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Natural image statistics in the dorsal and ventral visual field match a switch in flight behaviour of a hawkmoth

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Many animals use visual cues to navigate their environment. To encode the large input ranges of natural signals optimally, their sensory systems have adapted to the stimulus statistics experienced in their natural habitats[1]. A striking example, shared across animal phyla, is the retinal tuning to the relative abundance of blue light from the sky, and green light from the ground, evident in the frequency of each photoreceptor type in the two retinal hemispheres[2]. By adhering only to specific regions of the visual field that contain the relevant information, as for the high-acuity dorsal regions in the eyes of male flies chasing females[3], the neural investment can be further reduced. Regionalisation can even lead to activation of the appropriate visual pathway by target location, rather than by stimulus features. This has been shown in fruit flies, which increase their landing attempts when an expanding disc is presented in their frontal visual field, while lateral presentation increases obstacle avoidance responses[4]. We here report a similar switch in behavioural responses for extended visual scenes. Using a free-flight paradigm, we show that the hummingbird hawkmoth (*Macroglossum stellatarum*) responds with flight-control adjustments to translational optic-flow cues exclusively in their ventral and lateral visual fields, while identical stimuli presented dorsally elicit a novel directional flight response. This response split is predicted by our quantitative imaging data from natural visual scenes in a variety of habitats, which demonstrate higher magnitudes of translational optic flow in the ventral hemisphere, and the opposite distribution for contrast edges containing directional information.

Image statistics of natural visual scenes are rarely homogeneous, and certain features often cluster in distinct parts of the visual field[1,2]. Our optic-flow imaging across several different habitat structures (Figures 1A and S1) found that the highest levels of translational optic flow were generated in the ventral hemisphere across all habitats (Figure 1B), including closed ones like forests (Figure S1C). The frequency of high-contrast edges, such as could be used for directional orientation, was highest in the dorsal visual field (Figure 1C).

To assess whether the free-flight behaviour of hawkmoths showed responses matching these regionally clustered sensory inputs, we used a 1 m long flight tunnel that the insects could traverse to shuttle between two flight cages. Patterns made from transparent red plastic provided both directional cues, with an orientation component independent of the flight direction, and translational optic flow cues, the magnitude of which depended on the direction in which hawkmoths crossed the contrast edges of the stimuli (Figure 1D). Also, the side walls of the tunnel were covered with 5% contrast checkerboard patterns, adjusted to elicit the weakest centring responses possible while retaining controlled flights (Figure S2A,D).

As has been shown in Dipteran and Hymenopteran[5], hawkmoths exhibited a centring response to grating patterns generating strong translational optic flow cues when presented in their ventral and lateral visual fields (Figure 1E, top two panels). The strength of the responses, measured as the centred median position of the flight paths (Figure S2B) and their straightness (Figure S2H), was highest with the ventral gratings, reflecting the natural distribution of translational optic flow we measured (Figure 1B). The ventral gratings also induced the typical reduction in flight speed that has been described previously in other insects[5] (Figure S2E,J, middle panel).

When the same patterns were mounted on the tunnel ceiling, however, we observed a novel and

