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AN OCELLAR DORSAL LIGHT RESPONSE IN A DRAGONFLY

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One of the functional roles suggested for the insect ocelli is their involvement in flight behaviour such as the maintenance of stability by monitoring movements of the animal relative to the horizon (Hesse, 1908). In a recent study on second order ocellar neurones in locusts, Wilson (1978) concluded from physiological and anatomical considerations that this system is ideally suited 'to detect rapid movements of the whole visual field which represent instability in flight'. In fact, indirect behavioural evidence for this concept was provided by Mittelstaedt (1950), who observed that dragonflies with occluded ocelli go through a sequence of unstable flight attitudes and stalls when released in the presence of a single light source of small angular dimensions. We report here simple experiments which give direct evidence that the ocelli do function as equilibrium organs during flight.

Experiments were performed on imagines of *Hemicordulia tau* (Anisoptera, Corduliidae) mounted in a wind tunnel and flying at wind speeds between 2 and 4 m s^{-1}. Light sources for stimulation were arranged as in Fig. 1, and additional infrared illumination was provided where necessary to allow direct observations and video recordings. All stimulus sources had small angular dimensions in order to provide a minimum amount of stimulation to the compound eye system as a whole. Because the ocelli have wide visual fields and defocused optics, point sources are equivalent to extended sources (Wilson, 1978). The sources A, B and C were positioned to address the ocelli separately, and switching them evoked changes in head posture as shown in Fig. 2(*a–d*). When the source B was turned on, the head moved downward from the position 2(*a*) to the position 2(*b*). Similarly, activating source A or C evoked a head roll to the right or left (Fig. 2*c*, *d*). The rolling response was much more marked (rotation of up to 90°), when the sources A and C were activated in alternation. When the median ocellus was reversibly blinded with plasticine the movement (*a–b*) no longer occurred while the response (*c–d*) was not affected. Single frame analysis of video recordings showed latencies in the order of 40 ms, and the movements were completed within 100 ms.

To further identify the sensory organs which mediate the light evoked head movements, the head was continually illuminated with white light from one of the alternative positions D and E (Fig. 1). Under these conditions, passing a sharp 1 mm wide shadow across the head evoked the responses summarized in Fig. 2(*e–k*). When the

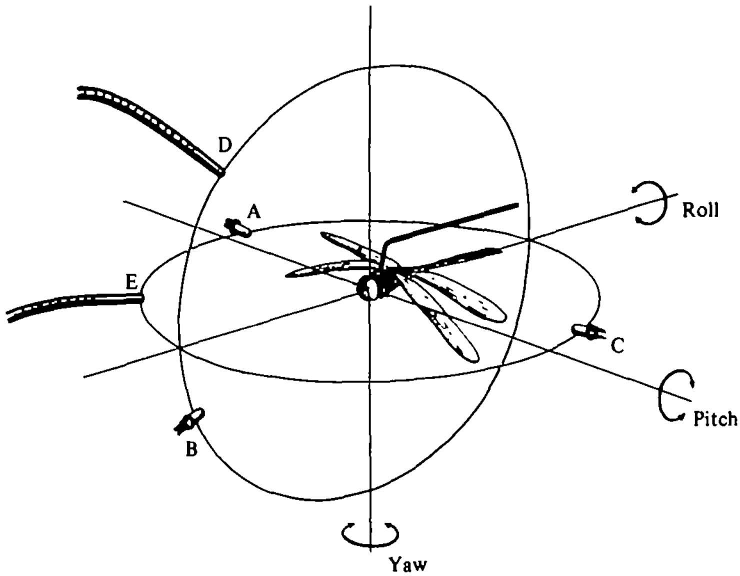

Fig. 1. Experimental set-up (not to scale). The intact animal is tethered on the synthorax to a fixed rod and mounted in a wind tunnel (not shown). A, B and C are 30 mW green light-emitting diodes positioned slightly off the ocellar optical axes in order to address the ocelli separately. D and E are two alternative positions of the end of a quartz light guide emitting white light from a 150 W xenon arc lamp. All light sources are 12 cm distant from the animal's head, subtending angles of less than 2°.

shadow was moved to shade the median ocellus, the head moved upwards around the pitch axis, while removal of the shadow evoked a downwards movement. This response occurred for both vertical and horizontal movements (Fig. 2*e–f*, *g–k*). When either lateral ocellus was shaded, the head rolled away from the shaded side (Fig. 2*h*,*j*). This response was independent of the direction of stimulus movement showing that we are not observing fixation responses mediated by the compound eyes.

