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The neuroecology of bee flight behaviours

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By combining functional, ecological and evolutionary perspectives, neuroecology can provide key insights into understanding how behaviour and the underlying sensory and neural processes are shaped by ecology and evolutionary history. Bees are an ideal system for neuroecological studies because they represent a numerous and diverse insect group that inhabit a broad range of environments. Flight is central to the evolutionary success of bees and is the key to their survival and fitness but this review of recent work on fundamental flight behaviours in different species – landing, collision avoidance and speed control – reveals striking differences. We discuss the potential ecological and evolutionary drivers behind this variation but argue that to understand their adaptive value future work should include multidisciplinary approaches that integrate neuroscience, ecology, phylogeny and behaviour.

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Introduction

Neuroecology focusses on studying variations in behaviour, cognition and neural processes in order to understand how natural selection acts on brains [1]. One advantage of neuroecology is that it combines functional, ecological and evolutionary perspectives to robustly answer a question, providing a deeper understanding of animal behaviour and the factors that shape it. The extraordinary diversity of bee species – members of the hymenopteran clade Anthophila [2] – provides neuroecology with an ideal animal system for understanding how brains and complex behaviours are shaped by ecology and evolutionary history. Many bee species live in elaborate societies with thousands of individuals: Some are capable of navigating over tens of kilometres [3], of locating miniscule flowers in dense dark forests [4] and of communicating information about food sources through dance language [5]. This heterogeneity

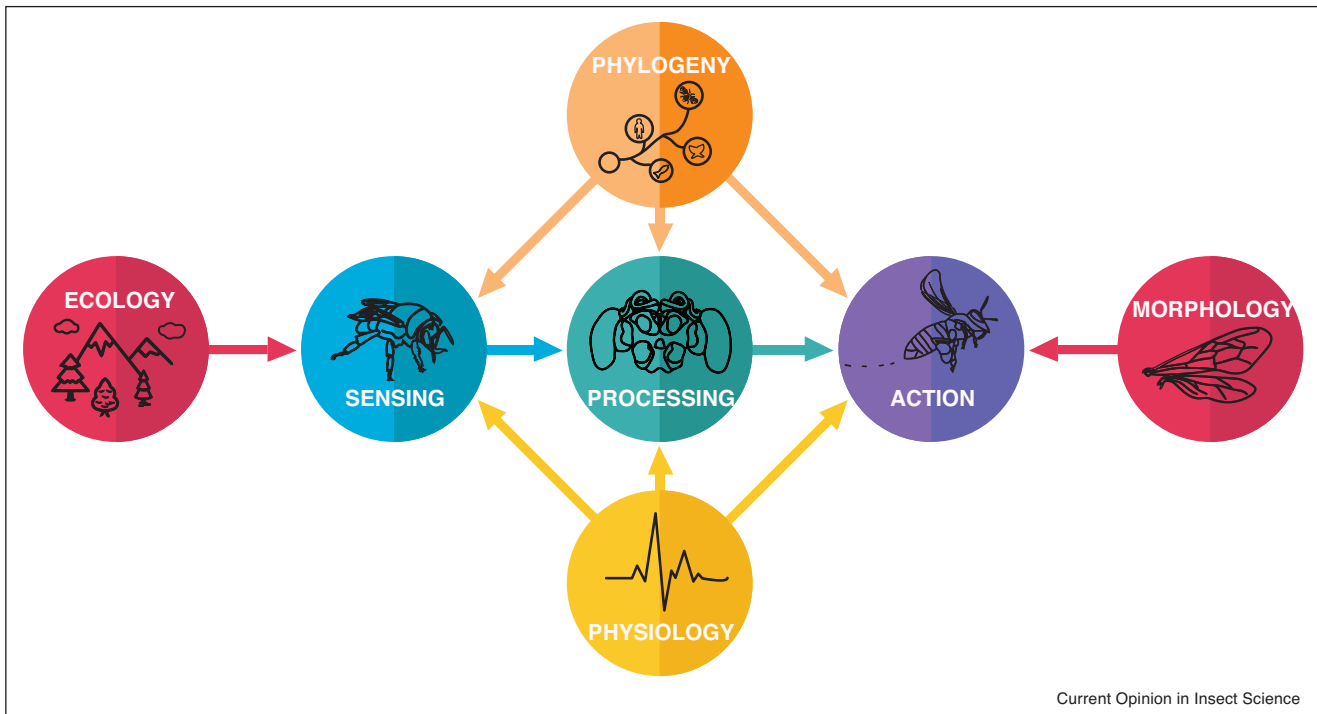
relates, at least in part, to their capacity to adapt to new ecological constraints, which is undoubtedly linked to their genetic, physiological, morphological and behavioural plasticity: Bees inhabit a variety of biomes across the globe and thrive in some of the most challenging environments on Earth, from the oxygen-poor altitudes of the Himalayas, to the wind-swept tundra of the Arctic and the dense tropical rainforest of the Amazon [6]. Nonetheless, we still understand little about how the miniature brains of bees (960 000 neurons in a 1 mm³ brain [7]) acquire and process the sensory information necessary to coordinate their behaviour. This is, in part, due to a lack of understanding of how ecology and other factors such as phylogeny, morphology and physiology shape the underlying sensory and neural processes (Figure 1). The goal of this review is to argue for the value of taking a neuroecological approach when studying bee behaviour. We use studies of flight control to illustrate the importance of considering the broader context in which bees operate in order to better understand the adaptive value of their behaviour.

