

Animal Cognition: The Self-Image of a Bumblebee

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Knowing one's body dimensions is a core aspect of individual experience and self-awareness. A recent study illustrates how bees take into account their own body size both in preparation for and while traversing small gaps.

The door is open just a little and you are in a hurry to get through. Are you small enough to fit? Should you squeeze sideways or can you walk in normally? As we interact with our environment, we take into account our own body size, our reach and our limitations. We first, as toddlers, learn to differentiate our body and its size in relation to our surroundings, and we continue to fine-tune our understanding of our size and shape as we grow¹. The awareness of our body is such an integral part to who we are that some argue it is one of the core components of self-awareness¹. Ravi *et al.*² now provide evidence that bumblebees take into account their individual body size, suggesting they too have some type of awareness of their bodies in relation to the wider world.

Bumblebees are perfect subjects for this question because workers of the same species vary greatly in size³. Their lifestyle as flower-visitors furthermore regularly demands flying through small gaps in dense vegetation. Ravi *et al.*² took advantage of this and presented their foraging bees (*Bombus terrestris*) with a challenge: to reach the outside world from their hive, bees in their study had to traverse a small gap in an obstructing wall. The researchers varied the size of this gap, from 20 mm (smaller than most bees' wingspans) to 60 mm wide (larger than most bees' wingspans), and filmed a large number of approaches and crossings of bees through the gaps with a high-speed camera.

Previous research would suggest that bees should attempt to fly straight through the centre of this gap, using the relative visual motion from their left and right eyes to determine how

best to avoid collisions⁴. This is exactly what bees did when their wingspan was much smaller than the gap width (Figure 1). When the bees' wingspan was larger than the gap, however, flying directly through would risk the bee's wings colliding with the hard edges. This not only can result in a flight crash but can also damage the fragile wings themselves, which can reduce a bee's flight efficiency and lifespan⁵. A bee's wingspan is longer than its body length, and much wider than the body's width in flight. When the gap was narrower or close in width to the bees' wingspans, bees did not attempt to fly straight through. Instead, they re-oriented their bodies and carefully flew sideways through the gap, sometimes even head-butting the edge or guiding their motion with their legs in a seemingly deliberate manner. Interestingly, this reorientation happened consistently as a function of the size of the gap relative to each bee's individual wingspan, rather than to the absolute size of that gap (Figure 1). Humans re-orient in a similar manner, twisting their shoulders once a gap becomes approximately 1.3 times the shoulder width or less⁶.

Ravi *et al.*² also observed that, before attempting to pass through, bees performed side to side scanning (peering) motions, apparently to judge the width of the gap. The initial amplitude for these side-to-side motions is consistent, no matter the individual's size², and very similar for all gap sizes (Figure 1). Bees must perform these peering manoeuvres since unlike animals with widely spaced eyes⁷, bees do not have stereoscopic vision. A bee hovering stationarily in front of a target will not be able to judge the size of this

target or how far away it is from the bee's position. Instead, the bee can use a strategy termed motion parallax^{8,9}. If you look at two objects, one far away and one close up, and move your head side to side, the object far away will appear to move less than the one close to you. Bees use this strategy by performing side to side flight, for example allowing them to distinguish hard-to-detect targets against a background or estimate the distance of objects^{8,10,11}. To gauge the width of a gap, bees here could be comparing the relative visual motion from the left and right edges of the gap during their deliberate physical peering, integrating visual information with their self-generated flight movements^{2,12}. This would allow the bee to judge the relative distances of each edge, and therefore assess the gap width².

Not only did bees perform these peering flights before traversing gaps, narrower gaps elicited more peering than larger ones, and larger bees consistently peered more and for longer than smaller bees. The number of back and forth peering passages and the time spent peering was directly associated with wingspan when the bee approached narrow gaps. Why is this? Irrespective of the bees' size, narrower gaps are likely to be more challenging to cross. More peering is likely to provide the bee with a more precise estimate of the size of that gap, especially if that information is only approximate. That bees with larger wingspans spent longer times peering than smaller bees indicates that even before reaching too-small gaps, these larger bees were more invested in collecting precise information. This is very similar to what



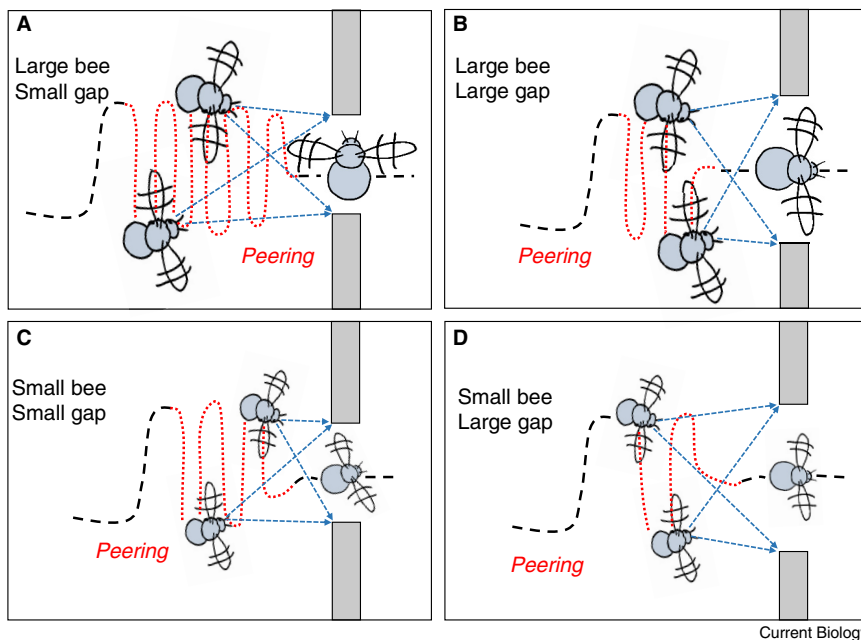


Figure 1. Bees' flight behaviour when steering through gaps.

