

## REVIEW

# The brain behind straight-line orientation in dung beetles

Basil el Jundi<sup>1,\*</sup>, Emily Baird<sup>2</sup>, Marcus J. Byrne<sup>3</sup> and Marie Dacke<sup>3,4</sup>

## ABSTRACT

For many insects, celestial compass cues play an important role in keeping track of their directional headings. One well-investigated group of celestial orientating insects are the African ball-rolling dung beetles. After finding a dung pile, these insects detach a piece, form it into a ball and roll it away along a straight path while facing backwards. A brain region, termed the central complex, acts as an internal compass that constantly updates the ball-rolling dung beetle about its heading. In this review, we give insights into the compass network behind straight-line orientation in dung beetles and place it in the context of the orientation mechanisms and neural networks of other insects. We find that the neuronal network behind straight-line orientation in dung beetles has strong similarities to the ones described in path-integrating and migrating insects, with the central complex being the key control point for this behavior. We conclude that, despite substantial differences in behavior and navigational challenges, dung beetles encode compass information in a similar way to other insects.

**KEY WORDS:** *Scarabaeus*, Insect, Polarized light, Navigation, Vision, Sun compass

## Introduction

While monarch butterflies and moths make annual migrations over large distances (Reppert et al., 2010; Warrant et al., 2016) and desert ants and bees navigate thousands of body lengths back to their nests (Giurfa and Capaldi, 1999; Wehner, 2003; Collett and Collett, 2000), dung beetles simply orient towards an unknown goal in the savanna. These ball-rolling insects also traverse their world in reverse: moving backwards, away from a defined point in space with the primary aim of avoiding their foraging conspecifics. The journeys of ball-rolling beetles further differ from those of other navigating insects in that they perform their entire journey along a single bearing. Here, we review the dung beetle's orientation strategy and its underlying neuronal network and place it in context through comparisons with the guidance strategies employed by other insects.

After forming its ball at a dung pile, a dung beetle quickly rolls it away by pushing the ball backwards with its head down along a straight-line path (Dacke et al., 2003a, 2011; Byrne et al., 2003; Dacke, 2014; el Jundi et al., 2014b; Smolka et al., 2016; Fig. 1). This makes its exit as swift and as efficient as possible. To keep a constant bearing, the beetle uses cues related to the sun, the moon

and the stars (Byrne et al., 2003; Dacke et al., 2003b, 2004, 2013a, 2014; Foster et al., 2017; el Jundi et al., 2014b, 2015a) (Fig. 1). Even though under certain circumstances (largely in response to artificial lights), dung beetles show a tendency to roll towards a light stimulus (Smolka et al., 2016) – a behavior that could be interpreted as a positive phototaxis – the beetles usually use the sky to exhibit menotactic orientation, or compass orientation. This means that the beetles, similar to flies (Warren et al., 2018; Giraldo et al., 2018), desert locusts (Mappes and Homberg, 2004), ants (Collett and Collett, 2000) and monarch butterflies (Merlin et al., 2012), are able to maintain any kind of bearing relative to the celestial cues (Fig. 2).

The wide range of celestial input – ultimately processed at the very center of the brain – effectively guides the beetle around bushes, grass and other obstacles until a suitable place to bury and consume the ball is encountered. For the beetles, each foraging event is a unique, one-way trip, through novel terrain that they have never seen before and might never see again. It should therefore not come as a surprise that ball-rolling dung beetles eschew landmarks as orientation cues and exclusively orient to the compass cues in the sky (Dacke et al., 2013b). Prior to rolling, diurnal dung beetles typically climb up onto their ball and perform a rotation. This relatively stereotypical rotation behavior is called a dance and has been proposed to facilitate the acquisition of celestial compass cues (Baird et al., 2012; el Jundi et al., 2016; Dacke and el Jundi, 2018).

Compass cues found in the daytime sky all originate from the sun. Apart from the sun itself, these include: a circular pattern of polarized light centered around the sun, an intensity gradient, and a spectral gradient created by the ratio between longer and shorter wavelengths between the sun and the anti-sun hemispheres (Coulson, 1988; Coemans et al., 1994; el Jundi et al., 2014b). Therefore, when the sun is covered by clouds, it is still possible – at least theoretically – to extrapolate the sun's position from these other cues. Do dung beetles, and insects in general, make use of this hardwired arrangement of celestial compass cues?

