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1 **Technical comment to:**

2 Solvi, C., Al-Khudhairi, S. G., & Chittka, L. (2020). Bumble bees display cross-modal
3 object recognition between visual and tactile senses. *Science*, 367(6480), 910-912.

4
5 **Title: A killjoy perspective on object representation by bumblebees**
6

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12

13 **Abstract:**

14 Solvi et al. (1) reported that bumblebees trained to discriminate objects by touch could
15 distinguish them through vision, and vice versa. We argue that this behavioural feat may be
16 explained by egocentric heuristics rather than an abstract representation of object shapes. We
17 call for more considerations of animals' ecology, neural circuitry and actual behaviours.

18
19 **Main text:**

20 Insect cognition research is living a golden age, with increasing numbers of studies showing
21 that insects can solve ever more impressive behavioural tasks despite their miniature brain. In
22 the latest example, Solvi et al. (1) describe an elegant experiment where bumblebees trained
23 to discriminate cubes vs. spheres, either visually (through a transparent screen) or by touch (in
24 the dark), could apparently also recognize them in the other modality. This suggests that
25 insects form a “modality-independent internal representations of object shapes”, an ability
26 that we humans are explicitly self-aware of.

27 This study is designed to demonstrate, in an insect, the existence of a ‘higher cognitive
28 process’ drawn from human psychology rather than the animal’s known neuro-anatomy or
29 natural behaviours. This approach undeniably drives the field of comparative cognition
30 forward by suggesting unsuspected and often sensational human-like cognitive abilities in
31 small-brained animals. However, this provides no insights on how or why these behavioural

feats are achieved; and because the incentive is to seek for complex phenomena, this approach is subjected to the risk of overlooking more parsimonious, ‘killjoy’, explanations (2). This is particularly true in insects, which perceive and interact with the world in very different ways than humans do. Such an approach ought to be supplemented with considerations for plausible mechanisms underlying the phenomena, ultimately enriching species comparisons (3).

Cross-modal transfers in insects are not new (4, 5), and in some cases we have a good understanding of how this is implemented in their neural circuits. For instance, insects can memorise directions based on wind ,or self-motion cues perceived through mechanosensors and subsequently recover these directions using visual cues (6–8). Because there is no a-priori reason to link these cues in any particular fashion, such transfers require the simultaneous experience of both cues at some point in the past, and involve Hebbian-like plasticity (i.e., cells that fire together wire together) in a well characterised area called the Central Complex (8, 9).

The fascinating aspect of the new study by Solvi et al. (1) is thus not so much about a cross-modality transfer per se, but the idea that such a transfer is achieved through an internal representation of object shapes. This seems at odds with previous work. For instance, flies (10) and bees (11) can learn to visually discriminate two triangles shown side by side, with one pointing up and one pointing down, suggesting – as in the present study – their ability to memorise shapes. However, this apparent ability vanishes if the triangles’ relative positions are slightly shifted vertically so as to align their centres of mass, showing that insects do not build a mental image of shapes, but extract instead a limited number of specific features. Congruently, insects’ visual receptors and neural processing are poorly suited to reconstruct the world’s shapes but remarkably efficient to pick-out task-relevant features (e.g., indicating the presence of flowers in bees, flying targets in predatory insects, or distant trees in fruit flies). Such filtering, so-called ‘matched-filters’, “severely limits the amount of information the brain can pick up from the outside world, but frees the brain from the need to perform more intricate computation to extract the information finally needed for fulfilling a particular task” (12). In sum, insects seem not equipped to build internal reconstructions of the outer world, but are excellent at using ecologically relevant task-related heuristics.

How could we reconcile Solvi et al.'s (*1*) results with such an idea? Without information about the sensory-motor experience of the bumblebees, we can only provide tentative explanations, more to sparkle the debate than to defend a strong belief.

First, bumblebees may have achieved mechano-visual associations during previous experience with edges, curved or flat surfaces, presumably here also through Hebbian-like plasticity. This would be exciting; however, it should be understood that such associations may link egocentric perceptions (i.e., centred on the animal viewpoint rather than the world) and thus do not imply any form of abstract object representation or 'world-centred' reconstruction. Such egocentric cross-modal transfers would require the unimodal perception to be similar to what it was during the past bi-modal experience. That is, the bumblebee would need to view the object from a short distance (close enough to touch it) to trigger the associated bi-modal representation.

Alternatively, bumblebees may have used a sensorimotor trick. Insects can visually guide their legs and antennae appropriately when trying to reach an object (*13, 14*). This visual control is based on egocentric features such as the apparent movement of proximal edges or surfaces (*13, 14*). Therefore, even though the objects presented in Solvi et al.'s (*1*) visual condition are covered with a transparent screen, bumblebees may visually adjust their appendages differently when preparing to touch the round sphere or the flat, edgy cube. These object-specific movements might bear similarities with the ones effected during the act of sampling the objects in the dark. 'Preparing to grasp the cube using vision' and 'sampling the cube in the dark' might involve similar movements, specific of the object. Because this self-induced experience – whether through proprioception, motor command or both – occurs just before the bumblebee receives the reward or the punishment, it is likely learnt as a salient cues allowing differentiation. An operant rather than Pavlovian conditioning, which would predict a spontaneous transfer across visual and dark conditions. This may sound far-fetched to us humans, but it would not be the first time insects use their own movements to solve object-recognition paradigms in unsuspected ways (*15*). Intriguingly, even for us, the object-specific movements effected when grasping are based on a limited set of egocentric visual features rather than our ability to form object-based representation (*16*).

In any case, both egocentric hypotheses predict that bumblebees tested in the light would need to approach the object within reach to recognise it as good or bad. As it turns out, this seems to be what they are doing. The example videos courteously shared by the authors showed that

the bumblebees tested in the visual condition approached (close enough to touch it) both the rewarded and punished objects equally often (21 vs. 22 instances). Their straight approaches reveal that they do see the targeted object... but have yet no information allowing discrimination. The bumblebee trained in the dark further displayed multiple attempts to reach the punished object through the glass with its legs or antennae before moving on. These behaviours seem hard to conciliate with the psychology-inspired idea of “a complete, globally accessible, Gestalt perception of the world”.

Surely, an analysis of the bumblebees’ actual behaviour is needed. Our egocentric explanations may prove to be wrong but we hoped it showed how consideration of insects’ neurobiology, ecology, and sensory-motor dynamics can lead to alternative, more mechanistically grounded explanations.

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