

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.

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

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7 **Authors:** Florent Le Moël¹, Sebastian Schwarz¹, Mathieu Lihoreau¹, Antoine Wystrach^{1*}

8 **Affiliations:**

9 ¹Centre de Recherches sur la Cognition Animale, CNRS, Université Paul Sabatier, Toulouse,
10 F-31062 Cedex 09, France

11 *Correspondence to: antoine.wystrach@univ-tlse3.fr
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13 **Abstract:**

14 Solvi et al. (*I*) 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.

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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. (*I*) 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

32 feats are achieved; and because the incentive is to seek for complex phenomena, this approach
33 is subjected to the risk of overlooking more parsimonious, ‘killjoy’, explanations (2). This is
34 particularly true in insects, which perceive and interact with the world in very different ways
35 than humans do. Such an approach ought to be supplemented with considerations for
36 plausible mechanisms underlying the phenomena, ultimately enriching species comparisons
37 (3).

38 Cross-modal transfers in insects are not new (4, 5), and in some cases we have a good
39 understanding of how this is implemented in their neural circuits. For instance, insects can
40 memorise directions based on wind ,or self-motion cues perceived through mechanosensors
41 and subsequently recover these directions using visual cues (6–8). Because there is no a-priori
42 reason to link these cues in any particular fashion, such transfers require the simultaneous
43 experience of both cues at some point in the past, and involve Hebbian-like plasticity (i.e.,
44 cells that fire together wire together) in a well characterised area called the Central Complex
45 (8, 9).

46 The fascinating aspect of the new study by Solvi et al. (1) is thus not so much about a cross-
47 modality transfer per se, but the idea that such a transfer is achieved through an internal
48 representation of object shapes. This seems at odds with previous work. For instance, flies
49 (10) and bees (11) can learn to visually discriminate two triangles shown side by side, with
50 one pointing up and one pointing down, suggesting – as in the present study – their ability to
51 memorise shapes. However, this apparent ability vanishes if the triangles’ relative positions
52 are slightly shifted vertically so as to align their centres of mass, showing that insects do not
53 build a mental image of shapes, but extract instead a limited number of specific features.

54 Congruently, insects’ visual receptors and neural processing are poorly suited to reconstruct
55 the world’s shapes but remarkably efficient to pick-out task-relevant features (e.g., indicating
56 the presence of flowers in bees, flying targets in predatory insects, or distant trees in fruit
57 flies). Such filtering, so-called ‘matched-filters’, “severely limits the amount of information
58 the brain can pick up from the outside world, but frees the brain from the need to perform
59 more intricate computation to extract the information finally needed for fulfilling a particular
60 task” (12). In sum, insects seem not equipped to build internal reconstructions of the outer
61 world, but are excellent at using ecologically relevant task-related heuristics.

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

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

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

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

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

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

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