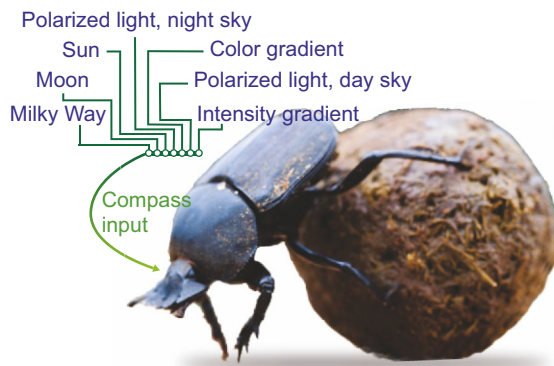
## Strategies for celestial cue integration

Recordings from the locust brain have described neurons with large receptive fields that are sensitive to polarization angles arranged around a 'point of gravity' (Bech et al., 2014). This undoubtedly allows the animal to identify the position of the sun from the polarization pattern. The same seems to hold true for *Cataglyphis fortis* ants, which readily switch from a sun to a polarization compass (Lebhardt and Ronacher, 2015). In addition, neurons in the locust brain give their greatest response in almost opposing directions, depending on whether they are stimulated with green light (relatively richer in the sun hemisphere) or UV light (relatively richer in the anti-sun hemisphere) (Pfeiffer and Homberg, 2007; Kinoshita et al., 2007). This matched filter at the neural level is perfectly suited for encoding the spectral gradient of the sky (Pfeiffer and Homberg, 2007). Similarly, bees interpret a green light spot as the sun direction during their dances, while a UV light spot is taken as a direction anywhere in the anti-sun hemisphere (Edrich et al., 1979; Brines and Gould, 1979; Rossel and Wehner, 1984).

<sup>1</sup>University of Würzburg, Biocenter, Zoology II, Emmy-Noether Group, 97074 Würzburg, Germany. <sup>2</sup>Stockholm University, Faculty of Science, Department of Zoology, Division of Functional Morphology, 10691 Stockholm, Sweden. <sup>3</sup>University of the Witwatersrand, School of Animal, Plant and Environmental Sciences, Wits 2050, South Africa. <sup>4</sup>Lund University, Department of Biology, Lund Vision Group, 22362 Lund, Sweden.

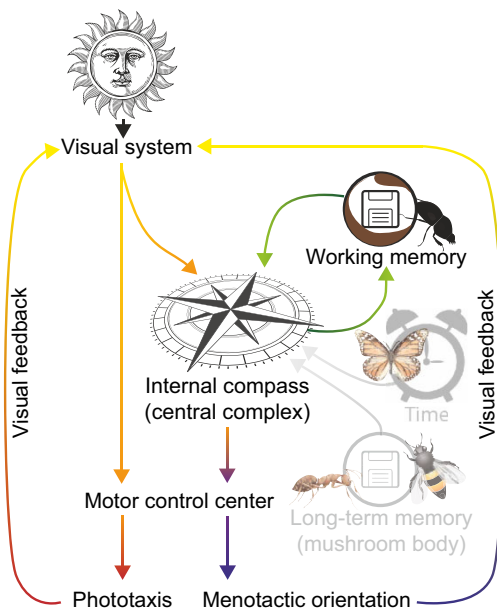
\*Author for correspondence (basil.el-jundi@uni-wuerzburg.de)

© B.e.J., 0000-0002-4539-6681; E.B., 0000-0003-3625-3897; M.J.B., 0000-0002-5155-2599; M.D., 0000-0001-6444-7483



**Fig. 1. Celestial compass cues used by dung beetles during straight-line orientation.** A South African dung beetle (*Scarabaeus lamarcki*) rolling a dung ball. Dung beetles are able to use a variety of celestial compass cues, such as polarized skylight, the sun/moon, light intensity and spectral cues, and even the stars for orientation.

Surprisingly, ball-rolling dung beetles ignore the spectral content of a single light stimulus and rather treat a green or UV light spot as the ‘sun’. Moreover, they are not able to directly transfer directional information from the sun to a polarization stimulus (el Jundi et al., 2016). Thus, dung beetles seem to lack any mechanisms that allow them to infer the position of one celestial cue from another. Instead, they form a short-term memory of the cues available in the sky in which different celestial cues are integrated and hierarchically weighted – a celestial snapshot – that is then used as template for



