burrows than males without hoods in *U. terpsichores*. Furthermore, the authors show for the first time that this effect is present whether the hood has been built by the crab itself or has been added experimentally, thus demonstrating that the use of the hood as a beacon is not contingent on the user having built the structure. The hood gives male fiddler crabs the option to switch from path integration to using a beacon for visual orientation back to their burrows and that gives them greater freedom of movement when they are courting. More generally, this new study by Kim and Christy demonstrates the importance of knowledge about the underlying behavioural mechanisms for understanding how selection works.

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References
