COMMENTARY

The evolution of honey bee dance communication: a mechanistic perspective

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ABSTRACT

Honey bee dance has been intensively studied as a communication system, and yet we still know very little about the neurobiological mechanisms supporting how dances are produced and interpreted. Here, we discuss how new information on the functions of the central complex (CX) of the insect brain might shed some light on possible neural mechanisms of dance behaviour. We summarise the features of dance communication across the species of the genus *Apis*. We then propose that neural mechanisms of orientation and spatial processing found to be supported by the CX may function in dance communication also, and that this mechanistic link could explain some specific features of the dance form. This is purely a hypothesis, but in proposing this hypothesis, and how it might be investigated, we hope to stimulate new mechanistic analyses of dance communication.

KEY WORDS: *Apis*, Central complex, Ellipsoid body, Exaptation, Optic flow, Orientation

Introduction

Honey bee (*Apis*) dance communication is arguably the most lauded of all forms of animal signalling. Bees dance to signal the location of valuable resources to their nestmates, and dances are effective in recruiting additional foragers to those resources (Seeley, 1995). It has been described as the only known form of 'symbolic communication' in the invertebrates (von Frisch, 1967). All bees in the genus *Apis* dance, but outside of *Apis* there is nothing quite like it. Thanks to visionary work by Martin Lindauer (1956, 1961), we have had a possible phylogenetic scenario for the evolution of dance for some time. It is still not clear, however, how a bee might convert a foraging trip to a functionally referential signal (*sensu* Blumstein, 1999), or how a recruit might interpret a dance to identify a forage location. Here, we discuss how new findings from insect neurobiology may shed some light on this problem. We begin by briefly summarising the features of dance communication across the genus *Apis*. We then review new research into how orientation and spatial relationships are processed by the central complex [CX, an unpaired cluster of neuropils (see Glossary) in the centre of the insect brain]. We argue that neural mechanisms of spatial processing may have been exapted for new functions in dance communication. Exaptation (*sensu* Deacon, 2012) refers to a new adaptive function evolving by a shift or expansion of existing functions. We propose that pre-existing mechanisms for spatial processing, involving mostly the CX, adopted new functions in the evolution of dance

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performance and dance following, and that this mechanistic relationship explains some of the specific features of honey bee dance communication. Having set out this hypothesis, we conclude by suggesting how it could be explored experimentally.

The structure of dance communication in *Apis mellifera*

In European honey bees (*Apis mellifera*), dances are performed in the contexts of foraging and nest site selection. On returning to the hive, successful *A. mellifera* foragers sometimes perform highly stereotyped dance movements (Fig. 1). For resources more than a few hundred metres away from the nest, the dance can be described as a repeating figure-of-eight movement performed on the vertical surface of the comb hanging inside the hive (Fig. 1). At the junction between the two loops of the figure of eight, the bee takes a stride and leans forward, vibrating her wings and waggling her abdomen rapidly from side to side in the famous and distinctive 'waggle run' of the dance (Dyer, 2002; Tautz et al., 1996). The wing vibrations produce both acoustic signals and jets of air directed behind the dancing bees (Michelsen, 2012). Features of the waggle run correlate with the distance and direction of the resources found by the forager. As these dances appear to represent quantitative information about the position of foraging sources in a new (and apparently arbitrary) form compared with the original information, they have been described as 'symbolic communication' (Couvillon, 2012; Dyer, 2002; Preece and Beekman, 2014; von Frisch, 1967). For foraging resources located close to the hive (typically less than 100 m), the duration of the waggle phase is extremely short; consequently, the figure-of-eight form deforms into a sickle or round shape, but the very brief waggle phases of these dances still contain some directional information (Gardner et al., 2008; Griffin et al., 2012; Preece and Beekman, 2014; Sen Sarma et al., 2004).

Apis mellifera: what is communicated when dancing?

Apis mellifera most typically dance on vertical wax frames within the dark nest cavity. The orientation of the waggle phase relative to vertical on the comb correlates with the direction of the resource relative to the solar azimuth on departure from the hive (Fig. 1); hence, the angle of the waggle run relative to vertical is considered a signal of direction for *A. mellifera* (von Frisch, 1967). There is flexibility to directional signalling in this species. European honey bees will sometimes dance on the horizontal board at the hive entrance in the sun, in which case their dances point directly towards the resource (Esch, 2012; von Frisch, 1967). If the image of the sun is reflected in a mirror such that it is visible at the bottom of the frames inside the dark hive, then the bees orient their waggle phases to signal the direction of the food relative to this image of the sun (Esch, 2012; von Frisch, 1967).