**Fig. 2. Celestial compass mechanisms and where they are encoded in the brain.** Visual signals can be used to control phototactic or menotactic orientation behavior. Although the central complex acts as the internal compass for menotactic behaviors, phototactic behavior driven by achromatic information could be processed without the use of such a control center. For many menotactic behaviors, such as the straight-line orientation behavior of dung beetles, a short-term memory of the heading direction needs to be stored somewhere in the brain. Several other insect species, such as the monarch butterfly, can maintain the same geographical heading for an entire day. For this, time-of-day information from an internal clock needs to be fed into the compass network. Homing insects, such as bees and ants, employ a long-term memory for visual landmarks or for the solar ephemeris to find their way home. This memory is most likely stored in the mushroom bodies.

maintaining a constant bearing (el Jundi et al., 2015b, 2016; Dacke and el Jundi, 2018). This celestial snapshot is taken during the dance (el Jundi et al., 2016), where the rotations about the vertical axis on top of the ball might be used to simultaneously scan and compare the visible celestial cues in each direction and to create a memory of neural activity patterns at different body orientations. Exactly how the dung beetle’s dance is encoded and memorized in the beetle brain is one of the most intriguing unanswered questions within this model system.

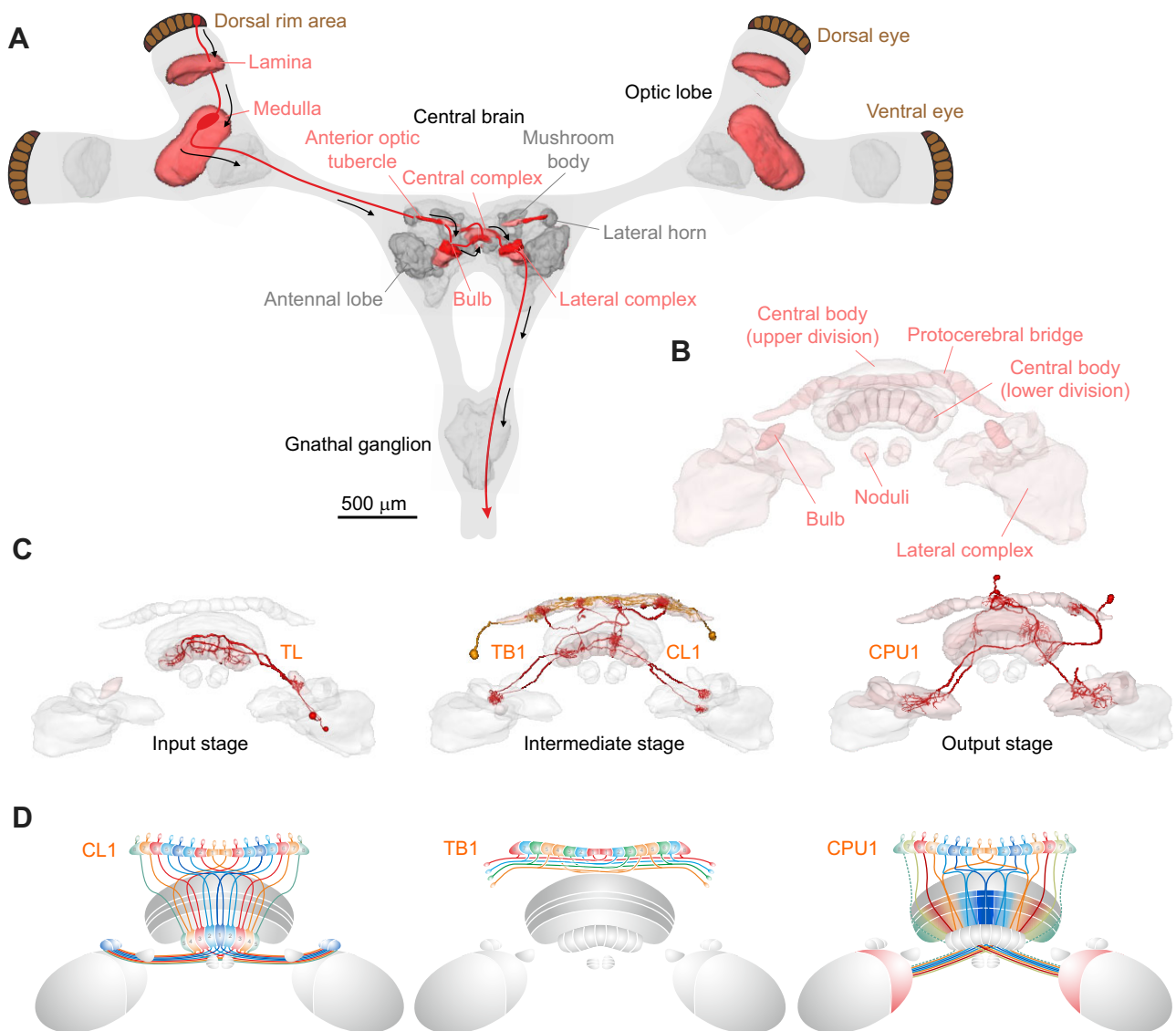
**The neural substrate of compass orientation**