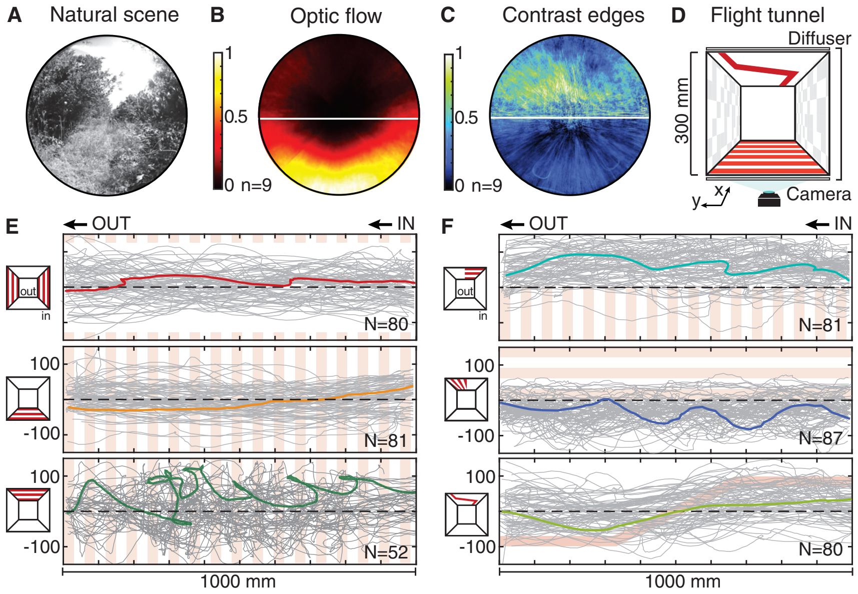

Figure 1. Natural image statistics and hawkmoth flight responses.
(A–C) The statistics of natural scenes are not homogeneously distributed across the visual field. Across nine open, semi-open (A) and closed habitats (see also Figure S1), the translational optic flow (B) was concentrated in the ventral visual field, and high-contrast edges containing directional information (C) were more frequent in the dorsal hemisphere. (D) The flight responses of hawkmoths were tested in a 1 m long tunnel, in which red patterns mounted on the tunnel walls in different parts of the visual field generated translational optic flow and directional cues. (E,F) Flight paths (grey, example in colour, see also Figure S2). N gives the number of flights; a longitudinal view into the tunnel is shown on the left, and the flight tracks are shown from the camera's perspective into the tunnel from below.

qualitatively different behaviour (Figure 1E, bottom panel): instead of traversing the tunnel centrally and with straight paths, the hawkmoths' flights showed a significant increase in lateral movement (Figure S2H) combined with a significantly lower flight speed compared to the other conditions (Figure S2E,J, bottom panel). Furthermore, we noted a strong reluctance of the hawkmoths to traverse the tunnel with the patterned ceiling at all, resulting in a lower number of successful flights during the same sampling period as the other conditions. We confirmed this by presenting gratings mounted on either the right or the left half of the ceiling. The hawkmoths significantly preferred to fly in the part of the tunnel without a dorsal pattern (Figures 1F, top panel, and S2G). For the same stimuli mounted on the floor, there was no side preference (Figure S2G).

Hawkmoths also avoided flying under longitudinal gratings (Figures 1F, middle panel, and S2G), indicating they generally avoided ceiling areas covered with high-contrast patterns, not only areas that generated translational optic flow. When the hawkmoths traversed the tunnel with the dorsal grating covering the whole ceiling, their flight paths showed an increase in components aligned with the main orientation axis of the stripes in the pattern (Figure S2K, bottom panel); conversely the ventral grating elicited straight flight paths perpendicular to the stripes' main axis (Figure S2K, middle panel). Together, these observations suggest that the hummingbird hawkmoths responded to the position and orientation of the dorsal patterns, in addition to their translational optic flow components.

To directly test if the animals aligned with a prominent dorsal orientation cue, we presented a single longitudinal stripe, which crossed from one to the other side in the central third of the tunnel ceiling. Most hawkmoths followed the change of pattern position with a change in flight direction (Figure 1F, bottom panel), evidenced by the significant difference in lateral position in the first and last third of the tunnel compared to the control and ventral condition (Figure S2I). Some hawkmoths even flew towards the tunnel side where the stripe was mounted on the ceiling (Figure S2K, bottom panel), indicating that the hawkmoths oriented their flight relative to the stripes' position and orientation.

Such behaviour has not been observed previously in hawkmoths, or any other insect species we are aware of. In its reliance on dorsal contrast cues for orientation, its closest equivalent might be the canopy orientation of ants, shown to use the pattern of a tree canopy to find their way back to their nests[6]. In *M. stellatarum*, the innate directional response to high-contrast edges in the dorsal visual field might be a strategy to avoid flying under dense vegetation: by aligning in parallel with tree lines, the likelihood of flying into a canopy-covered area is reduced. This would fit well with their natural abundance in open and semi-open habitats, and their inclination to escape from perceived threats with an upward flight motion, strongly hindered by a canopy. Further experiments will elucidate the nature and adaptive value of this intriguing behaviour.

The qualitatively different flight responses to stimuli in different visual regions we observed in hummingbird hawkmoths — a translational optic flow response to lateral and ventral contrast patterns, and flights directed by the oriented components and the position of dorsal patterns — have not been previously reported from other flying insects. Regional anisotropies in the response gain to translational optic flow, however, are well documented: *Heliothis virescens* moths use dorsal and ventral random-dot patterns equally well to stabilise their flights in a wind tunnel, though they rely stronger on dorso-lateral than ventro-lateral patterns[7]. In line with that, *Manduca sexta* hawkmoths control their flights well with the ventral, but not the dorsal half of their visual field occluded[8]. The opposite gain distribution was found in fruit flies, which showed stronger responses to ventrally presented translational side-slip than a dorsal one[9]. No avoidance of dorsally presented patterns was observed in either of these species, and the stimuli used in these studies did not contain contrast edges that could have induced a directional response. A honeybee study with striped patterns on all sides of a flight tunnel did not report any directional responses to the stripes' dorsal contrast edges, though the simultaneous presentation across the visual field might have masked region-specific effects[10]. Our novel findings therefore provide a framework for future comparative studies on insects and other flying animals, to investigate whether different visual pathways govern flight responses in different parts of the visual field, and how these exploit regional variations in natural scene statistics to optimally adapt the behavioural responses to different visual habitats.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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