The duration of the waggle phase in time correlates with the distance of the resource from the hive (Gardner et al., 2008; Schürch et al., 2013). More precisely, the duration of the waggle phase correlates with the amount of retinal image flow (i.e. optic flow; see

Glossary

Allothetic
A navigational reference external to the subject.

E-vector
Electric vector – the component of light that interacts with matter (Horváth and Varjú, 2004). Functionally, also the angle of polarisation.

Idiothetic
A navigational reference internal to the subject.

Neuropil
A region of dense nerve tracts, connectivity and synaptic contacts in the insect brain (Strausfeld, 2012).

Optic flow
The progression of objects in a visual scene across the eye as an animal moves through the scene (Zeil et al., 2009).

Path integration
The integration of all distances travelled and all angles steered, which results in the shortest return path (home vector) (Collett and Collett, 2000a).

PiggyBAC
A transposon system that has proved effective for the stable introduction of gene sequences into the genomes of various insect species (Schulte et al., 2014).

Polarisation
The scattering of light by the Earth's atmosphere. In a theoretical world, the degree of polarisation is 100% if the incident angle between light and molecules in the atmosphere is 90 deg (Wehner, 2001).

Polarotopy
Neural organisation based on a compass-like representation of E-vectors (polarisation angles).

Rotational optic flow
The lateral progression of objects in a visual scene across the eye as an animal turns (Zeil et al., 2009).

Translational optic flow
The progression of objects in a visual scene across the eye around the axis of movement through the environment, caused by the animal's movement (Zeil et al., 2009).

Glossary) experienced by the bee during her flight (Esch et al., 2001; Srinivasan et al., 2000). The amount of optic flow is usually highly correlated with distance travelled (Barron et al., 2005; Tautz et al., 2004), and the relationship between waggle duration and the distance to the resource is best described by a linear function, albeit with significant variation around a linear fit (Gardner et al., 2008; Schürch et al., 2013). The speed and number of dance circuits performed correlates with the relative value of the gathered resources (Barron et al., 2007; Tautz, 2008).

Recruits attend to the movements of the dancer, often following close behind her. Recruits must follow more than one waggle phase in order to gain information on the location of the indicated resource (Tanner and Visscher, 2008), but how they 'read' the dance is still unclear. Multiple stimuli could signal the position and movements of the dancer, including physical contact with her body by the antennae of the followers (Rohrseitz and Tautz, 1999; von Frisch, 1967), substrate-borne vibrations generated by the dancer (Tautz, 1996) and acoustic signals (Kirchner et al., 1991, 1988; Michelsen, 2003), as well as air flows and narrow directional jets of air generated by the vibrating wings of the dancer (Michelsen, 2003, 2012). Any or all of these might be used by followers to track a dancer's movements. In *A. mellifera*, there is considerable variation in waggle runs both within and between dances for the same location (Couvillon et al., 2012; Schürch and Couvillon, 2013; Schürch et al., 2013). Authors disagree over whether recruits must follow behind the dancer to gain information from the dance (Judd, 1995; Michelsen, 2012; Rohrseitz and Tautz, 1999), or whether recruits can read a dance from side-on (Tanner and Visscher, 2009). Either way, following more waggle runs increases the chance of a recruit successfully locating a foraging source, and presumably recruits have the capacity to improve their estimate of resource location by combining (and perhaps averaging) information obtained from successive waggle runs (Tanner and Visscher, 2009, 2008).

Odours detected by recruits during the waggle dance also provide important information, but the contribution of odours to dance communication in *A. mellifera* has been controversial (Couvillon, 2012; Esch, 2012; Wenner and Wells, 1990). Dancers produce a specific pheromonal bouquet, which attracts recruits to them, but this does not provide any spatial information (Esch, 2012; Thom et al., 2007). The specific floral odour of the resource collected by the dancer is also a source of information used by recruits to help them locate the indicated resources (Couvillon, 2012; Esch, 2012; Gruter et al., 2008; Grüter and Farina, 2009).