The anatomy of the dung beetle brain is similar to that of all insect brains, which are built on the same generic neuroarchitecture (Strausfeld, 1976; Ito et al., 2014). Generally speaking, olfactory information, which is used by the beetles to locate the dung pat (Tribe and Burger, 2011), is mainly processed by the antennal lobes, the mushroom bodies and the lateral horns (Immonen et al., 2017). The celestial cues that help guide the beetle away from the dung pat are mainly processed by a different set of brain regions: the optic lobes, the anterior optic tubercles, the lateral complexes and the central complex (Immonen et al., 2017; el Jundi et al., 2018).

Like all insects tested so far (apart from cockroaches), dung beetles possess a specialized region in their eyes, called the dorsal rim area (DRA) (Dacke et al., 2002, 2003b, 2011; Labhart and Meyer, 1999; Homberg and Paech, 2002). This can be used as a starting point to follow its associated neurons back into the brain areas involved in the processing of the celestial polarization pattern (Fig. 3A; for other insects, see Homberg, 2004; Pfeiffer and Kinoshita, 2012; Zeller et al., 2015; el Jundi et al., 2014a). The first integration center for polarized light in the brain of the beetles is the lamina (Immonen et al., 2017) (Fig. 3A). As in several other insect species, such as locusts and bees, the dung beetle DRA photoreceptors not only project to the lamina, but also to a distinct area of the medulla [dorsal rim area of the medulla (DRAME)] in the optic lobes (Homberg and Paech, 2002; Schmeling et al., 2015; Pfeiffer and Kinoshita, 2012; Zeller et al., 2015; Immonen et al., 2017). In dung beetles, as in flies (Fortini and Rubin, 1991), the DRAME cannot be separated morphologically from the rest of the medulla. What this difference signifies is not known.

From the medulla, a tract of specific neurons, called transmedulla or line tangential neurons, transmit information to the central brain; specifically, to the beetle’s lower unit complex of the anterior optic tubercle (Immonen et al., 2017). The neurons of this tract show a notable similarity to the fibers of the transmedulla neurons presented in locusts and bees (Homberg et al., 2003; Pfeiffer and Kinoshita, 2012). They not only arborize in the DRAME, where they receive polarization information, but additionally branch through a layer of the medulla, where they receive unpolarized light input from the main retina. This makes transmedulla neurons perfectly suited for combining polarized light and sun direction information before being processed in the central brain (el Jundi et al., 2011). Interestingly, in dung beetles, the transmedulla neurons branch in a layer of the dorsal region of the medulla (Immonen et al., 2017), suggesting that sky compass information is only received from the dorsal pair of eyes (many dung beetles have four eyes, two dorsal and two ventral, separated by the canthus). This is consistent with behavioral experiments, which show that if the dorsal visual field is obscured by a miniature cap, dung beetles cannot move in a straight line (Byrne and Dacke, 2011; Dacke et al., 2013a).

From the anterior optic tubercle, information is sent via tubercle-to-bulb neurons to the ipsilateral bulb of the lateral complex (el Jundi et al., 2018). These neurons have also been described in a variety of



**Fig. 3. The sky compass network in the dung beetle brain.** (A) Frontal view of a dung beetle brain. Celestial compass information, such as polarized light, is encoded in the optic lobe, the anterior optic tubercle, the bulb and the central complex (red pathway and red brain areas). After being processed in the central complex, the information is transferred to descending neurons in the motor control center in the thoracic ganglia (red arrow). (B) The neuroanatomy of the dung beetle's central complex. This brain region consists of four brain areas (protocerebral bridge, upper and lower division of the central body, and noduli) which can further be divided into slices (protocerebral bridge and central body) and layers (central body and noduli). The central complex network is tightly associated with the lateral complex, which consists of the subunits of the lateral accessory lobe, bulb and gall (not indicated here). (C) Three-dimensional reconstruction of different neurons warped into the same 3D model of the central complex. Whereas TL neurons (left) form the input stage of the sky compass information, CL1 and TB1 cells (middle) represent an intermediate processing stage. CPU1 neurons (right) provide the main output pathway of the central complex to the lateral complex. TB1 neurons interconnect different slices of the protocerebral bridge, whereas CL1 and CPU1 neurons interconnect slices of the protocerebral bridge with the lower (CL1) or the upper (CPU1) division of the central body. (D) Schematic drawings of the regular connectivity pattern of CL1 (left), TB1 (middle) and CPU1 (right) neurons in the dung beetle central complex. B, C and D are adapted from el Jundi et al. (2018).

