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Bee happy: emotion-like states in an insect

Bumble bees show dopamine-dependent changes in decision-making indicative of affective state

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In his book *The Expression of The Emotions in Man and Animals* Charles Darwin (1872/2009, p.347) noted that: “even insects express anger, terror, jealousy, and love by their stridulation”. Almost 150 years later, spurred by an interest in the evolutionary roots of emotional (affective) processes and their underlying mechanisms, there has been a sudden upsurge of research into the question of whether insects and other invertebrates may indeed have emotion-like states (1-4). Recent work has focused on negative states, but on page XXX of this issue, Perry et al. (5) broaden the scope to consider positive emotions. They show that feeding bumblebees a sucrose solution, which is assumed to induce a positive state, leads to positively-biased decision-making under ambiguity, analogous to optimism in humans and an indicator of positive affect in both humans and other species (6-8). It also counteracts the negative impact of a simulated predator attack on bee foraging behaviour, and both effects appear to be dopamine-dependent.

Emotions are quintessentially subjective experiences – positive or negative *feelings* such as happiness or anger – so how can such private states be studied in non-human animals? One way is to provide an operational definition of emotion that allows researchers to identify what state an animal is in and hence to search for associated underlying mechanisms, and physiological, behavioural and cognitive markers which, unlike feelings, can be measured objectively. A recent suggestion is to use general properties of human emotion including valence (positivity or negativity; a key defining characteristic of human emotion (7,9)), arousal or scalability, persistence after a stimulus or event, and generalization across situations – so-called ‘emotion primitives’ (1) – to identify affective states in other species.

Another operational definition is that emotions are states elicited by rewards and punishers, where a reward is something for which an animal will work and a punisher is something that it will work to avoid (7,9,10); on this basis, an animal exposed to a punisher is in a negative affective state. Even if researchers disagree, such definitions lay out assumptions that can be argued and improved, and make it clear exactly why a particular method for inducing an emotion, or a particular measure of emotion, is being studied. Many scientists are agnostic about whether these operationally defined states are consciously experienced in animals, and it is possible that some species subjectively experience emotion whilst others exhibit behavioural and physiological indicators of emotion (‘emotion-like’) without any accompanying feeling (11).

In their study, Perry et al. used a rewarding sweet solution to induce a positive emotional state, in line with the second operational definition. They then sought to confirm this state using a cognitive bias test (6) which is based on findings that human emotions bias decision-making under ambiguity – happy people are more likely to make optimistic judgements about ambiguous situations than unhappy people (7) – and is now used widely in animal emotion research (8). Bumblebees were trained that on any trial a cylinder was placed either on one side of a foraging arena next to a green card or on the other side next to a blue card. One of the location-colour combinations indicated that the cylinder contained a 30% sucrose solution reward whilst the other indicated that it contained just water, and the bees learnt to fly faster to the cylinder on trials with the first configuration. Occasional trials were then used to test their responses to ambiguity by presenting the cylinder between the two trained locations and next to an intermediately coloured (blue/green) card. The prediction was that bees in a positive affective state would fly faster to intermediate cues, analogous with an ‘optimistic’ judgement of ambiguity (6).

Consistent with this prediction, Perry et al. found that bees given an unexpected 60% sucrose reward to induce a positive affective state prior to an ambiguity trial, did indeed fly faster to the cylinder than non-rewarded bees. They then tested the idea that emotional states generalise across contexts (1) finding that an unexpected 60% sucrose solution also improved the speed of recovery (resumption of foraging) from a subsequent predator attack simulated by brief restraint. Finally, they investigated underlying mechanisms and showed that the ameliorating effect of sucrose on response to simulated predation disappeared when a dopamine antagonist (fluphenazine) was topically applied prior to the test,

whilst the antagonist on its own had no general effect on activity following predation. Fluphenazine also prevented sucrose-induced 'optimistic'-like responses to ambiguity in the cognitive bias test.

Taken together these findings suggest that an unexpected sugar reward induces a putatively positive state that persists for at least a short time, has effects across both positive (foraging) and negative (simulated predation) contexts, alters behaviour as predicted in a cognitive bias test specifically designed to assess the valence of affective states, and is mediated by dopaminergic circuitry. Such a state satisfies a number of the criteria identified by the operational definitions of emotion mentioned earlier (1,10).

It is possible that the induced state, rather than having affective properties, was simply one of general increased activity resulting from the energizing effects of sucrose. In an attempt to discount this interpretation, Perry et al. showed that sucrose-induced faster flight in the ambiguity test was not observed in other foraging contexts, and did not occur to novel stimuli, indicating that it was unlikely to be an effect of a general activity increase. In the absence of a specific control in the simulated predation context, it remains possible that sucrose may have been exerting its effects via a general energizing effect on the speed of recovery following restraint.

However, the finding that a dopamine antagonist blocked the effects of sucrose in the foraging and predator tests provides further evidence that the same underlying state was at work in both contexts. For example elevated activity of reward-sensitive dopaminergic neurons, which could be likened to a primitive positively valenced state, may bias action selection in favour of active or approach behaviour to relevant stimuli (12). On its own, however, this process would not explain the specificity of such a response to ambiguous as opposed to novel stimuli. Moreover, given that dopamine is also involved in punishment processing (12,13), we might expect that fluphenazine would have interfered with dopamine-mediated suppression of action in response to simulated predation in the absence of a sucrose reward, but this was not observed.

The study of Perry et al. extends recent work on invertebrate emotion, in particular by focusing on positive states and their impact across contexts. It also provides further support for the hypothesis that one function of affective states is to act as a Bayesian prior on decision outcome probabilities that guides decision-making, particularly under ambiguity where current information on outcomes is lacking (9). Given the likely adaptive value of such emotion-cognition interactions it is not surprising that insects, like other taxa, possess emotion-like systems to implement them. Many questions remain to be answered including whether cross-context effects are indeed the result of an internal state that is mediated by the same underlying neural mechanisms, the extent to which such states exhibit other operationally defined properties of emotion and hence warrant the label, and whether induced negative states also show cross-context effects and are mediated by the same or different neural processes. Whether 'emotion-like' states in insects are accompanied by emotional feelings remains unanswered, but the possibility of insect consciousness is now the topic of exciting new theories and vigorous debate (14,15 and references therein).

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FIGURE

Cognitive bias test of affect-induced changes in decision-making under ambiguity. Bees are trained to associate one set of cues with a sucrose reward in a cylinder and another set of cues with no reward in the cylinder. They learn to fly faster to the cylinder when the cues predict reward. In ambiguity tests, 'ambiguous' cues are presented at one of three locations intermediate between the training cues and the bees responses are recorded. Before these tests some bees experience an affect manipulation (unexpected sucrose reward) to put them in a putatively positive state. The prediction is that these bees will make a positive evaluation of the cues as predicting reward and hence fly faster to the cylinder than those in a less positive, or negative, state.