Variation in dance across *Apis* and beyond: insights for a model of dance evolution

Dance is unique to the genus *Apis*, but social recruitment of foragers is certainly not. Opinions still differ as to whether the sister group to tribe Apini are the Bombini (bumblebees) or Meliponini (stingless bees) (Oldroyd and Wongsiri, 2006; Thompson and Oldroyd, 2004), but both of these tribes feature social recruitment of foragers to food sources. Bumblebees do not signal the location of found resources, but they do advertise that they have found something by an energetic zig-zagging run within the hive to alert nestmates (Dornhaus and Chittka, 1999, 2001). The floral odour clinging to
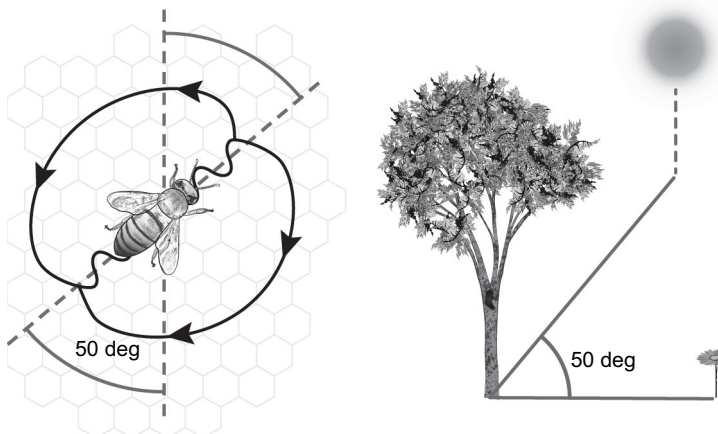

Fig. 1. Schematic diagram of the waggle dance of *Apis mellifera*. Dances advertise resources found by foragers. The dance is usually executed on vertical combs inside the hive (left). The angle of the waggle phase of the dance relative to vertical on the comb corresponds to the direction to the advertised resources on departure from the hive relative to the solar azimuth (right). The duration of the waggle phase correlates with the amount of optic flow experienced during the flight to the resources. At the end of the waggle phase, the forager loops back to the beginning and repeats the movement.
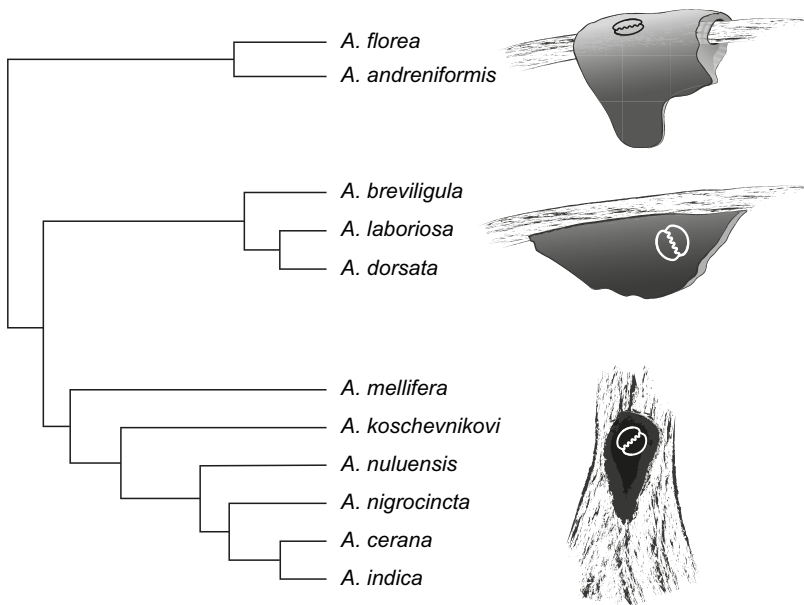
50 deg

50 deg

Fig. 2. Diversity of dance and nest forms within the genus *Apis*. Dwarf honey bees *Apis andreniformis* and *Apis florea* dance on the horizontal surface (black dance trace) at the top of their nests suspended from tree branches, and orient their waggle phases to point toward the advertised resources. Giant honey bees (the *Apis dorsata* clade) dance on the vertical surface (white dance traces) of their comb and orient their waggle phases with respect to gravity, similar to the dances of the cavity-nesting species (the clade including *Apis mellifera*). Phylogeny adapted from Lo et al. (2010).

the returning forager provides information to recruits about the discovery (Dornhaus and Chittka, 1999, 2001). The stingless bees are by far the most diverse group of these three tribes (with 36 genera within the tribe; Michener, 2000), and their social recruitment mechanisms vary. The most commonly reported are non-directed alerting runs rather similar to those of bumblebees, but some species have directional social recruitment systems (Lindauer, 1961; Lindauer and Kerr, 1958; Nieh, 2004). It seems reasonable to propose that social recruitment of foragers is ancestral to the Apini (l'Anson Price and Grüter, 2015).

Apis is the only extant genus of Apini. Mapping the differences in the dances between the extant species of the genus to the consensus *Apis* phylogeny suggests a plausible scenario for how dance may have evolved (Fig. 2). This model for dance evolution was first proposed by Lindauer (1957) and has been updated by Oldroyd and Wongsiri (2006), Couvillon (2012) and l'Anson Price and Grüter (2015).