insects, including fruit flies (Omoto et al., 2017), monarch butterflies (Heinze and Reppert, 2011), desert locusts (Pfeiffer et al., 2005; el Jundi and Homberg, 2012) and honey bees (Zeller et al., 2015), and form large microglomerular complexes in the ipsilateral bulbs (Träger et al., 2008; Heinze et al., 2013; Seelig and Jayaraman, 2013; Held et al., 2016; Schmitt et al., 2016; el Jundi et al., 2018). The input neurons of the dung beetle's central complex, termed TL neurons (in flies termed ring neurons; Hanesch et al., 1989), then transfer information from the bulbs to the lower division of the central body of the central complex. The sky-compass network of the dung beetles, from the eyes to the central complex, shows striking similarities to the ones described in other insects (Homberg et al., 2011; Pfeiffer and

Kinoshita, 2012; Zeller et al., 2015) and suggests that traveling insects rely on the same basic neural networks for straight-line orientation, migration and path integration. And, at the core of these networks, lies the central complex.

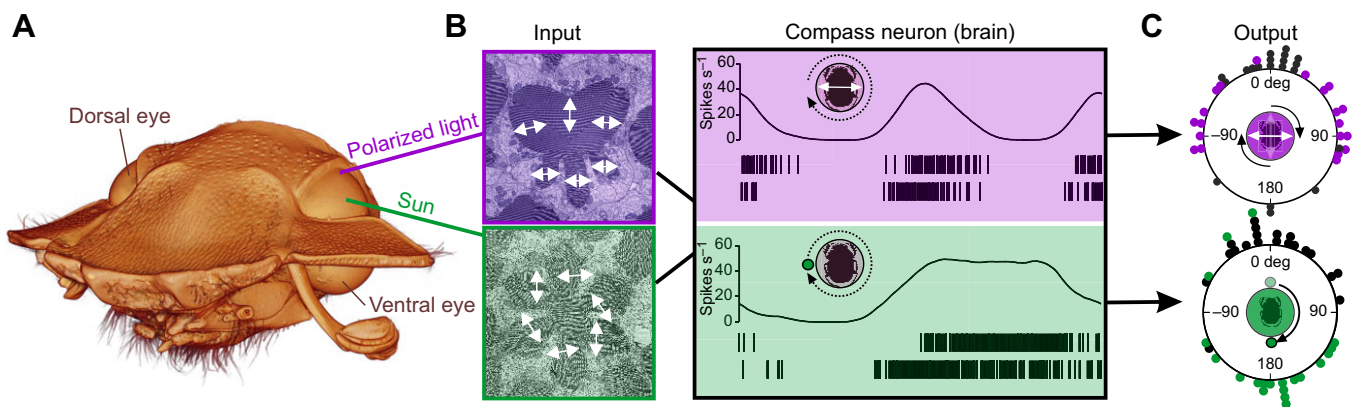
The central complex is a midline-spanning neuropil that seems to act as the main center for orientation in many insects (Pfeiffer and Homberg, 2014). The dung beetles' central complex can be divided into four subdivisions: the upper and lower division of the central body (termed ellipsoid and fan shaped body in flies), the paired noduli and the protocerebral bridge (Fig. 3B). The protocerebral bridge and the central body can be further divided into 16 columns or slices. In addition to this, the central body can also be divided into

layers (Immonen et al., 2017). Whereas the TL neurons transfer information to all slices of the lower division of the central body, most central-complex neurons branch only in one slice of the central-complex neuropil (Fig. 3C). For instance, the neuron types termed CL1 and CPU1 branch in one slice of the protocerebral bridge and in one slice of the lower division of the central body (CL1) or the upper division of the central body (CPU1) (el Jundi et al., 2018) (Fig. 3C). According to the number of slices, there are at least eight classes of CL1 neurons, each of them branching in a different slice of the protocerebral bridge. Another type of neuron, called TB1, interconnects different slices of the protocerebral bridge with each other (el Jundi et al., 2018) (Fig. 3C,D). Again, similar to CL1 neurons, there are at least eight classes of TB1 neurons that ramify in different slices of the protocerebral bridge. The polarity (input versus output regions) of the dung beetle central-complex neurons suggest an information flow from TL neurons to CL1 neurons to TB1 neurons to CPU1 neurons (Fig. 3C). The CPU1 neurons form the main output signal of the central complex and relay the skylight information either indirectly or directly to descending neurons in the lateral complex. Again, this proposed information flow in the dung beetle central complex aligns with that suggested for other insects (Heinze et al., 2009; Franconville et al., 2018) and further strengthens our argument that dung beetles encode compass information in a similar way to other insects. In addition, the neurons of the protocerebral bridge (CL1, CPU1 and TB1) in the dung beetle central complex reveal a regular connectivity pattern (el Jundi et al., 2018) (Fig. 3D). As shown for the central complex in the locust brain, this regular neuroarchitecture is essential for establishing a map-like representation of polarization angles in CPU1 and TB1 neurons (Heinze and Homberg, 2007, 2009).