When approaching a gap, bees perform peering behaviour, in red. This allows them to view the gap from several perspectives (blue arrows), allowing them to gauge the gap's width. Large bees (A) peer more than small bees (C) approaching small gaps. When the gap is smaller or close to bees' wingspan, bees re-orient their body to avoid collisions (A,C versus B,D).

is observed in dogs¹³, and suggests that bees take into account their own size before attempting to navigate through small spaces.

How do insects know, or learn, their own body dimensions? Walking locusts and grasshoppers perform similar peering motions before crossing gaps in their path¹⁴, and their knowledge of their own body size seems to be dependent on experience of a complex environment¹⁵. A recent study by Krause *et al.*¹⁶ explored this question in detail with fruit flies. The researchers controlled the visual experience of flies and determined that their memory of body size relied on visual feedback from their surroundings. Specifically, visual experience paired with walking was necessary and sufficient for the fruit flies to form a long-lasting memory of their body size. The team assessed the willingness of individuals to walk across gaps of varying widths, where larger flies tended to cross or attempt to cross larger gaps than their smaller conspecifics. Krause *et al.*¹⁶ state that flies are able to tell their size from their vision while walking because their step length is correlated with their leg length

and body size, but in flight bees do not have that kind of easily-scaled information. How bees acquire information about their body dimensions remains unknown. It is possible that some such information is acquired in a tactile manner while they spend the first days after emergence from the pupa in the darkness of the hive, and that such information is later accessible in the visual modality¹⁷. It is also possible that the information is only acquired once a bee starts its flight activities, but learning body dimensions in this life stage through trial-and-error via collisions with obstacles in flight is likely to be inefficient and hazardous.

Being able to account for their own body size is clearly an advantage for any animal moving through habitats rich in obstacles. Knowing one's own body and its dimensions is often hailed as a component of self-awareness in both humans and other animals^{1,18}. Although it is still not fully understood, body awareness is linked to other emerging self-aware behaviours in children (referring to themselves in speech and recognising themselves visually)¹.

Exploring how bees acquire and perceive information about their own individual bodies could provide a new angle in the quest for exploring the possibility of conscious experience in insects^{19,20}.

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Cell Biology: Resolving How DNA Is Damaged during 3D Migration

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Cells migrating through confined spaces are subject to mechanical stresses that can deform the nucleus and even rupture the nuclear envelope. A new study reveals that nuclear deformation is sufficient to trigger double-strand breaks at sites of active DNA replication.

Historically, cell motility investigations focused on the molecular machinery and membrane dynamics at the leading and trailing edges of migrating cells to understand how cells move across rigid surfaces¹. In three-dimensional (3D) matrix environments, however, such as those modeled by microfluidic devices and type I collagen gels, this focus has shifted inwards and revealed the nucleus to be a conductor of the molecular symphony regulating and driving 3D cell movement².

While the cell's ability to move the large, bulky nucleus through tight spaces can dictate the speed of 3D cell migration^{3,4}, the nucleus is not inert cargo. The nucleus is actually required for cells to migrate in 3D environments⁵ and can transform the mechanical force required for 3D migration⁶ into hydraulic pressure to push the leading edge forward⁷. The nucleus also functions as a mechanosensor, able to find the path of least resistance for migrating dendritic cells⁸, as well as activate actomyosin contractility in response to confinement to help push the nucleus through particularly narrow openings^{9,10}. Thus,

the nucleus sits at the center of many of the internal and external forces that characterize 3D cell motility. As a result of these substantial forces, the nucleus experiences significant mechanical stresses that can deform and elongate the nucleus, even leading to the periodic rupture and subsequent repair of the nuclear envelope^{11–13}. Critically, the deformation of the nucleus and the rupture of the nuclear envelope can both lead to DNA damage and genomic instability^{11,14}.

In a new paper published in this issue of *Current Biology*, Shah *et al.*¹⁵ sought to understand the mechanism by which DNA is damaged when the nucleus deforms without rupturing. They predicted that this mechanism is distinct from how DNA damage occurs following rupture of the nuclear envelope based on the following rationale. Once the nuclear envelope ruptures, the nucleoplasm is no longer sequestered from the rest of the cell. This allows nuclear-localized DNA repair factors to escape into the cytoplasm and exposes the DNA to cytoplasmic nucleases, resulting in DNA damage¹⁴, a mechanism unlikely to occur when the

nuclear envelope remains intact. By carefully comparing multiple cell lines, Shah *et al.*¹⁵ now report that actively replicating cells can sustain damage to their DNA following the deformation of intact nuclei.

The authors examined a number of cell lines to discover the distinct mechanisms by which DNA can become damaged during 3D migration (Figure 1). The cells were transfected with tumor suppressor p53-binding protein 1–mCherry (53BP1–mCherry) to detect DNA double-strand breaks (DSBs) and a nuclear localization sequence tagged to GFP (NLS–GFP) to monitor nuclear envelope integrity. By performing live cell imaging in microfluidic devices containing either narrow ($\leq 10 \mu\text{m}^2$; damage-inducing) or wide ($75 \mu\text{m}^2$; no damage) constrictions, they could monitor the extent of DNA damage, nuclear deformation, and rupture in single cells as they moved through the device. The authors discovered two distinct modes of DNA damage during confined migration that reproducibly occurred in specific cell types (Figure 1). While nuclear rupture predominated in