The dwarf honey bees (*Apis andreniformis* and *Apis florea*) are basal to the genus (Fig. 2). These nest by forming a single sheet of comb hanging from a tree limb. Dances are performed on a horizontal surface at the top of the comb, and dancers point their waggle runs directly to the resource using celestial cues and/or landmarks to orient the dance (Dyer, 2002). It has been proposed (Couvillon, 2012; von Frisch, 1967) that ancestral honey bees communicated first by excitatory runs (perhaps similar to bumblebees) that involved shaking of the body and were aligned toward the foraging site. The simple waggle dance could be thought of as re-enacting the departure direction of the forager bee from the hive. Over time, it is assumed that the dance evolved to became more stereotyped to resemble the neat figure-of-eight waggle dances of the extant dwarf bees. Orienting dances relative to gravity on a vertical comb and adding acoustic signals to the waggle phase are considered to be derived dance features. Vertical dances evolved in species that build combs in cavities (*A. mellifera* and *Apis cerana*) or under ledges (*Apis dorsata* and *Apis laboriosa*), where there is no horizontal dance floor. Sound pulses and air jets are interpreted as adaptations to make waggle dances more apparent in low-light environments such as a cavity, or underneath a sheet of close-packed bees (as in the giant honey bees like *A. dorsata*). In the migratory *A. dorsata*, dances also occur in the context of the migration of the

colony. Dances precede the departure of the colony from either its original nest site (Dyer and Seeley, 1994) or bivouac sites along the colony migration route (Robinson, 2012). In this special case, dances appear to indicate the direction in which the swarm should move on departure, but it is not clear whether they indicate any specific distance (Dyer and Seeley, 1994; Robinson, 2012). The cavity-nesting species *A. mellifera* and *A. cerana* have dances that are so similar it is possible for them to function across species (Su et al., 2008; Tan et al., 2008).

A phylogenetic analysis of dance evolution suggests therefore that the original dances can be thought of as 'a symbolic enactment of the foraging flight' (Couvillon, 2012; von Frisch, 1967; Wilson, 1971), as the waggle run points directly in the direction to be flown. If this interpretation is correct, then the evolutionary innovation that may have led to the dance motor pattern could have initially been as simple as an outbound forager delaying her departure from the hive and performing part of her departing flight vector (including beating her wings) while still clinging to the comb. The neat figure-of-eight looping behaviour that is so characteristic of dancing may have evolved later as a mechanism to enable the dancer to hold a position on the comb for multiple circuits while being followed.

The waggle dance of *A. mellifera* still indicates the vector from the hive to the food source, but uses a gravitational reference to substitute for a celestial reference. From this perspective, the mechanisms supporting dance communication must therefore involve the mechanisms of orientation of flight. Below, we summarise new findings on the neural mechanisms of orientation and path integration (see Glossary) in bees and other insects, and propose how they might function in dance communication.