Common to all bee species is their ability to fly: Whether locating and moving between food resources, navigating home or searching for a mate, many important behaviours are carried out on the wing. Getting airborne, avoiding obstacles and making a safe landing in an ever-changing three-dimensional environment requires a brain that can rapidly and reliably process information about how the animal is moving through its environment, particularly with reference to the ground and other nearby obstacles. Early investigations into the neural basis of flight control using the European honeybee *Apis mellifera* discovered that they rely primarily on the pattern of motion generated on the retina (known as optic flow) as they move through the world [8]. Since this pioneering work, other bee species from a diverse range of lineages and habitats have also been shown to use optic flow for flight control – the forest-dwelling honeybee *Apis cerana* [9••], the open grassland-dwelling bumblebees *Bombus terrestris* [10–12] and *Bombus impatiens* [13] and the tropical rainforest-dwelling nocturnal sweat bee *Megalopta genalis* [14]. Below, we present the findings of such investigations and how differences in the sensory and neural mechanisms underlie flight behaviours in bees.

Landing

While all aspects of flight control present enormous processing challenges to the bee brain, landing is arguably one of the most difficult to orchestrate. To land successfully, a bee must identify a suitable target, such as a hive entrance or a flower, and then simultaneously regulate its position and speed before extending its legs in time to

Figure 1



An overview of the factors that affect bee flight behaviour and a sketch of how their interactions might shape it. Currently, little is known about these relationships, but important insights could be gained through neuroecological approaches. Such insights could aid in the better understanding of the neural and sensory processes underlying behaviour and how these are shaped by phylogeny and ecology. Such information could be valuable for the development of effective bee conservation practices.

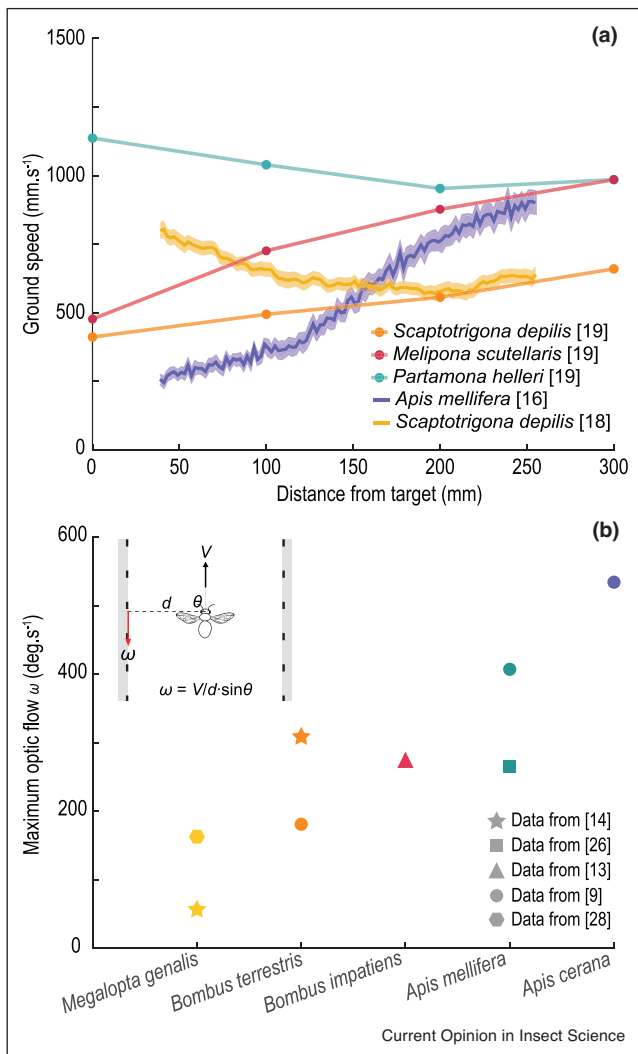
ensure a secure contact. This is similar to what pilots of aircraft must achieve to land safely — forward speed and altitude must be reduced before extending the wheels before contact with the ground, all while taking into account wind speed and direction. Studies on landing in *A. mellifera* have shown that they reduce their speed when approaching a surface by holding some value of the magnitude of optic flow constant; such that flight speed decreases to near-zero when contact with the surface is made (Figure 2a, purple line) [15,16]. This elegant strategy, similar to the one used by human pilots [17], makes it tempting to think that it might be universal among bees as well as other flying animals. However, Tichit *et al.* [18**] recently found that the stingless bee *Scaptotrigona depilis* accelerates when landing but they are nonetheless capable of performing controlled touchdowns with well-timed leg extensions (Figure 2a, yellow line). In their comparison of landing in stingless bees, Shackleton *et al.* [19**] also reported high touchdown speeds in *S. depilis* and *Melipona scutellaris* (Figure 2a, orange and red lines, respectively). More remarkably, they found that *Partamona helleri* consistently increased their speed before crashing kamikaze-style into their nest (Figure 2a, green line; see the supplementary material of [19**] for video examples). While the honeybee's strategy of reducing

