



## Essay

# Honeybee waggle dance error: adaption or constraint? Unravelling the complex dance language of honeybees



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The honeybees' (genus *Apis*) waggle dance is the only known example of a symbolic language in a nonprimate species. Through a complex series of stereotyped movements, a bee returning from a foraging trip can indicate to her nestmates the direction, distance and quality of a nectar, pollen or nest resource she has located. The 'waggle' component of the dance (indicating directional information) contains an inherent error and this error becomes smaller the further the site danced for. The imprecision in the dance effectively spreads dance followers over a patch that remains relatively constant with increasing distance to a resource. This error has been proposed to be a colony-level adaptation and to confer an advantage in the context of foraging. An alternative explanation for the error in the bees' dance is that the bees simply cannot be more precise due to constraints inherent to the dance. Here we analyse all studies to date that have investigated the bees' dance error. We conclude that the error in the honeybee waggle dance is nonadaptive and that the bees dance as best they can.

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In its most general sense, animal communication refers to the transfer of information by an animal that elicits a change in the behaviour of the recipient of the information. Animals communicate with each other in a range of contexts. For example, social breeders communicate their dominance rank (Abrams & Matsuda, 1994; Ligon & McGraw, 2013), potential mating partners their sexual receptivity (Rowland, Baube, & Horan, 1991) and resistance to parasites and diseases (Hamilton & Zuk, 1982), and prey species deter predators by indicating their unpalatable or poisonous characteristics (Pearson, 1985).

Tinbergen (1952) suggested that animal communication has its origin in an animal's 'reaction pattern': innate behaviour elicited as a reaction to the animal's environment. Such behaviours provided the raw material for communication systems to evolve. Tinbergen described in detail how 'ordinary' behaviour, such as feeding or locomotion, can be shaped into display behaviour employed during courtship or aggressive interactions. More generally, if receivers have the ability to detect cues produced by other individuals, they can use this information to adapt their own decision making. If 'eavesdropping' on such cues does not benefit the sender, no selection will take place on improving the information content of the

cue. If, on the other hand, the sender does benefit, selection will act on increasing the effectiveness of the cue, thus selecting for a communication signal (Lloyd, 1983). Even though direct selection towards benefiting the sender will be the main driving force behind more effective communication systems, if receivers are closely related to the sender, indirect selection on the receivers can increase the signal's efficacy even further.

Many social insects have elaborate recruitment systems that greatly increase the foraging efficiency of the colony (reviewed in Jarau & Hrnčir, 2009). Individuals within insect colonies tend to be close relatives, thus increasing the benefit of effective means of communicating. Yet, there is an inherent trade-off between effort and usefulness; communication is most worthwhile when the benefits of sending the signal exceed the cost of its production. Most often, benefits are greater when groups are larger because more individuals can be employed to search the environment and report back the location of any discovered resources (Beekman & Ratnieks, 2000; Dornhaus, Powell, & Bengston, 2012). In general, the larger the colony, the more elaborate the communication mechanisms are (see Beckers, Goss, Deneubourg, & Pasteels, 1989 for a discussion on recruitment mechanisms in ant species).

Many social bees recruit nestmates to profitable food sources they have found. In its most primitive form, as found in bumblebees (Dornhaus & Chittka, 1999), recruitment in bees comprises nondirectional excitatory runs performed by the returning forager in the nest. Because the returning forager carries with her the scent of the

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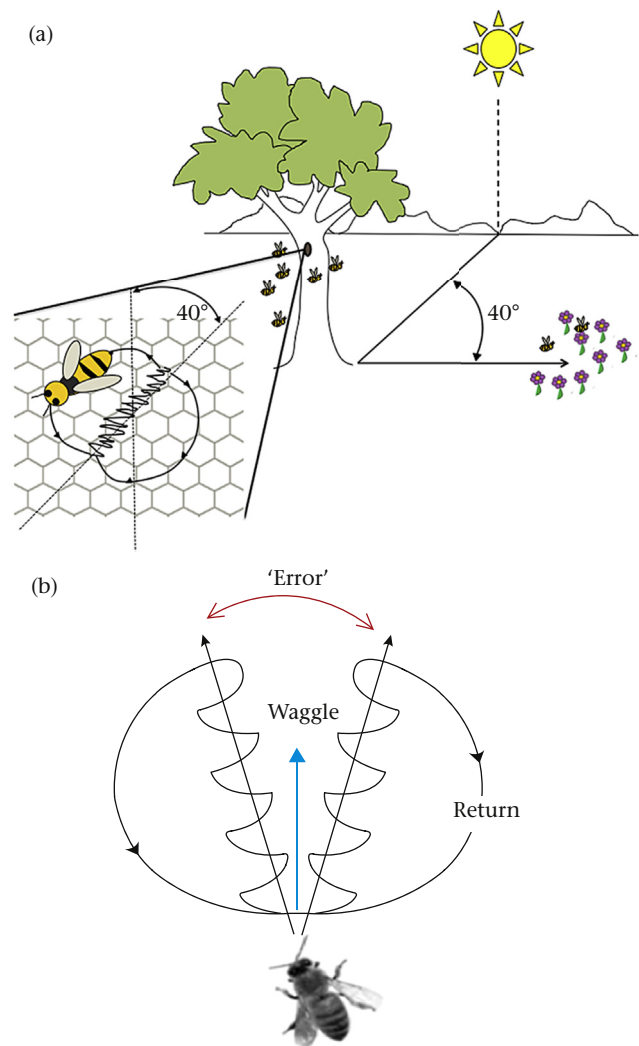
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flowers on which she has been foraging, nestmates learn not only that there is something out there worth leaving the nest for, but also the smell of the source. The stingless bees (comprising several hundred species distributed over more than 36 genera, Michener, 2000) and the honeybees (12 species all within the genus *Apis*, Lo, Gloag, Anderson, & Oldroyd, 2010) are highly social bees that live in permanent colonies, in contrast to the seasonal colonies of bumblebees. Stingless bees use a diverse array of recruitment communication systems ranging from odour trails left behind on vegetation en route to the food source to the potential referential encoding of food location (reviewed in Nieh, 2004). In contrast, all species of honeybee use the same communication mechanism: the waggle dance. The honeybees' dance probably had its origin in the excitatory behaviours described earlier in bumblebees that are also present in some species of stingless bees (Nieh, 2004). The most primitive form of the dance can still be found in the red dwarf honeybee, *Apis florea*, a bee species that is probably most similar to the common ancestor of *Apis* (Beekman, Gloag, Even, Wattanachaiyingcharoen, & Oldroyd, 2008; Dyer & Seeley, 1989; Makinson, Oldroyd, Schaerf, Wattanachaiyingcharoen, & Beekman, 2011). Some authors have proposed that the honeybees' dance originally evolved to allow the bees to select a nest site and that the dance was only later co-opted in the context of foraging (Beekman et al., 2008; Beekman & Lew, 2008).