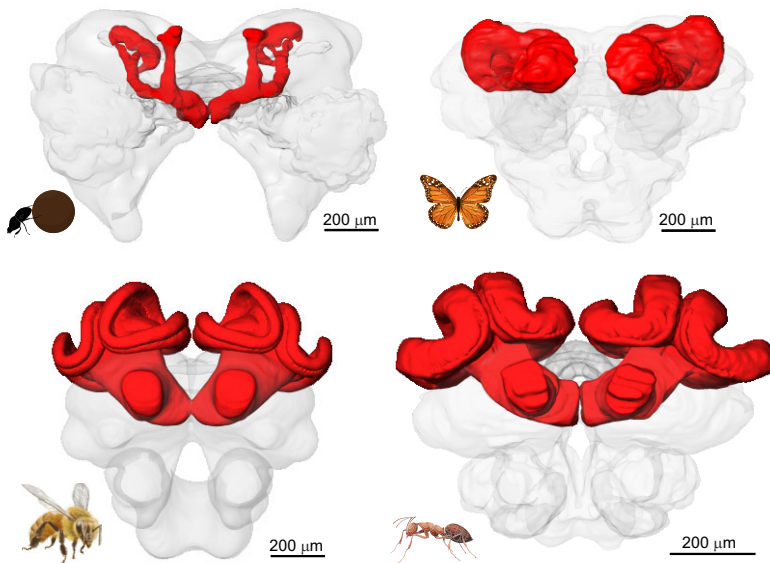
A more dynamic map of head-direction information for visual information, possibly representing the sun, has been shown in CL1 neurons in *Drosophila* (Seelig and Jayaraman, 2015; Green et al., 2017; Giraldo et al., 2018). The occurrence of such a modular neuroarchitecture also in the dung beetle central complex, combined with a highly regular connectivity pattern of the central-complex

neurons, suggests that this region of the brain may hold a similar map of different skylight cues. The neurons encoding the celestial snapshot stored by the dung beetles need to have a flexible tuning that enables them to update or replace the celestial snapshot at any moment in time. As the central complex dynamically encodes visual signals and combines them with motor feedback from the legs (Seelig and Jayaraman, 2015), it represents the ideal neural substrate for encoding the dance and storing the snapshot. In addition, the central complex contains the types of neurons (CL1/2, TB1, CPU1/2/4) that would allow the animal to steer its ball along a straight path by matching the stored celestial snapshot to the current view and generating compensatory rotations when the match fails (Heinze, 2017; el Jundi and Dacke, 2018).

To understand how the different skylight cues (Fig. 1) are coded in the beetle brain (Fig. 4A,B), neuronal activity can be recorded while simulating a full body rotation under the natural sky. This is achieved by rotating a polarizer in the dorsal visual field of a constrained beetle, while simultaneously recording from the central-complex neurons (TL, CL1, CPU1 or TB1) in the brain. During a 360 deg polarizer rotation, these neurons respond with a sinusoidal modulation of their firing activity, with two maxima and two minima (el Jundi et al., 2015b) (Fig. 4B). Similar recordings have been obtained from the brains of butterflies (Heinze and Reppert, 2011; el Jundi et al., 2014a), bees (Stone et al., 2017) and locusts (Homberg et al., 2011; Homberg and el Jundi, 2013) under the same circumstances. To simulate a beetle orienting to the sun or the moon, a green light spot (ersatz sun/moon) can be moved on a circular orbit around the beetle's head. Now, the very same compass neurons that earlier showed a response to polarized light, show a higher firing activity at a certain position of the celestial-body stimulus, suggesting that the same neurons process both stimuli in the beetle's brain (Fig. 4B). Taken together, this convincingly shows that at least two different sky compass cues are integrated in the same network in the dung beetle brain and are used as heading information during orientation (Fig. 4C). A similar response can be observed in locusts (Pfeiffer and Homberg, 2007; el Jundi et al., 2014a; Pegel et al., 2017) and monarch butterflies (Heinze and Reppert, 2011).