The CX and its role in orientation and path integration in walking and flying insects
Recently, a series of studies of the CX has transformed our understanding of how insects process their position in space (Fig. 3) (Pfeiffer and Homberg, 2014; Plath and Barron, 2015; Turner-Evans and Jayaraman, 2016; Varga et al., 2017). The CX consists of the protocerebral bridge (PB), the central body (CB) and the noduli (NO) in pterygote insects (Fig. 3). The CB is divided into an upper division [CBU, termed fan-shape body (FB) in the fruit fly] and a lower division [CBL, termed ellipsoid body (EB) in the fruit fly].
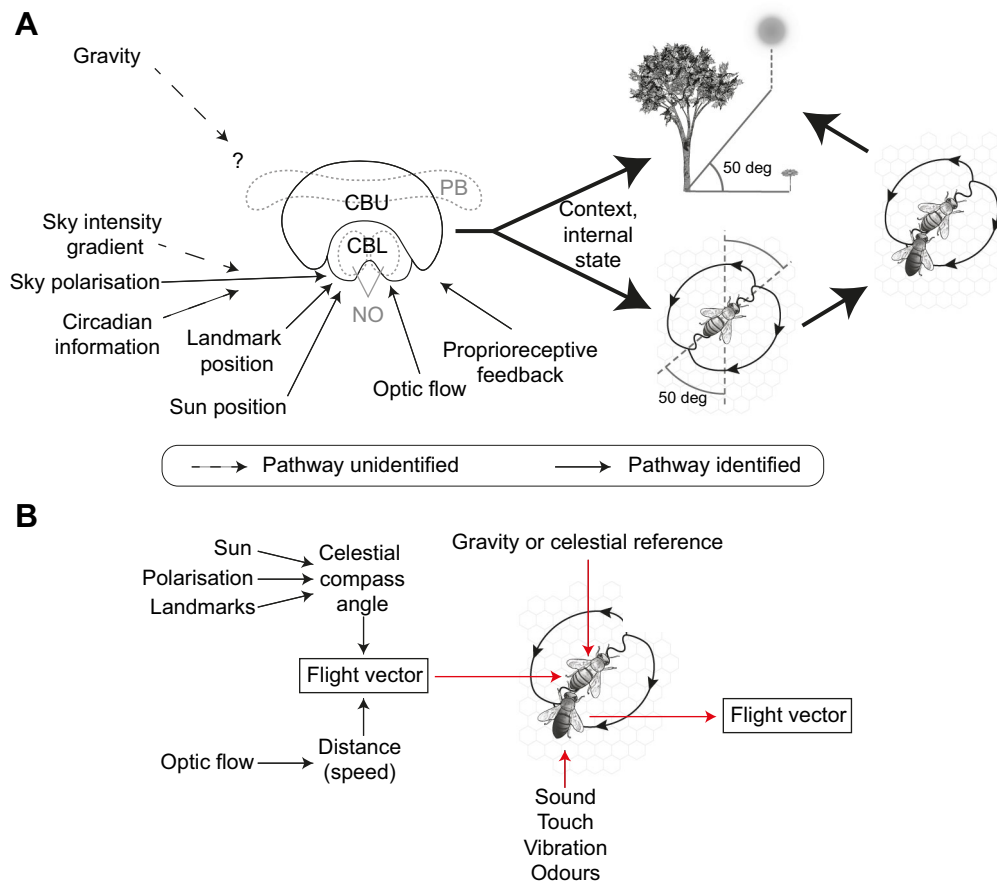
Fig. 3. Inputs to the central complex involved in orientation, and proposed to also be involved in dance. (A) The CX is composed of the central body upper unit (CBU), the central body lower unit (CBL), the protocerebral bridge (PB) and the noduli (NO). The figure shows a summary of inputs that have been identified in various insect species entering the CX (solid arrows) and potential inputs to the CX with as-yet unidentified pathways (dashed arrows). The relevant references are included in 'The CX and its role in orientation and path integration in walking and flying insects'. We propose that these inputs, which carry different forms of spatial information, along with processing within the CX support both the calculation of the vector displayed in the dance (upper right) and the execution of the dance movement (lower right). Which behaviour is performed (dance or flight) depends on the context and state of the bee. (B) Information flow between dancer and recruit. For the dancer, celestial information and optic flow information gathered during flight are integrated into a single flight vector reflecting the shortest path between the hive and the resources. The flight vector information is transformed to specific dance movements: dance orientation and waggle duration, oriented relative to either gravity or celestial references depending on the bee species. Odours attract recruits to dancers, and recruits sense the dance movement through sound, touch and vibration. Recruits then transform information gathered from the dance to a flight vector. Red arrows indicate which parts of this hypothesis present the greatest challenges for a neurobiological interpretation.

The CX receives sensory information via tangential neurons from the surrounding protocerebrum; the majority of this sensory input is visual information indirectly relayed from the optic neuropils. The tangential neurons have ramifications outside of the CX and connect to the PB (TB neurons), the CBU (TU neurons), the CBL (TL neurons) and the NO (TN neurons). Information is transmitted between the PB, CBU and CBL via columnar neurons, which create a columnar organisation (vertical slices) in all three structures. In the NO, two distinct layers are found, which are interconnected exclusively with the CBU or with the CBL. Important input and output regions for the CX are the adjacent lateral accessory lobes (LAL) in either hemisphere. (For more details on CX architecture and connectivity, see Heinze et al., 2013; Heinze and Homberg, 2008; Lin et al., 2013; Wolff et al., 2015.)