The responses are independent of the direction of incident light (D or E, Fig. 1). Under condition E the pseudopupil of the compound eye (Horridge, 1978) is quite separate in location from the ocelli. Passing a shadow across the compound eye caused no response. Moving an illuminated object in front of the head was also ineffective, provided that its shadow did not pass across the head. This provides further evidence that the compound eyes do not take part in the response.

Finally, we note that light-evoked head movements were observed consistently in all animals tested ($n = 55$), provided that they were in flight. No signs of habituation were observed. This lack of habituation is a prerequisite for any sensory-motor system to function as an equilibrium organ.

Our experiments demonstrate that the ocelli mediate a set of fast directional responses such that the apex of the head is turned towards the direction of maximum overall illumination, in analogy to the dorsal light response (Mittelstaedt, 1950). Under natural conditions, appropriate changes in illumination are caused mainly by the relative movement of the horizon. The responses are directed to compensate for

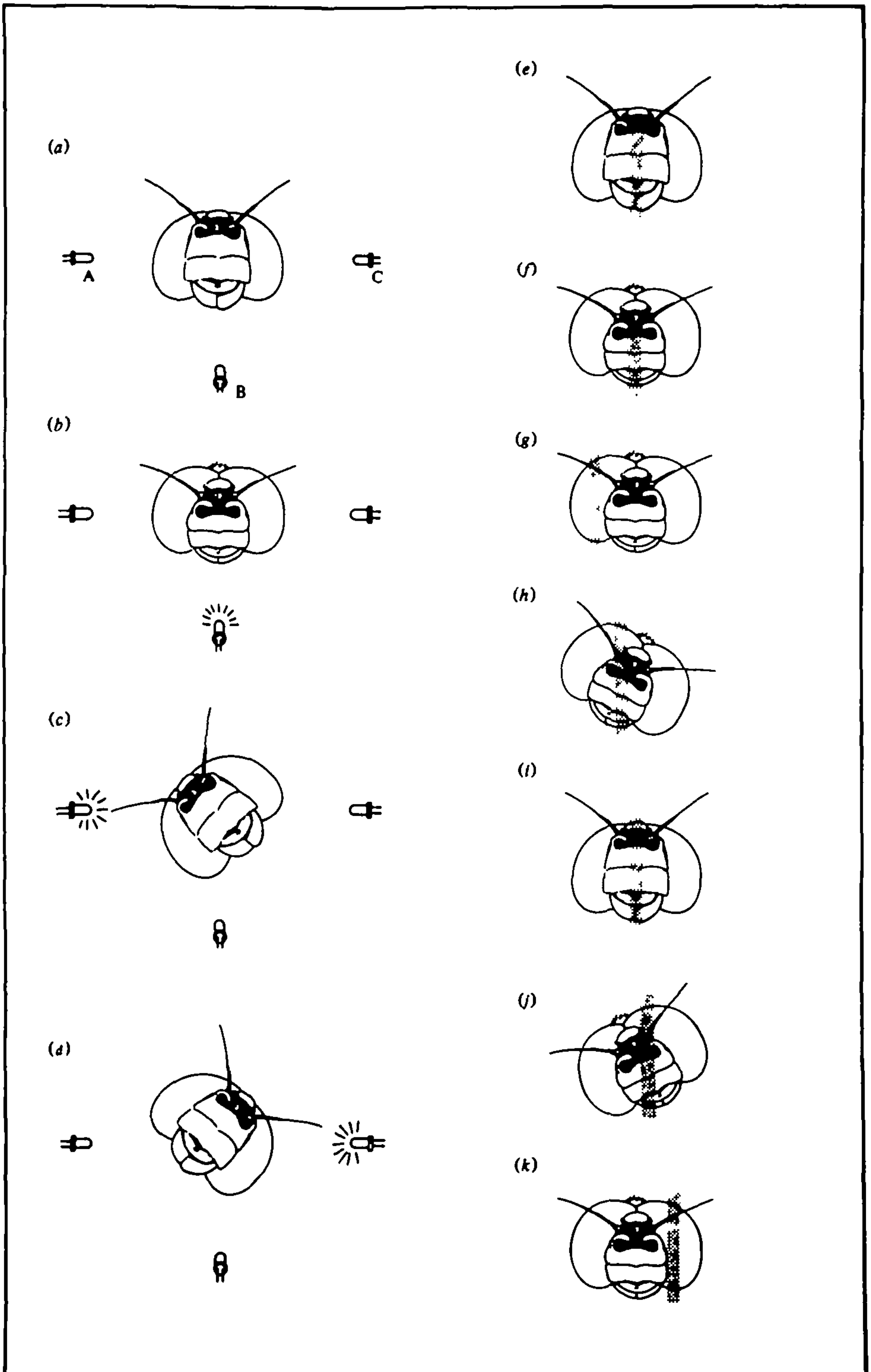

Fig. 2. Head positions of a flying dragonfly, drawn from video recordings. (*a–d*) Responses to changes of illumination as indicated (A, B and C, see Fig. 1). (*e–k*) Responses to changes in the position of a shadow under condition D or E. (*e,f*) Head movement around pitch axis evoked by vertical movement of shadow across median ocellus. (*g–k*) Sequence of head movements around roll and pitch axes evoked by lateral movement of shadow across all three ocelli in sequence.

such changes, and hence the ocellar system is capable of functioning as a flight equilibrium organ by monitoring the horizon, as proposed by Wilson (1978).

The question arises as to the role of this head stabilization. For the compound eye mediated dorsal light responses of dragonflies (Mittelstaedt, 1950) and locusts (Goodman, 1965) it has been clearly shown that head movements around the roll axis are monitored by neck proprioceptors, leading to corrective wing movements so as to realign the body with the head. An analogous