Detection of flow direction in high-flying insect and songbird migrants

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Goal-oriented migrants travelling through the sea or air must cope with the effect of cross-flows during their journeys if they are to reach their destination [1–3]. In order to counteract flow-induced drift from their preferred course, migrants must detect the mean flow direction, and integrate this information with output from their internal compass, to compensate for the deflection. Animals can potentially sense flow direction by two nonexclusive mechanisms: either indirectly, by visually assessing the effect of the current on their movement direction relative to the ground; or directly, via intrinsic properties of the current [4]. Here, we report the first evidence that nocturnal compass-guided insect migrants use a turbulence-mediated mechanism for directly assessing the wind direction hundreds of metres above the ground. By comparison, we find that nocturnally-migrating songbirds do not use turbulence to detect the flow; instead they rely on visual assessment of wind-induced drift to indirectly infer the flow direction.

Billions of insects and songbirds carry out compass-guided nocturnal migrations between Europe and Africa by flying in high-altitude airstreams [5,6], where they must cope with unfavourably-directed flows. The mechanisms by which these two taxa, differing substantially in flight performance and sensory capabilities, detect flow direction while flying high above the ground at night have eluded discovery. We answer this question by carrying out a comparative analysis of >10,000 radar tracks of individually migrating noctuid moths (Autographa gamma) and songbirds, and associated wind vectors, during multiple spring and autumn migrations over northern Europe (see Supplemental Experimental Procedures).

Fluid-dynamic theory [4] posits that fine-scale turbulence is anisotropic — that is, not equal in all directions — and stronger in the downstream direction. Thus, if a flying animal can detect these weak turbulent fluctuations, it can identify the flow direction. Crucially, the theory predicts that due to the Ekman spiral, an animal attempting to align its heading with the mean flow will tend to misalign slightly to the right of the downstream in the Northern Hemisphere (and to the left in the Southern Hemisphere) [4]. To determine if A. gamma moths and songbirds use these anisotropic turbulence cues to detect the flow direction, we analysed distributions of the ‘downwind offset’, δ, the angle between the self-propelled flight heading and the downwind direction (Figure 1), in relation to the taxon-specific seasonal preferred direction of movement (PDM) of both taxa [6] (see Supplemental Experimental Procedures). We modified the absolute values of δ in two ways. Firstly, we calculated the ‘corrected downwind offset’, δCORR, by assigning a positive value if the heading corrected for wind-induced drift (that is, the heading was closer to the PDM than the flow was; Figure 1A), but a negative value if the heading increased the drift (that is, it was further away; Figure 1B). Secondly, we calculated the ‘turbulence downwind offset’, δTURB, by assigning a positive value if the offset matched the prediction of the fluid-dynamic theory (that is, the heading was to the right of the flow; Figure 1B) and a negative value if it did not match the theory (that is, heading to the left of the flow; Figure 1A).
On occasions when the air flow was close to the seasonal PDM (i.e. the angle \( \omega \) between the flow and PDM was < 25°) the distribution of \( \delta_{\text{CORR}} \) for A. \( \gamma \)amma moths was not significantly different from zero (n = 30 migration events, \( \delta_{\text{CORR}} = +2.3° \), 95% CI = ±6.6°; Figure 1C), indicating that moths did not correct for small amounts of drift when travelling close to their preferred direction, and on average flew downwind. However, the distribution of \( \delta_{\text{TURB}} \) was significantly different from the expected value of zero and skewed to the right (n = 88, \( \delta_{\text{TURB}} = +2.8° \), 95% CI = ±6.8°; Figure 1C), indicating that moths did not correct for larger amounts of drift when travelling close to their preferred migration flow direction via turbulence cues and other zooplankton [9], and juvenile sea turtles [10] have also been postulated to directly detect currents, such sensory capabilities may prove to be widespread across the animal kingdom. However, our results indicate that nocturnally-migrating songbirds do not directly detect currents via turbulence cues; instead they probably rely on visual assessment of their movement relative to ground features to compensate for drift. In the study region (southern Sweden), migrating songbirds will be able to see a variety of landscape features including a prominent coastline and artificial light from several large cities in the immediate area, and these ground features presumably provide reliable references against which it is possible for songbirds to assess the degree of crosswind drift.\n
When downwind drifts were further away from the seasonal PDM (i.e. \( \omega > 25° \)) then offsets were consistent with both groups partially correcting for drift (moths: n = 88, \( \delta_{\text{CORR}} = +2.8° \), 95% CI = ±6.8°; Figure 1C), in line with the predictions of the turbulence mechanism of flow detection. In the few cases where the downwind direction for the songbirds was close to their seasonal PDM, the distribution of both \( \delta_{\text{CORR}} \) and \( \delta_{\text{TURB}} \) was centred around zero and was not significantly skewed towards either the PDM or the right (n = 10, \( \delta_{\text{CORR}} = -2.9° \), 95% CI = ±20.1°, Figure 1E; \( \delta_{\text{TURB}} = -3.5° \), 95% CI = ±20.0°, Figure 1F).


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