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Desire-state attribution: Benefits of a novel paradigm using the food-sharing behavior of Eurasian jays (*Garrulus glandarius*)

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ABSTRACT

In recent years, we have investigated the possibility that Eurasian jay food sharing might rely on desire-state attribution. The female's desire for a particular type of food can be decreased by sating her on it (specific satiety) and the food sharing paradigm can be used to test whether the male's sharing pattern reflects the female's current desire. Our previous findings show that the male shares the food that the female currently wants. Here, we consider 3 simpler mechanisms that might explain the male's behavior: behavior reading, lack of self-other differentiation and behavioral rules. We illustrate how we have already addressed these issues and how our food sharing paradigm can be further adapted to answer outstanding questions. The flexibility with which the food sharing paradigm can be applied to rule out alternative mechanisms makes it a useful tool to study desire-state attribution in jays and other species that share food.

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Recently, we have developed a new behavioral paradigm to study desire-state attribution in Eurasian jays (*Garrulus glandarius*).[1] Like other corvid species, the male Eurasian jay shares food with his female partner during breeding season. This courtship behavior is important for the formation and maintenance of the jays' long-term pair bonds.[2,3] This cooperative behavior allows us to investigate whether or not the male can respond to what is currently the food of the highest value for the female, i.e. what food she currently desires. This might be beneficial to the male because by sharing food of high value, he could signal his quality as a mate to the female.

The female's desire can be manipulated using specific satiety, which refers to the devaluation of a particular type of food that is experienced after excess consumption of that food.[4-6] In our original food sharing test, the male jay adjusted his sharing behavior to the female's specific satiety by sharing less of the food that the female was sated upon.[1] However, to be considered desire-state attribution, the male's behavior must not be explainable by a simpler mechanism. Below we discuss how our food sharing paradigm can address this issue by testing whether alternative mechanisms might underlie the male's sharing pattern.

Behavior reading

The male's response to the female's specific satiety would not qualify as desire-state attribution if it could be explained by the male responding solely to the female's behavior. To rule out the possibility that the male is responding solely to the behavior of the female at the time of sharing ('stimulus bound behavior reading'[7]), we ran an experiment in which the male did not see the female during pre-feeding and thus did not know what food she was pre-fed.[1] Thus, the female's behavior during the sharing phase was the only cue available to the male. Here, the male did not share with the female the food that she desired, suggesting that the food sharing effect cannot be explained by 'stimulus-bound behavior reading.'

It is further necessary to consider whether during the pre-feeding phase the female might elicit behaviors that directly indicate her desire, in which case the male would not need to posit a desire-state to her. To rule out the possibility that the male's sharing behavior is an effect of behavior reading during the pre-feeding phase our paradigm will need to be adapted such that it eliminates the female's behaviors that could directly indicate her desire during the pre-feeding phase. A further possibility would be to test whether the male could respond to the female's

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change in desire in the absence of all female's behaviors during the pre-feeding phase: instead of seeing the female eat, the male could be informed of this fact in a different manner such that he needs to *infer* that she has eaten a particular food.[7,8]

Self-other differentiation

To qualify as desire-state attribution, the male's sharing behavior has to be a response to the *female's* specific satiety and not to the male's own desire. In the original study, we ruled out the possibility that the male's own desire could have been affected by seeing the female become sated on one type of food: when the male could not share with the female during the test phase but only chose food for himself, his eating behavior did not show the same pattern as his sharing behavior.[1] Thus, the male's sharing pattern must have been a response to the female's and not his own desire.

In addition, the food sharing paradigm allowed us to investigate the extent to which the male can disengage from his own desire to share with the female what *she* (rather than what *he*) wants. By manipulating both the female's and the male's desires using specific satiety, we showed that when their desires conflicted, the male's sharing pattern took the female's desire into account but was also biased by his own desire.[9] Interestingly, a similar bias occurs when human adults and children respond to conflicting desires.[10-13] Thus, our finding provides further evidence for self-other differentiation in the male jay, and also supports the desire-state attribution hypothesis by suggesting that the same mechanism might underlie human and Eurasian jay responses to others' desires.[7]

Behavioral rules

A further question to consider is whether the male's sharing behavior could be the result of a simple behavioral rule such as "feed the female what you have not seen her eat." The results discussed above[9] speak against this explanation, because a behavioral rule is unlikely to be affected by a bias of the male's own desire.[14] Further, if the male was relying on a behavioral rule, his sharing pattern would be a response to a specific perceptual cue,[7,15] in this case the female eating a particular food. Thus, a behavioral rule is inflexible in 2 ways: firstly, it requires that the eliciting cue is always present and secondly, the same eliciting cue can only ever elicit the same behavior. Consequently, the use of a behavioral rule could be rendered unlikely in 2 ways. The male's reliance on the eliciting cue could be ruled out if the male responded to the female's desire in an inference based experiment, in which he has knowledge of what food the female is being pre-fed but does not see her eat. The flexibility in the male's behavioral respose to the same perceptual cue could be shown if the male exhibited a sensitivity to *how much* food the female has eaten and thus the degree of specific satiety she is experiencing, or a sensitivity to what food the female *prefers*, for instance after seeing the female choose between 2 available food sources.[16]

In summary, while our current results show that the male's sharing behavior is in line with the desire-state attribution hypothesis, several behavioral criteria still remain to be tested. Our food sharing paradigm can be modified to test whether the male's behavior satisfies these criteria and thus presents a novel means to investigate desire-state attribution in jays and potentially also other species that employ food sharing behaviors.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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