**Fig. 4. The neural tuning of celestial compass cues in the dung beetle brain.** (A) Dung beetles perceive sky compass cues, such as the sun/moon and the skylight polarization pattern through their dorsal eyes. (B) Left: photoreceptors in the dorsal tip of the dorsal eye are specialized to detect polarized skylight information in the UV range (upper panel). The photoreceptors of these ommatidia are characterized by rhabdoms with microvilli oriented in only two orthogonal directions. In the remaining dorsal eye, the microvilli of the photoreceptors are arranged in all possible directions (lower panel) and are therefore better suited to detect other celestial cues, such as the sun's position. White arrows indicate the orientation of the microvilli of the rhabdoms. Right: compass neurons in the brain integrate information from the polarization analyzers and the main retina of the dorsal eye and therefore respond to a rotating polarizer (upper panel) and to a green light spot that moves on a circular path around the head (lower panel). (C) When rolling in an indoor arena (upper circular plot), dung beetles respond to a 90 deg turn of a polarizer by changing their heading direction (purple circles). No change of heading occurs if the polarizer is not rotated between two rolls (black circles). When a green light spot is the only reference cue, beetles maintain the same heading in consecutive rolls (black circles) and turn their heading direction by 180 deg if the green light spot is presented in the opposite hemisphere (green circles). Ommatidia shown in B are adapted from Dacke et al. (2003a). Circular plot of the behavioral response to polarized light (upper panel in C) is adapted from el Jundi et al. (2015b).



**Fig. 5. Relative size of the mushroom bodies in insects with different orientation strategies.** Although the compass systems of dung beetles and monarch butterflies do not show a high reliance on landmarks, other insects, such as ants and bees, memorize landmarks and the pattern of the panoramic skyline to find their way back to their nests. Frontal views of the central brains of these insects reveal relatively small mushroom bodies in dung beetles (upper left) and monarch butterflies (upper right), while this brain area is much larger in honeybees (lower left) and ants (lower right). This suggests that large mushroom bodies are crucial to storing and memorizing landmark sceneries. The honey bee central brain 3D model is adapted from Brandt et al. (2005). The *Cataglyphis noda* ant 3D central brain is adapted from Grob et al. (2017; kindly provided by R. Grob and W. Rössler). The 3D model of the monarch butterfly central brain is adapted from Heinze and Reppert (2011; kindly provided by S. Heinze). The dung beetle central brain 3D model is adapted from el Jundi et al. (2018).

But how are different celestial cues combined and weighted in central-complex neurons? The night-active dung beetle *Scarabaeus satyrus* uses the polarization pattern of light centered on the moon as its main reference for orientation. However, if these nocturnal beetles are coaxed into rolling a ball during the day, they will switch to using the sun as their primary compass cue (el Jundi et al., 2015b). This dynamic weighting of celestial cues can also be observed in neurons of the central complex in the beetle brain (TL, CL1; Fig. 3C,D). If a polarization and a sun stimulus are presented in combination, the compass neurons switch from decoding the position of a celestial body (the sun) at high light intensity to encoding the direction of polarization at low light intensities (el Jundi et al., 2015b). Thus, the cue hierarchy seems to be set in a dynamic manner, following the relative light intensity of the compass cues. The functional reason underlying this switch is probably that the sky-wide polarization pattern allows the animal to spatially sum information across the entire dome of the sky (rather than from one spot), which provides a higher photon catch in beetles adapted for nocturnal orientation. Behavioral experiments also confirm that the sky-compass network of the beetles is sensitive enough to encode the dim lunar polarization pattern that arises from a crescent moon (Dacke et al., 2011; Smolka et al., 2016).

Similar to the beetles, when an ant transports a large piece of forage, this needs to be dragged backwards rather than carried forwards. Accordingly, the ant now needs to navigate in reverse when returning to its nest (Ardin et al., 2016a; Pfeffer and Wittlinger, 2016). This will unavoidably present the forager with an inverted view of celestial cues as well as terrestrial landmarks. Fortunately, the ants' estimations of the directions they need to travel to find their nest in reverse are as good as when running forwards (Ardin et al., 2016a; Schwarz et al., 2017). How the central complex could manage this is still not fully understood, but a recent model nicely suggests how the central complex could work as a holonomic internal compass that is not constrained by body orientations (Stone et al., 2017).

