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Too much noise on the dance floor

Intra- and inter-dance angular error in honey bee waggle dances

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Successful honey bee foragers communicate where they have found a good resource with the waggle dance, a symbolic language that encodes a distance and direction. Both of these components are repeated several times (1 to > 100) within the same dance. Additionally, both these components vary within a dance. Here we discuss some causes and consequences of intra-dance and inter-dance angular variation and advocate revisiting von Frisch and Lindauer's earlier work to gain a better understanding of honey bee foraging ecology.

A honey bee forager who has found a good resource (e.g., a high quality/quantity source of nectar or pollen) returns to the hive and performs a waggle dance, a communication event that recruits nestmate foragers and directs them to the specific resource location.[1,2] The directional information is encoded in the waggle run, the portion of the dance where the bee waggles her body from side to side for a particular length of time while moving at a particular angle on the vertical comb.[2,3] How long she waggles in seconds roughly corresponds to how far she flew from the hive in kilometers. Her waggle orientation clockwise from vertical corresponds to the angle of the resource relative to the sun.[1-3]

A forager will repeat these waggle runs many times within a dance, and these successive waggle runs vary in both the distance and angle component.[2,4,5] Potential recruits—and biologists decoding waggle dances to determine where a forager has been—average the waggle runs to obtain a single distance and a single direction.[6,7]

Decoding waggle dances to determine where bees collect food has advanced our understanding of both the basic[8-10] and applied[11] aspects of honey bee foraging ecology. However, as with any research utilizing a communication system, proper application of waggle dance decoding involves an understanding of the sources and consequences of system noise.

In Couvillon et al. (2012), we describe one particular type of communication noise, an intra-dance angular variation that ebbs and flows depending on the mean angle the bee is dancing.[12] This ebb and flow, we hypothesize, is due to gravity: when a bee is dancing horizontally (either left or right) on a vertical comb, she performs a dance with higher scatter, as measured as intra-dance angular SD, compared with a more vertically-oriented (either up or down) dance on the vertical comb.[12] Because of the movement of the sun and the subsequent changes in dance angle, the periodicity of the change in scatter is approximately 6 h. The scatter—and its periodic changes—does not affect the overall angular dance mean obtained by averaging successive runs.

However, in addition to this intra-dance error about the mean, there is another type of angular variation that also depends on the angle at which the bee dances; however, this error ["*Restmissweisung*," (residual misdirection) as von Frisch called it] does affect the mean angle.[2,13] The bees, depending at which angle they dance, systematically communicate certain angles incorrectly.