speed to near-zero when landing makes intuitive sense from a safety perspective this approach is, rather surprisingly, not employed by all bee species. The accelerated landing strategy of the stingless bees appears to be optimised for their specific ecological constraints because it would minimise the risk of predation at the hive [18**,19**,20] and increase foraging efficiency by reducing traffic congestion at their narrow hive entrances [18**].

Collision avoidance

Avoiding collisions is essential for efficient flight but non-trivial for bees whose visual system lacks the capacity to measure depth from stereopsis [21]. The most efficient way for a flying animal to avoid collisions is to maximise the distance to nearby obstacles. Evidence that bees do this first came from the observation that, when flying between two obstacles — such as when flying between the walls of a narrow tunnel — *A. mellifera* would keep an equal distance between them (although see Ref. [22] for a case in which they instead follow walls). Srinivasan *et al.* [23] found that the bees were maximising the distance to each wall by balancing the rate of optic flow perceived in each eye. Since this study, several other bee species have been found to use a similar strategy, including the Asian honeybee *A. cerana* [9**] and the bumblebees *B. terrestris*

Figure 2



Comparisons of landing and preferred rate of optic flow across bee species. **(a)** The speed of different bee species as they approach a landing target (data taken from the cited references). Note that for *Apis mellifera*, the landing target was a food source, whereas for the other species it was their nest entrance. For *A. mellifera* ($n = 26$) and *Scaptotrigona depilis* ($n = 52$), data for each flight was interpolated at 2 mm intervals and then averaged. The shaded area represents the standard error of the mean. For details on the remaining data, see Ref. [19*]. **(b)** The rate of optic flow ω perceived laterally from the direction of flight ($\theta = 90^\circ$) along an experimental tunnel for different bee species (data calculated from cited references). The inset illustrates the calculation of optic flow and the general experimental context, with a bee flying between two walls (grey lines) displaying a high contrast pattern (black dashed lines). The maximum rate of optic flow ω in degrees was calculated from the forward speed V , the distance to the tunnel wall with a pattern d , according to: $V/d \cdot \sin\theta \cdot 180/\pi$ (for further details of the calculation see Refs. [25,26]).

[12] and *B. impatiens* [13]. However, a recent study by Chakravarthi *et al.* [9**] highlighted clear differences in the underlying control mechanisms of this behaviour in *A. mellifera*, *A. cerana* and *B. terrestris*. When flying along a

