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ANALYSIS OF VISION AND GAZE CONTROL IN INSECTS

Roland Hengstenberg
Max-Planck-Institut für biologische Kybernetik, D-72076 Tübingen

Visual perception is greatly facilitated when the eyes are properly aligned with the surroundings and gaze is held stable on the target of interest. This demand is in conflict with the desire for high mobility and maneuverability. Hence vertebrates, mollusces, crustacea and some insects have evolved means to stabilize their eyes temporarily on the visual scene while moving through their habitats.

Flies, for example, have a preferred body posture like most other animals: when walking on even ground their body axis is roughly horizontal and the back is directed upwards. In flight, their attitude is similar, only the body axis may be more elevated, especially at low flight speeds. Very probably the fly's eyes, other sense organs and the sensory nervous system have been adapted during evolution to work best in this preferred orientation.

Flying insects have, in principle, all six degrees of freedom to move in space: they can translate along their body axes (thrust, lift, side-slip) and rotate about these axes (roll, yaw, pitch). After any voluntary or involuntary change of flight attitude the necessity to keep balance requires that the insect returns to its normal, upright posture. During perturbations and such corrective flight maneuvers, however, vision may become disturbed by misdirection of the gaze axis, by misalignment of the eyes and by motion blurring. Hence a means to stabilize the eyes would seem advantageous.

Flies and most other insects have two kinds of eyes: three small ocelli, each with a single underfocused wide-angle lens and several hundred photoreceptors: they are best suited to sense the mean brightness of large parts of the surroundings. In flies, the visual fields of the ocelli are directed upwards.

The two large compound eyes consist of several thousand so called ommatidia, each with a narrow-angle lens, focused to infinity and 8 photoreceptors falling in two main classes: six peripheral ones (R1-R6) that are the main inputs to the motion perception system and two central ones (R7, R8) arranged in tandem that serve other purposes. The lenses of both types of eyes are part of the head capsule and therefore rigidly coupled. Gaze can only be shifted by either turning the head or the whole body.

The blowfly *Calliphora* can turn its head horizontally (yaw ±20°) and vertically (pitch ±20°) and can rotate it around the body axis (roll ±90°). In this study only roll turns are considered which play an important part in flight control.

Head movements of insects can hardly be observed in free flight but flies can be studied during tethered flight in a wind-tunnel. Fixing the fly coaxially to the shaft of a servomotor allows to turn the animal. The walls of the tunnel are lined with varying patterns, illuminated from the outside and can be turned by a second motor.

This way either the fly and/or its optical surround can be turned arbitrarily. Head movements of the fly, relative to its trunk, are observed with a small video telescope through the entrance nozzle of the windtunnel.

When a fly is held stationary during flight and the surroundings are not moved, it nevertheless turns its head continuously in different directions, sometimes saccade-like. At the same time it varies its wingbeat amplitudes and the posture of its hind-legs, apparently in an attempt to perform one of the coordinated flight maneuvers that characterize the tortuous and unpredictable flight paths of blowflies.

When a fly is turned unexpectedly around its body axis it generates simultaneously a corrective flight maneuver and a compensatory head turn which alone may correct for about 2/3 of the imposed perturbation.

Which sense organs and sensory cues tell the fly the direction and speed of its motions? By turning the panorama, instead of the fly, it can be shown that corrective head turns are elicited visually. Conversely, turning the fly in visually featureless surroundings elicits also a corrective head turn, apparently due to a mechanosensory perception of body rotation. By systematic variation of the stimuli and surgical manipulations of different sense organs, four visual and four mechanosensory response components could be identified: (a) a response to coherent motions of extended patterns, (b) a response due to the orientation of visual contours in the frontal visual field, (c) a large tonic dorsal light response, all mediated by the compound eyes, and (d) a small phasic dorsal light response mediated by the lateral ocelli. (e) The body motion response is mediated by the halteres which are gyroscopic sense organs for rotations. They are homologous with the hindwings of other insects but have been massively transformed to serve the new purpose. (f) wing-load differences are perceived through strain receptors in the wing base, (g) the direction of gravity is sensed by the weight distribution among the legs through leg proprioceptors but only during walking and finally (h) neck-proprioceptors also influence head posture i. e. the alignment of head and trunk.

The different sensory components have different dynamic characteristics and complement each other: mechanosensory components have short latencies and elicit larger responses at high motion speeds than visual responses that tend to have longer latencies and operate best in the lower speed range. All components operate autonomously, which is a necessary condition, if the different components are to complement one another.

During walking and flight different combinations of sensory and motor components are used for head stabilization and locomotor control. This requires appropriate, status dependent routing and weighting of the respective neural signals. It can be shown that the major sensory components, mentioned above, influence head posture and locomotion in parallel. At present, the major efforts are directed to determine the specific characteristics of the component responses and to identify the neural circuits subserving them.

Stabilization of the fly's eyes tends to support visual perception on several levels of processing: (a) Reduction of retinal image velocity improves contrast transfer especially for high spatial frequencies. (b) Correct localization of a target in the visual field allows specific processing in retinotopic networks. (c) Correct orientation of targets facilitates their assessment, for example in object recognition. (d) Rotational stabilization facilitates more sophisticated evaluations of retinal image flow, e.g. distance perception by utilization motion parallax. For insects, which have too small a triangulation base for stereopsis over reasonable distances, this improvement is probably the most important one.

Literature:

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