Conceptually, perhaps it is easiest to think of our described variation as a 6-h

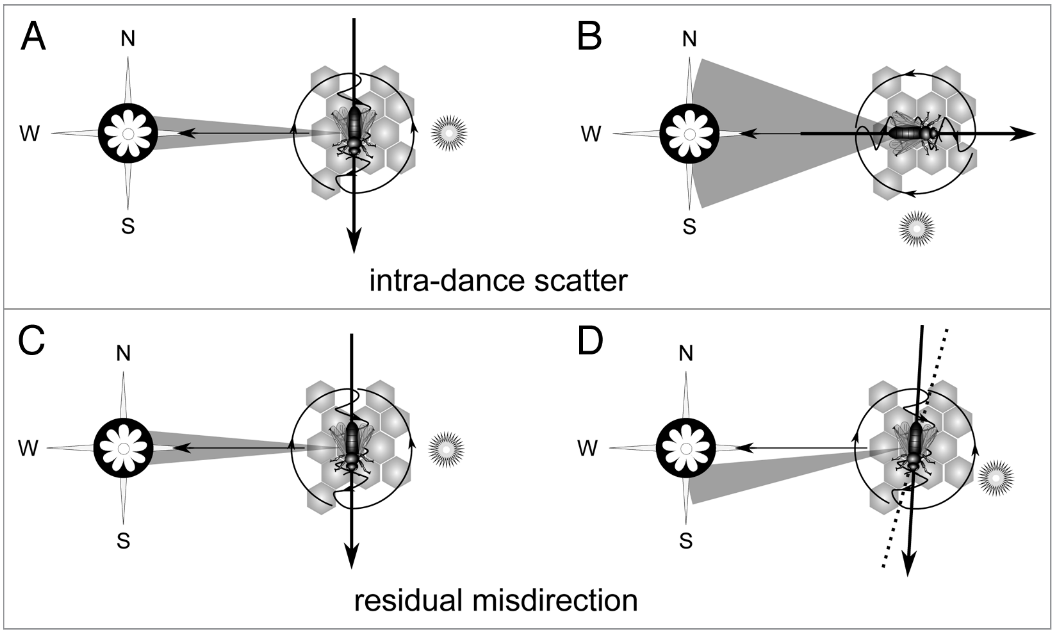

Figure 1. Honey bee waggle dances possess both within-dance angular scatter (**A and B**, gray wedge) and residual misdirection (*Restmissweisung*, **C and D**, gray wedge). A honey bee is dancing on a comb to indicate the position of a food source (flower on black circle) west of the hive (solid black arrow indicating the direction of the dance on the comb). When she begins to dance, the sun is in the east and therefore directly opposite the food, so the bee dances downward (**A**) with high precision. As the day progresses, the sun's location on the horizon moves from east to south, so the food is now 90° right of the sun and the bee is likewise dancing at 90° on the comb (**B**) with low precision, even if she still indicates the correct mean angle. This change in precision is due to intra-dance angular error from gravity.[12] Additionally, the same bee may experience a systematic angular misdirection, where danced angles are erroneously attracted to the axes.[13] A bee dancing downward (**C**) is unaffected by *Restmissweisung*, and she will dance with high accuracy as well as high precision. However, the bee may have trouble dancing for 190° (dashed line) and, instead, will dance with low accuracy (**D**) closer to 180° (solid black arrow).

fluctuation in intra-dance angular precision with no change in angular accuracy (**Fig. 1A and B**).[12] In contrast, von Frisch's described angular misdirection is a systematic fluctuation in angular accuracy (**Fig. 1C and D**),[13] independent of the precision. Additionally in our intra-dance variation, the scatter of waggle run angles within a dance increases around some axes (90, 270°) and decreases around others (0, 180°). For the *Restmissweisung*, angles seem attracted to the horizontal and the vertical axes. In other words, a bee wanting to dance for 190° may find herself dancing closer to 180° (**Fig. 1D**).

What are the consequences of angular variation? Our intra-dance angular scatter is most likely the easiest to handle for both potential recruits following the dance and biologists eavesdropping on the conversation: taking an average effectively reduces the intra-dance noise.[5]

The *Restmissweisung* is a different story. Von Frisch demonstrated that the recruited bees were unaffected by the misdirection.[2,13] However, he must have realized that the *Restmissweisung* would complicate matters for dance decoders. Even small residual misdirection translates into large errors in the plotting of long-distance foraging locations. For example, if residual misdirection is 10°, the estimated location of a resource at 1 km will be off by almost 200 m; this error will increase to over 800 m at 5 km (**Fig. 2**). Honey bees are known to forage far beyond these distances,[9] making this phenomenon problematic for ecologists wanting to investigate where bees collect their food. For von Frisch and Lindauer, working in the 1960s, the issue remained unresolved.

Now, 50 years on, we have at our disposal modern statistical tools that might be able to make sense of the pattern of residual misdirection. This understanding will allow for better, more accurate use of the honey bee language. By investigating this noisy dance floor of the honey bees, we see that the original work of von Frisch and Lindauer may prove to be, still, a magic well for discoveries in honey bee foraging ecology.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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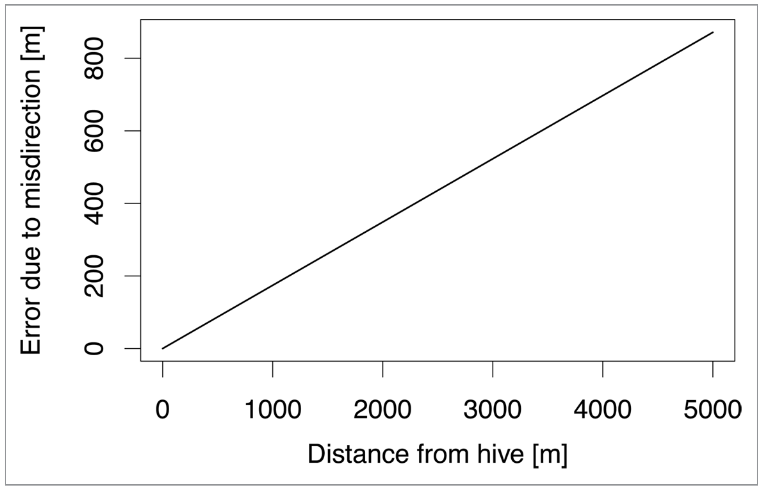

Figure 2. Error due to residual misdirection increases linearly with increasing distance to the resource from the hive. Here we demonstrate how *Restmissweisung* of 10° in dance angle translates into errors in meters away from the resource location.