Gap affordance judgments in bumblebees: same as humans?

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Abstract: When flying through narrow gaps, bumblebees of different body sizes fly either straightforward or sideways depending on the relation between their wingspan and the width of the gap (Ravi et al., 2020). They thus behave like humans when walking through narrow passages, which raises the question of the mechanisms underlying their own-body perception.

Moving through the environment requires choosing the safest path that ensures the least physical damage to reach the expected place as quickly as possible. In most of the cases, this selection consists in adapting our behavior with respect to the size of the obstacles encountered: bypassing some, jumping others, tilting the head forward to pass under a beam or turning the shoulders when an opening becomes too small. Taking this into account, James Jerome Gibson introduced in the seventies the term "*affordance*", a central concept in his ecological theory of visual perception (Gibson, 1979). Affordances are possibilities for action that depend on both an observer's capabilities and the properties of the environment (Gibson, 1979). This complementarity is well illustrated by the case of humans passing through an opening while walking, which implies making judgments about action capabilities. In this case, one begins to turn the shoulders for an opening that is 1.3 times the width of one's shoulders (Warren & Whang, 1987). This ratio (critical opening width / shoulder width) is invariant in humans, whether we are small or tall, i.e. whether we have small or large shoulders.

A relevant question for the affordance concept is whether it is universal and thus observable in other species beyond humans. Adopting a Gibsonian framework, a recent paper by Ravi et al. (Ravi et al., 2020) has addressed this question in bumblebees and analyzed *whether these insects take into account their own size to adopt the best flight maneuver while passing through a gap*.

Bumblebees navigate large distances and negotiate complex and cluttered environments during their flight maneuvers. Avoiding collisions is thus important to them, as their wings are delicate structures that can be easily damaged. Moreover, they exhibit a particular characteristic that cannot be found in other flying social insects such as honey bees and wasps: individuals within a colony vary significantly in size and interindividual body-mass differences can reach up to a factor of seven. Due this size variation, bumblebees constitute a very interesting model to test how differences in the perception of the own-body size may affect navigation decisions.

The particular behavior that was studied was the flight through a gap in a wall obstructing the passage along a tunnel to which the bees were previously trained. To pass through the gap, the flying bees had to estimate the horizontal extent of the gap to decide whether flying through it required maneuvering or could be straightforward. The results reported show that this decision was mediated by motion cues extracted in flight at the edges of the gap (Ravi et al., 2020).

Bee navigation relies heavily on optic flow (Egelhaaf & Kern, 2002), which is the pattern of apparent motion of objects, surfaces, and edges in a visual scene caused by the relative motion between an observer and a scene. Optic flow allows assessing the distance to objects encountered as objects closer to an observer move faster in the retinal field than distant objects (i.e. motion-parallax), so that approaching a target induces higher optic flow while moving away from it decreases it. Motion cues can be extracted at the edge of objects through parallax and allow evaluating the distance of targets with respect to their background based on differences in their relative retinal speed. Edges are therefore contrasting regions in terms of motion-parallax cues and are privileged by insects to estimate distances and facilitate landing (Egelhaaf & Kern, 2002). In the experiments of Ravi et al. (Ravi et al., 2020), bumblebees facing the edges of the obstructing wall within the tunnel performed consistent peering maneuvers while maintaining the gap in their frontal visual field. In this way, while oscillating in suspended flight in front of the gap edges, they extracted information about the gap extent, which they could then refer to their own size considered from one extended wing to the other extended wing.

Peering movements increased in amplitude in the case of narrow gaps, thus showing that the bees privileged information extraction before engaging in a potential difficult maneuver. Segregating the flight behavior of bees according to their size (i.e. their wingspan) showed that larger bees, whose passing through a narrow gap was more compromised, performed more peering than smaller bees, thus showing that appreciating the difficulty of the maneuver was relative to body size. Yet, the most interesting result was observed when the animal passed through the gap once it had evaluated its extent: when the gap was large, the bees simply flew straightforward; yet, when it was narrow, the bees re-oriented their body axis and flew sideways (i.e. they varied their yaw angle in 90° to pass through the gap). Like humans who rotate their shoulders to avoid frontal collision with edges when passing through a narrow gap, the bees also changed their flight axis and passed laterally, to avoid wing contact with the edges. Differences depending on wingspan were particularly interesting in the case of intermediate-size gaps. For smaller bees, such gaps posed no problem and they flew directly through them; for larger bees, on the contrary, the risk of frontal collision was high so that they passed sideways. This result indicates that the perception of the own-body size relative to the size of the physical aperture determined different strategies when facing the same gap.

In sum, bumblebees behave like humans in front of a challenging, narrow gap. They quickly adapt their flight trajectory to the point that they can even fly entirely sideways when negotiating extremely small openings. As in humans, what determines the strategy adopted is not the absolute size of the opening but its size relative to the bumblebee’s own size, i.e. the ratio between the critical opening and the wingspan, which remains invariant, irrespective of the size of the bumblebees. Are bees cognitively aware of their own size? This question is difficult to answer but the behavioral results indicate that body size is taken into account and determines their flight maneuvers.

In humans, several experiments have shown that the Visual Eye Height (VEH)—the distance in the visual scene from the horizon (corresponding to the observer’s line of gaze) to the ground on which the observer is standing—constitutes an important reference in perceiving the passability of an aperture (Warren & Whang, 1987). VEH is a static information that can be extracted and used even when the head is restrained and under monocular vision. Other sources of information, in particular dynamic ones, could also play a role such as those linked to head sway or stride length during walking. On Earth, VEH can be used as a reference because the observer’s eye height and the object to be perceived (e.g., the edges defining the aperture) share a common surface: the ground. Thus, this information cannot be used in flight so that it would be inaccessible to bumblebees. These insects determined gap size using optic flow, which is also used to estimate distances travelled (Egelhaaf & Kern, 2002). As smaller bees fly faster than larger bees (Crall, Ravi, Mountcastle, & Combes, 2015), the optic flow units used to this end are directly related to body size, so that gap-size information would be equally scaled to body size. In addition, navigation towards and from exploited flowers in a field of bushes and tall grass, provides multiple opportunities to improve progressively body-size scaling via individual experience. Bees perform numerous foraging flights along their live as individual and collective survival depend on these activities. In these flights, cumulative collisions with herbs and leaves – which do not inflict serious damages to the wings – could refine the bees’ own-body perception. Thus, studying bumblebees offers the interesting possibility of discovering the nature of the information allowing these body-scaled actions in suspended flight. Whether humans would use similar information under comparable conditions – in flight or for instance when astronauts move in microgravity conditions –remains to be determined but bumblebees could already give us some clues.

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