For a foraging flight, it is essential that a bee is able to identify the directions of the home hive, the foraging site and its current heading relative to some common reference. It has long been known that the pattern of polarised light in the sky is a vital reference by which bees orient. More recent research in several insects has shown that neurons in the CX form a map-like organisation of E-vector

orientations (el Jundi et al., 2014; Heinze and Homberg, 2007; Pfeiffer and Homberg, 2014) which can provide celestial compass information that will help an insect to identify its orientation relative to celestial cues. The compass neuron network comprises groups of excitatory and inhibitory tangential and columnar neurons with activity maxima elicited by different azimuths of the celestial body or different E-vector angles (see Glossary). Polarotopy (see Glossary) in the network has been suggested to be stabilised by antagonistic integration across neurons that are active at E-vector angles shifted by 90 deg (Bockhorst and Homberg, 2015). The celestial compass pathway has been reconstructed in the honey bee (Brockmann and Robinson, 2007; Held et al., 2016; Mota et al., 2011; Zeller et al., 2015), and is very similar to the described pathways found in other bees (Pfeiffer and Kinoshita, 2012) and locusts (Homberg et al., 2003; Homberg and Paech, 2002).

It seems that processing within the CBL helps a moving insect maintain a heading relative to celestial or other visual cues, or to execute a turn to a new heading. Activity in one column of the EB corresponds to the orientation of the animal in relation to either visual stimuli (allothetic cue; see Glossary) or the proprioceptive

signals provided by walking (idiothetic cue; see Glossary) (Seelig and Jayaraman, 2015). Interestingly, the EB activity is maintained beyond the presentation of either visual stimuli or the animal moving – thus providing a possible mechanism for spatial working memory in flies (Seelig and Jayaraman, 2015). These findings were based on calcium imaging, capturing activity profiles created by all neurons in the EB at once. A recent study based on extracellular recordings in the cockroach CBL region discovered neurons that responded variously to allothetic and idiothetic cues alone or in combination (Varga and Ritzmann, 2016), corroborating the findings in the fruit fly (Seelig and Jayaraman, 2015) for head-direction cells in insects. This would support orientation relying on external and self-motion cues. Two recent publications have provided some substantial experimental evidence towards an additional integration of orientation angles and angular velocity: Green et al. (2017) and Turner-Evans et al. (2017) have identified a type of neuron (tile neuron) which connects the EB to the PB. Activity in these neurons correlates with angular velocity and activity changes caused by turns of the animal preceded activity changes in the head-direction cells found in the EB. Thus, information about orientation changes of the animal are constantly updating the representation of the orientation in relation to external landmarks in the EB.

The CBL is also important for organising an insect's change in orientation relative to the external landmarks or cues; most of the relevant studies have been done with walking or tethered insects. For example, initiation of locomotion and turning behaviour in cockroaches and crickets is preceded by a change in firing rate of neurons recorded from the CBL region (Guo and Ritzmann, 2013; Kai and Okada, 2013; Martin et al., 2015). Further, stimulation of neurons with predictive firing patterns elicited the same walking and turning responses observed when recording from these cells (Martin et al., 2015). We note here that these studies are based on extracellular recordings; it is therefore possible that some neural responses were recorded from neurons bypassing rather than entering the CBL.

The CX is core to mechanisms underlying orientation and movement in the environment. However, it remains to be investigated how the insect brain integrates the spatial information gathered on a foraging flight to be able to navigate a direct route (a single vector) from a nest to a food source and back. Ethological studies suggest that some insects (especially walking ants and flying bees) use path integration to find the shortest route, and even use novel short-cuts from food sources to the nest (Collett and Collett, 2000b; Wehner and Srinivasan, 2003). A recent study provided evidence for a form of path integration in the fruit fly that exhibited search behaviour at the location of a food source which was independent of visual and olfactory cues (Kim and Dickinson, 2017).

A study in the tropical nocturnal sweat bee *Megalopta genalis* has traced and recorded from tangential and columnar neurons and confirmed that these are tuned to different *E*-vectors in this species (Stone et al., 2017). An exciting new finding of this work is that TN neurons entering the NO might have the capacity to encode information on speed. These neurons respond to translational optic flow (see Glossary, caused by forward motion) but not rotational optic flow (see Glossary; caused by turning). Individual TN cells show increasing activity with translational optic flow (in either direction) with increasing stimulus velocities, suggesting a system capable of detecting speed of movement. Stone et al. (2017) discovered frequent co-staining of these TN neurons with CPU4 neurons (columnar neurons connecting the PB and the CBU),

suggesting that CPU4 neurons could combine polarisation-based compass information received from the compass network with speed information received from the NO. Modelling of this circuit proposes that it could be capable of path integration calculations (Stone et al., 2017). This network has the potential to support coding of a home vector during a foraging flight. This proposed network of CPU4 neurons could be utilised to produce the vector indicated by dancers also.

How orientation mechanisms and the CX might be involved in generating the dance

The hypothesis that the CX is involved in dance signalling was first suggested by Brockmann and Robinson (2007). As the waggle phase signals the outbound vector to the resource, it is most parsimonious to propose that the generation of the dance accesses the accumulated path information within the CX network that is gained through flying to the food source. We propose therefore that the directional and distance information provided by the CX system is utilised by all oriented behavioural responses.