narrow tunnel with asymmetrical optic flow (i.e. the tunnel contains one ‘textured’ wall that displays vertical contrast cues that provide front-to-back motion and one ‘featureless’ wall where these cues are minimised), *B. terrestris* consistently flew closer to the featureless wall than the honeybees, even when the spatial frequency and contrast of the patterns on the textured wall was altered. More extreme differences in collision avoidance behaviour were reported in a comparative study between the nocturnal sweat bee *M. genalis* and *B. terrestris* [14]. When presented with asymmetrical optic flow, *B. terrestris* flew closer to the featureless wall (consistent with an optic flow balancing strategy), whereas *M. genalis* continued to fly along the midline, as they did when both walls were textured. Why bumblebees respond more strongly to optic flow asymmetry than honeybees and why *M. genalis* does not appear to respond at all is unclear. The answers potentially lie in the large ecological and phylogenetic differences between the species: For example, *A. mellifera* and *A. cerana* are also the most similar in ecology and phylogeny and they have the most similar response to asymmetric optic flow. The nocturnal *M. genalis* belongs to the Halictidae family and has visual adaptations that render them 27 times more sensitive to light than the other species [24], while the honeybees and bumblebee belong to the Apidae family and typically do not forage after the sun sets. Perhaps *M. genalis*’ visual sensitivity trade-off prevents them from efficiently using optic flow for collision avoidance. They may instead use brightness cues, as another rainforest bee *Euglossa imperialis* does [25], to detect and negotiate spaces between obstacles between the densely packed vegetation. Habitat and diel activity differences as well as other morphological and physiological factors are likely to shape the differences in the behaviour between bee species, but we currently do not have sufficient data to explore this in detail.

Flight speed

Differences in how bee species use visual information to control their flight can also be seen when comparing their flight speed. Chakravarthi *et al.* [9**] found that, in the same 30 cm wide tunnel with asymmetric optic flow cues, different species flew at different speeds, with *A. cerana* flying at $\sim 150 \text{ cm s}^{-1}$, *A. mellifera* at $\sim 100 \text{ cm s}^{-1}$ and *B. terrestris* at $\sim 60 \text{ cm s}^{-1}$. Similarly, Baird *et al.* [14] found that *M. genalis* flew 4 times slower ($\sim 15 \text{ cm s}^{-1}$) than *B. terrestris* ($\sim 60 \text{ cm s}^{-1}$) in the same 14 cm wide tunnel with symmetric optic flow cues. Flight speed has previously been shown to be regulated using optic flow in both *A. mellifera* and *B. terrestris* (the only two species in which this has been studied to date [10,26,27*]). The flight speed differences observed in Chakravarthi *et al.* [9**] and in Baird *et al.* [14] therefore appear to reflect variation in how these species use and/or measure optic flow for flight control. This is supported by a comparison of the maximum rate of optic flow experienced by different bee species when flying along experimental tunnels in

different studies (Figure 2b). Further evidence for differences in how optic flow information is processed across bee species comes from a comparative study into the effect of light intensity on flight control in *M. genalis* and *B. terrestris* [28]. As light intensity decreased, *B. terrestris* flew slower — a response that is associated with an increase in the integration time of their photoreceptors [29]. In contrast, flight speed in *M. genalis* was unaffected by large changes in light intensity, suggesting that they do not use temporal integration to improve sensitivity in dim light and that they may have increased their reliance on other sensory cues, such as mechanosensory information about airspeed, to control their flight [28].

Although we do not yet know exactly how different factors drive the differences in flight speed between bee species, it is possible that these may be related to variation in the distances they typically fly when foraging (i.e. their foraging range). Beutler [30] proposed that the largest energetic cost to flying long distances for bees is the time spent not collecting food and that the cost of an increased foraging range can be offset by increased flight speed. If this is indeed the case, it follows that the relative differences in flight speed observed between species may also reflect differences in the distance over which they typically fly and forage from the nest. The foraging range of a species is notoriously difficult to determine. However, relative differences in the estimates of the foraging ranges of the species discussed here [31–34] are consistent with estimates of their relative differences in their cruising speed [9**,14,12,26] (Table 1). It is also possible that other elements of flight control are driven by the typical flight range and habitat of a species. Long flights through dim, cluttered habitats would require much greater accuracy in collision avoidance and speed control than shorter flights through bright, open environments. This may explain why the nocturnal rainforest-dwelling *M. genalis* have the slowest relative flight speed among the