### Spatial memory and landmark orientation

Dung beetles, like fruit flies (Warren et al., 2018; Giraldo et al., 2018), do not seem to rely on a time-compensated sun compass. For the short journeys of the beetles (~2–20 min), this is not a limiting factor, but to get back to their set routes after temporarily losing

contact with their balls or tumbling down an incline, they still need to form some sort of memory of their direction of travel (el Jundi et al., 2016; Dacke and el Jundi, 2018). Dung beetles seem to form this memory during their dance (el Jundi et al., 2016). In fact, to store and memorize a route or direction is essential for almost every compass orientation behavior. In fruit flies, spatial orientation memory appears to be dependent on the activity of distinct TL neurons (Neuser et al., 2008; Ofstad et al., 2011), most probably the same as those that encode for skylight signals in dung beetles (el Jundi et al., 2015b). In addition, a model of the central complex suggests that a type of neuron, termed CPU4, could act as the neural substrate for memorizing directional information (Stone et al., 2017; Heinze, 2017). Both of these neurons are found in the dung beetle central complex. Even though we do not know how long dung beetles retain memory of their direction, behavioral experiments suggest that they can store a given direction for at least 30 min (J. Smolka and M. Dacke, unpublished). Given that the functionality of the central complex is conserved across insects, this is the part of the brain where we would expect to find the memory for directional information in dung beetles.

Dung beetles are not the only animals that can be seen to stop and rotate prior to orientation or when moving along their path. During their initial forays from the nest, ants will stop and perform 'pirouettes', where they rotate about their vertical axis while occasionally pausing in the direction of the nest (Müller and Wehner, 2010). The desert ant *Ocymyrmex* appears to use these pirouettes to obtain 'snapshot' views of the nest and its surroundings that can be remembered for weeks. In general, hymenopterans display navigation behaviors that rely on long-term memories of their visual surroundings (Collett et al., 2003; Cheeseman et al., 2014; Menzel et al., 2005; Degen et al., 2016; Graham and Cheng, 2009; Fleischmann et al., 2018). Other ant species and wasps are well known to take such snapshot views, called panoramic snapshots, to aid their homeward navigation while foraging (Judd and Collett, 1998; Zeil et al., 2003; Buehlmann et al., 2016; Stürzl et al., 2016), and bees form a memory for the solar ephemeris (the sun's position at given times of the day) relative to local landmarks (Dyer and Gould, 1981; Towne and Moscrip, 2008; Kemfort and Towne, 2013). These panoramic snapshots and landmark memories are believed to be stored in the mushroom bodies (Collett and Collett, 2018), which provide enough 'storage capacity' for a large

number of snapshots (Ardin et al., 2016b). Compared with hymenopterans and monarch butterflies, both flies and dung beetles (Fig. 5) have relatively small and simple mushroom bodies (Strausfeld et al., 2009). In addition, the mushroom bodies of the ball-rolling dung beetles seem to lack any visual input (Immonen et al., 2017) and follow the architecture of scarabs with specialized feeding habits (Farris and Roberts, 2005). These simple mushroom bodies correspond with the possible function of the mushroom bodies in landmark memory, an orientation mechanism that dung beetles do not seem to use (Dacke et al., 2013b).

## Conclusions

In conclusion, we find that the neuronal network behind straight-line orientation in dung beetles has strong similarities to those described in ants, butterflies, flies and locusts, with the central complex as a key control station for this behavior. Considering the substantial differences in behavior and navigational challenges between these different groups of insects, this is somewhat surprising. Interestingly, the relative size of the mushroom bodies does differ between species, potentially corresponding to their possible role in landmark memory. Whether an increase in the relative size of the mushroom bodies or a visual input from the eyes to the mushroom bodies can be identified in desert-living navigating dung beetles that, like path-integrating ants, repeatedly return to a nest (Scholtz, 1989) remains to be investigated.

An interesting phenomenon of the straight-line orienting beetles is that if a beetle is robbed of its ball and forced to return to the dung pat to make a new one, it will depart from the dung pile in a new direction, which it will maintain for the rest of this – hopefully more fruitful – journey (Baird et al., 2010). How beetles reset their bearing, or even select the first bearing, is an open question. On moonless nights, dung beetles can still travel accurately along their selected bearings, and do so by menotactic orientation to the Milky Way (Dacke et al., 2013a; Foster et al., 2017). How this dim cue is encoded in the sky-compass network, or how the hierarchy between the different celestial cues is controlled and set, represents some of the future directions of our continued investigations into the compass system of the beetles.

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## Competing interests

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