mechanism has been described for yaw movements in flies (Liske, 1977), but head and body can also turn simultaneously (Land, 1975). For the case of pitch attitude control, corresponding data are still missing. In any case, even though wing movements were not monitored in the present experiments, it is reasonable to infer that, in free flight, head stabilization is associated with reorientation of the body in a direction which will increase stability in flight.

Thus it appears that the visual component of equilibrium control in flying insects such as the dragonfly consists of inputs from a dual system, involving both compound eyes and ocelli. A comparison of the two types of eyes reveals a fundamental difference: while the compound eyes have high spatial resolution (Laughlin, 1974), only low frequency spatial information is conveyed by the second order ocellar neurones (Wilson, 1978). On the other hand, both systems have similar temporal characteristics (Ruck, 1958), but it is interesting to note that light adapted ocellar neurones signal only changes in overall intensity (Chappell & Dowling, 1972).

As pointed out by Wilson (1978), the lack of spatial resolution gives the ocelli an advantage over the compound eyes for the detection of rapid changes of the visual field as a whole. Dragonflies are capable of remarkable aerodynamic manoeuvres, and during a rapid turn it is vital to process information about flight attitude as quickly as possible in order to maintain flight stability. As a consequence of the low pass spatial filter characteristics of the ocelli, that information is available in the second order neurons. While information on overall changes in illumination is conveyed by the compound eyes, this must occur through higher order convergence, necessarily involving a time delay. It seems that the ocellar system is more suited to the rapid fulfilment of this task.

We conclude therefore that the compound eyes provide the fine resolution needed to define the actual position of the horizon, while the ocelli monitor rapid changes of that position, allowing fast corrections of attitude which are vital for the maintenance of flight stability.

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