As discussed above, for *A. mellifera*, the directional information obtained relative to the sun during flight must be translated into directional information relative to gravity when dancing on the vertical comb. How could this be done? A possible inference from the physiological properties of the CX (Seelig and Jayaraman, 2015; Turner-Evans et al., 2017) and the proposed model of how it performs path integration (Stone et al., 2017) is that it is not bound to any specific form of spatial reference. The circuit will operate to any spatial reference frame, be it celestial, landmark-based or proprioceptive. Thus, there may not need to be a specific mechanism for switching of a reference frame in the CX, but information on gravity must be available to the CX system if gravity is to be used as an orientational reference frame.

One candidate site for sensing orientation relative to gravity (i.e. geosensing) is the neck, as any inclination of the thorax in relation to the head due to gravity would lead to a different pressure of the head onto the thorax. Manipulations of mechanosensory hairs located at the neck lead to disorientated geotactic behaviour and a disorientated dance (Lindauer and Nedel, 1959; von Frisch, 1967). Projections from these hairs to the suboesophageal ganglion have been found in the honey bee (Brockmann and Robinson, 2007). Other possible sites for geosensing include the joint between the thorax and the abdomen, and the leg joints (Srinivasan, 2011). However, these have not been investigated in relation to dance behaviour to our knowledge, and how geosensing might be integrated into the CX network still needs to be explored.

Dancers can also update their directional estimate of the food source over the course of the day as the sun moves across the sky, demonstrating a time-compensation aspect to their celestial compass (for discussion, see Srinivasan, 2011). When bees are stopped from foraging for a time after learning a food source and then receive some nectar from that food source, some bees start to dance the direction of the food source, indicating the correct position of the sun at that time despite having not left the hive to update their information on solar position (Lindauer, 1960). Zeller et al. (2015) identified a possible circuit for interaction between neurons carrying polarisation information (see Glossary) and neurons sensitive to circadian information, suggesting a possible locus for time compensation of the celestial compass. This system could also be involved in the generation of time-compensated dance output.

How distance information is transformed from flight to dance is currently challenging to understand. The amount of optic flow experienced in flight en route to the food source determines the

duration of the waggle phase (Esch et al., 2001). For dance, however, the distance aspect of the vector output of the CX network must be transformed to a waggle phase of a certain duration rather than a flight of a certain amount of optic flow. How this might be done is not clear.

How might the dance be interpreted by recruits?

The key information that dance followers gain from the dance is that a profitable food source exists, along with information on its direction, an estimate of distance, and its odour. As discussed above, recruits mostly track the position of the dancer using their antennae (Dyer, 2002; Esch, 2012; Michelsen, 2012). Open-nesting honey bees can also see the dancer. Recruits must transform a vector indicated by the sensed dance movement back into a flight vector. In open-nesting species, the direction component of the dance is usually oriented with respect to celestial cues; therefore, the direction estimated from the dance is in the same reference frame as that of a flight. For cavity-nesting species, however, the direction estimated from the dance can be oriented with respect to gravity. In flies and cockroaches, the CX heading estimation is not bound to any specific reference frame (Seelig and Jayaraman, 2015; Varga et al., 2017). If the same is true for bees, then the CX system could enable direction estimation to operate with respect to any reference frame. No 'switching mechanism' would be needed within the CX as the context of the currently executed movement would provide the reference. To translate a dance vector into a flight vector, however, it must be the case that flight heading orients to visual and/or celestial cues and does not use gravity, whereas dance and dance-following headings orient to gravity.

How distance information signalled by the duration of a waggle phase might be translated by a recruit back to the amount of optic flow perceived during flight is another tough question. As discussed above, evidence suggests quite a high level of imprecision in both the execution of the waggle movement and the vectors flown by recruits. Perhaps this imprecision reflects sensorimotor constraints in the translation of vector information stored by the CX into dance movements, and back again (Beekman et al., 2005).

Recruits are also able to pick up odour cues from the collected resource from the dancer, and it is common for the dancer to donate nectar to recruits via trophollaxis (Farina, 2000; Farina et al., 2005). In this case, the well-studied mechanisms of olfactory learning in the bee antennal lobe and mushroom body (Galizia, 2014) would enable the recruit to associate the odour of the dancer with nectar reward, which would establish the odour of the nectar source as a rewarding goal (Reinhard et al., 2004a,b).