The honeybee waggle dance has been argued to be unique in that the bees are able to adjust the accuracy of their information communication by 'tuning' their dance, incorporating increased or reduced error depending on the distance to the advertised location, resource type and size of the area they are indicating (Dyer, 2002; Gardner, Seeley, & Calderone, 2007; Towne & Gould, 1988; Weidenmüller & Seeley, 1999). Here we review the evidence for such adaptive tuning after first describing the honeybees' dance.

## THE HONEYBEE WAGGLE DANCE

In 1973, Austrian researcher Karl von Frisch received the Nobel Prize in Physiology or Medicine for his description of the honeybees' unique symbolic communication (von Frisch, 1967). The symbolic language of the bees' dance is the most astounding example of nonprimate communication that we know of (von Frisch, 1967). The waggle dance provides information to nestmates about the profitability of resources found, and allows dance followers to be recruited to these resources. On return to the nest some successful foragers perform a linear 'waggle' in which the dancer shakes her abdomen from side to side vigorously, then turns to the left or right and circles back to repeat the waggle, in the process tracing a figure of eight pattern (Fig. 1a). During the waggle phase of the dance, a returning forager communicates a spread of vectorial and spatial information indicating the direction and distance flown (Fig. 1b; Towne & Gould, 1988; Weidenmüller & Seeley, 1999). The dancing bee uses gravity (when dancing in the dark) and the angle relative to the solar azimuth (when dancing in view of the sky) to indicate where a resource can be found (von Frisch, 1967; Oldroyd & Wongsiri, 2006). The duration of the waggle phase increases with increased distance to the resource, and the rate of the dance, measured by the vigour of the waggle and the speed of the dancer's circular turn, correlates with the quality of the resource as perceived by the foraging bee (nicely reviewed in Seeley, 1995). The consequence of both the adaptation of the number of waggle phases in a dance and the speed of the return phase is that dances for better resources last longer and are more 'livelier' or 'enthusiastic' (Seeley, Mikheyev, & Pagano, 2000). Such dances attract more followers, thus more nestmates will be recruited to those resources (Seeley, 1994; Seeley, Camazine, & Sneyd, 1991). As a result, even though individual bees only experience the quality of their



**Figure 1.** The waggle dance and dance 'error'. (a) Each waggle run indicates the distance and direction to a resource, where the distance is approximately equal to the duration of the waggle ( $1 \text{ s} \approx 1 \text{ km}$ ), and the direction is the angle of the resource relative to the sun and gravity. The number and speed of complete circuits (waggle phase and return to the starting position) indicate profitability. On alternate waggle runs, the indicated vector direction varies, leading to error. (b) The angle of divergence between successive waggle runs is not constant, and increases as the distance to the target increases (see Fig. 2; Beekman et al., 2005; De Marco et al., 2008; Gardner et al., 2007; Tanner & Visscher, 2010a; Weidenmüller & Seeley, 1999). For more distant targets (>500 m) the direction is indicated by precisely aligned dances; however, dances for closer targets have error to either the left or the right based on the direction of the turn that precedes the waggle phase. Bees following the dance average the vector information in the waggle dance to fly to a resource. Dances for targets closer than 100 m are often called 'round dances' as the waggle phase becomes so short the bees appear to be performing circular movements (von Frisch, 1967). These 'round dances' are in fact just a deformed waggle dance as direction is still encoded in the movement (Gardner et al., 2008; Griffin et al., 2012; Sen Sarma et al., 2004). Based on Figure 2.9 in Seeley (1995).

particular patch, collectively the workers focus on those patches that are most profitable (Camazine & Sneyd, 1991; De Marco, 2006; Seeley, 1986; Seeley et al., 1991).

## DANCING WITH AN ERROR

The vectorial component of the dance contains an inherent error. The degree of angular vector variation or 'error' in the dance decreases with increasing distance to a resource (Beekman, Doyen, & Oldroyd, 2005; Gardner et al., 2007; Towne & Gould, 1988). The

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