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 nest-mate 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 basic8-10 and applied11 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 [“Restmisseusung,” (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
fluctuation in intra-dance angular precision with no change in angular accuracy (Fig. 1A and B). In contrast, von Frisch’s described angular misdirection is a systematic fluctuation in angular accuracy (Fig. 1C and D), 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.

The Restmissweisung is a different story. Von Frisch demonstrated that the recruited bees were unaffected by the misdirection. 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, 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.
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.