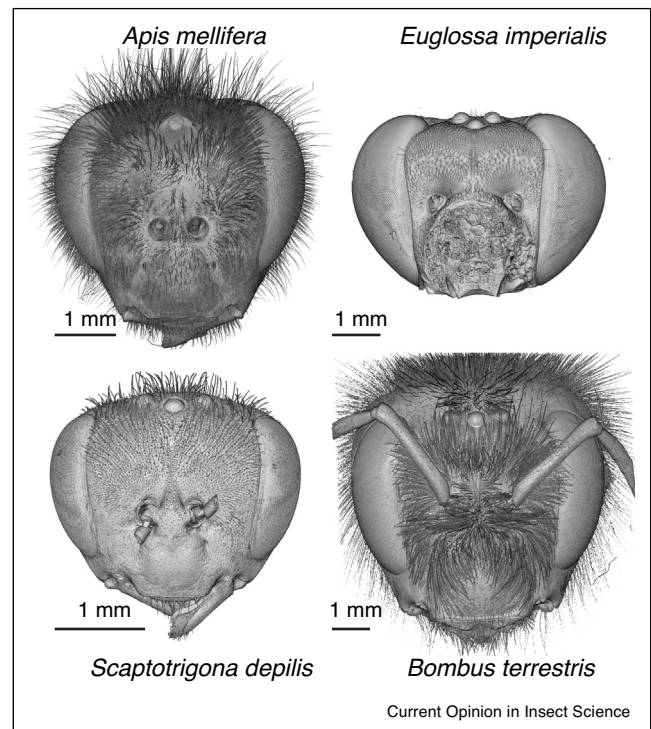
Table 1

Relationship between foraging distance and flight speed in different bee species

Species	Estimated foraging distance (m)	Estimated maximum optic flow (deg s ⁻¹)	Estimated cruising flight speed ^a (m s ⁻¹)
<i>Megalopta genalis</i>	240 [31]	58 [14]	1
<i>Bombus terrestris</i>	630 [32]	181 [12]	3.2
<i>Apis mellifera</i>	1570 [33]	265 [26]	4.6
<i>Apis cerana</i>	650 [34]	522 [9**]	9.1

^a Estimated from the maximum optic flow for a 1 m distance to nearby objects calculated from the flight speed and distance to the tunnel walls in each experiment given in the third column. For further details on the calculation, see Refs. [25,26].

Figure 3



X-ray microtomographic images (for details of the method see Ref. [38**]) of bee heads revealing the diversity of visual morphology (compound eye and ocelli) across species. Each image is a volume rendering (orthographic view) of the dried head of a male (*Euglossa imperialis*) or a female worker (*Apis mellifera*, *Scaptotrigona depilis*, *Bombus terrestris*). Note that the heads have been scaled to have the same width so that each scale bar is individual-specific and that the antennae were removed in all individuals apart from *B. terrestris*.

species tested [14,28]. Similarly, how a species measures visual information for flight control is also likely to be shaped by the type and distribution of available flowers, competition and predation [35] as well as to morphological constraints such as body size [36] (which will also affect brain size) and wing shape [37].

Vision and flight

Variation in the strategies underlying landing, collision avoidance and speed control highlighted here show that bee species acquire and process visual information in multiple ways. While we currently lack information on the relationship between visual features and flight control, previous work on bee vision and on behaviours carried out in flight, such as foraging and mating, suggest that they are strongly associated. For example, in *B. terrestris*, smaller body size has been related not only to reduced eye volume, spatial resolution, sensitivity [38**] and brain volume [39] but also to a reduced foraging rate compared to larger individuals [40]. In different bumblebee species, the mating strategy – whether they perch and

wait for females or patrol scent-marked territories – has been correlated with differences in male eye morphology [41]. Further support for the importance of ecology and phylogeny in shaping sensory systems and flight behaviour comes from studies of the morphology and physiology of bee eyes. Comparisons of visual resolution and sensitivity across bumblebees [42] honeybees [43], and the Apidae family [44*] reveal a great diversity that correlates with their visual habitat and the light-intensity range over which a species is normally active. How the diversity of eye morphology (Figure 3) and physiology across bee species has evolved and how this morphological variability affects flight behaviour are open questions waiting to be answered by neuroecological approaches.

Conclusion

While studies on vision and flight control in bees provide compelling evidence for the tight association between sensory systems, ecology, phylogeny and behaviour (Figure 1), our understanding of the relationship between these factors is currently limited. Insights into the adaptive value of complex behaviour in bees could be achieved with a more integrative neuroecological approach that combines neurobiological studies of bee brains and sensory systems with descriptions of species-specific behaviour, ecology and phylogeny. This can be best achieved through comparative approaches at both the species and individual level that utilise and integrate the methods and expertise of neurobiologists, ethologists and ecologists. The knowledge gained from such partnerships will also play an important role in conservation efforts by providing critical insights into if and how the neural and sensory world of different bee species can explain their vulnerability to rapid environmental change and actions that can be taken to prevent further species declines.

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Conflict of interest statement

Nothing declared.

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