Investigating the neural basis of the waggle dance

By emphasising the relationships between aspects of dance behaviour and aspects of orientation and foraging behaviour, and by considering the properties of neural systems now known to be involved in orientation and foraging, we have proposed that neural systems might have been exapted during evolution to new functions in dance. This is, of course, a hypothesis that needs to be tested. Dance is, by its nature, a movement and a social interaction, which means that it cannot be studied using harnessed bees; this, in turn, rules out using electrophysiological approaches with current technology. However, the anatomical and electrophysiological exploration of neuronal pathways involved in spatial orientation and navigation in other insect systems now has great momentum, and will certainly provide insights that will help us understand orientated behaviours, including dance.

The challenge that we face is to relate the responses of specific groups of neurons to what the animal is doing in its natural environment. el Jundi et al. (2014) artfully demonstrated a roadmap for how that might be done by first manipulating the natural stimuli to carefully observe the change in behaviour, then demonstrating that the same changes in behaviour occur in response to carefully selected artificial stimuli applied in a lab setting, and finally by recording neuronal responses to these artificial stimuli using electrophysiology. Can we apply these principles to similarly dissect the dance to its mechanism?

If we can find out which cues trigger a switch between using path integration information to execute a flight vector or to execute a dance vector, we would be one step closer, at least, to understanding the dance behaviour. We also urgently need a better understanding of dance as a pattern of motor activation. The behaviour is well described (Tautz et al., 1996), but what muscles are involved? Models have been invaluable in bridging neural properties to function and behaviour (Stone et al., 2017). If we could combine models of path integration and spatial navigation with knowledge about the motor patterns generated in the waggle dance, we could probably make some progress.

Neuropharmacological methods have been used to explore dance (Barron et al., 2009, 2007) and to uncover how dance changes as a result of ingestion of pesticide (Schricker and Stephen, 1970). To make further progress, targeted neuropharmacology by microinjection of specific agonists and antagonists into specific brain regions (Søvik et al., 2016) could provide a method for testing the role of the CX in dance. Substances known to alter dance behaviour and navigation after systemic treatments could be injected into different brain regions to determine whether bees would still be able to find food sources that had been visited before. A challenge is whether the bee could recover well enough from such an invasive procedure to participate in dances or follow them before the pharmacological agent has worn off. Perhaps injection of microcapsules into the head capsule could be a method of delivering a slow-release drug to areas of the bee brain. The ultimate goal would be to combine long-term acting drugs such as irreversible antagonists with long-term observation of treated bees in the hive to uncover changes in behaviour. Radio-frequency identification (RFID) tagging of bees (Perry et al., 2015) is a useful tool for this kind of research.

Very ingenious neurogenomic analyses have identified some candidate genomic pathways that are potentially involved (Sen Sarma et al., 2010, 2009). Other techniques that would be transformative could be genetic transformation of bees with piggyBAC (see Glossary) and CRISPR/Cas9 or similar technologies (Kohno et al., 2016; Schulte et al., 2014), or bee-scaled microcanulae or microelectrode backpacks (similar to those now used in free-ranging small mammals; Fan et al., 2011). We acknowledge that highly insightful recordings have been made from free-moving insects (Kai and Okada, 2013; Martin et al., 2015), but currently it will be technically challenging to record from a bee that is interacting with other bees in a hive such that she may undertake or follow a dance.

Conclusions

In this Commentary, we have discussed the hypothesis that processing in the CX could contribute to both the production and interpretation of the honey bee waggle dance. We acknowledge that the core of this hypothesis was first proposed by visionary neuroethologist Harald Esch who wrote: 'The role of image motion during foraging and dancing can help to investigate the

"nature" of bee dances. The waggle dance might be a "symbolic replay" of a foraging flight… We suspect that the whole waggle dance is an act of conditioning: A recruit "learns" the location of a feeding site during attendance of a symbolic replay of a foraging flight inside the hive. A food sample delivered by the dancer through trophallaxis serves as a reward. We know that bees can perform most of the behaviors that are required for this task' (Esch, 2012).

Although there has been enormous success in dissecting the phenomenon of dance behaviour, thus far there has been little progress in studying the neural mechanisms involved. This is because it is an extremely hard task. Bees only dance in a hive, and no one has yet persuaded any bees to execute dances in a laboratory setting, making the dance a very difficult phenotype to investigate experimentally. Learning more about the neurobiology of the bee brain has allowed us to flesh out this hypothesis. If indeed dance evolved by exaptation of orientation and learning systems, then while dance can still be described as a functionally referential signal, the form of the dance is far from arbitrary and reflects a hive-bound replay of a foraging flight.

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