VISUALLY CONTROLLED HEAD MOVEMENTS
IN PERCHED ANISOPTERAN DRAGONFLIES

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Small, moving, visual targets commonly excite fast saccadic head movements (head--cocks) in perched dragonflies. Head-cocking in response to natural stimuli has been examined by video-recording perched individuals of 7 libellulid and 1 gomphid species in the field during periods of feeding or sexual activity. Head-cocks varied in duration from 40 to > 1000 ms (mean 350 ms) and they usually occurred many times per minute. Typically a head-cock consisted of 3 components: a fast saccadic movement in the rolling and/or pitching plane; a brief period of stasis or of slow, smooth head movement, often involving a yaw component and interpreted as visual tracking; and finally a fast return to the rest position. A minority of head-cocks was followed by take-off, normally in the direction to which the head had been aimed. In species which kept their forelegs lifted off the ground when perched (e.g. *Orthetrum*), yawing was sometimes amplified by a turning of the prothorax on the synthorax, and also sometimes by rotations of the whole body on the legs. Head-cocks could be evoked by throwing or swinging stones 10-20 cm in front of a perched dragonfly, but their mean duration was significantly less than that of spontaneous head-cocks. No head-cocking has been seen in perched aeshnids or in the zygopterans examined. Head-cocks are believed to aim the acute zones of the eyes at a target, and they may also allow its distance to be estimated by stereopsis since the axes of some ommatidia in a forward--looking acute zone either side of the frons converge a few cm in front of the insect. Head cocks may also determine the direction of take-off through the action of proprioceptors in the neck.

INTRODUCTION

Dragonflies are well known to use one of two principal strategies in feeding and in reproductive behaviour – perching and flying (CORBET, 1962). Fliers, such as most aeshnids, may be on the wing continuously during active periods and can search in a large area but, compared to perchers, they pay a higher energetic cost

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and may suffer a visual impairment as a result of their movement. Animals can see better when they are immobile, for example during hovering, stalking or perching, and the visual cost of forward flight has been estimated to be equivalent to a loss of 2-3 log units of light intensity (HORRIDGE, 1977). Perching libellulids and gomphids usually choose sites where they can maintain a high body temperature, and from which they can scan a large area and take off rapidly in pursuit of prey or conspecifics.

Observations have shown that alert, perched dragonflies make frequent and abrupt head-cocks, sometimes of large amplitude. These resemble the saccades of other animals and they are presumed to be in response to moving visual targets. Only a small minority of head-cocks is followed by take-offs. Head-cocks may allow the dragonfly to scrutinize a visual target using the acute zones of the compound eyes where visual resolution is high, and also to estimate its distance by stereopsis. Many libellulids have two acute zones, recognisable from the large size of the pseudopupil where they are found: these are a 40° zone in the fronto-dorsal region of the eye comprising large-diameter ommatidia (LAND, 1989), and a smaller forward-looking zone on either side of the frons where the ommatidia are narrower (HORRIDGE, 1977).

HORRIDGE (1977) has drawn attention to the many arthropods which make abrupt turns or saccades towards visual targets. For example hunting spiders move the whole body round to face a target (LAND, 1971), mantids make fast turns of the head (LISKE & MOHREN, 1984; CORRETT, 1990; ROSSEL, 1991), crabs move only the eyestalks (HORRIDGE, 1966), while many running (MILLER, 1979) or flying insects (COLLETT, 1980; EGELHAAF, 1987) perform saccades by turning the whole body.

The aim of this report is to draw attention to the high frequency of head-cocking in perched dragonflies, in which both a saccadic and a smooth-tracking component can be distinguished. The marked variability of the take-off threshold following head-cocks is also emphasised, which perhaps gives some insight into the 'motivational state' of an insect.

MATERIAL AND METHODS

Observations and video recordings have been made on 6 *Onychogomphus uncatus* (Charp.) (mature males), 4 *Libellula fulva* Müll. (mature males and females), 4 *L. quadrimaculata* L. (mature males), 1 *Orthetrum brunneum* (B. de Fonsc.) (mature male), 15 *O. cancellatum* (L.) (teneral, immature and matures of both sexes), 9 *O. coerulescens* (Fabr.) (mature males and females), 4 *Sympetrum danae* (Sulz.) (mature males) and 15 *S. striolatum* (Charp.) (teneral, immature and mature males and females), all when perched in sunlight during feeding, and in some cases also when reproductively active near water. They were made between 10.00 and 16.00 h. on several days during July and August, 1993 and 1994, in England at sites near Oxford and at Thursley National Nature Reserve, and in France on the River Vidourle (Hérault) and also in the vicinity of canals in the Venise Verte (the eastern area of the Parc Naturel Régional du Marais Poitevin).

Video records (SONY Hi-8 × 24) were made of head movements occurring spontaneously (pre-

sumed to be to natural targets) or which were evoked by small stones (ca 5 mm diameter), thrown or attached to a thread and swung 10-20 cm in front of the perched insect. They were analysed in single frames at 40 ms intervals. Sketches of head positions were made on transparent paper on the monitor and also from frozen specimens examined under a binocular microscope.

Fig. 1. The three planes of head movements: X = pitching; – Y = rolling; – Z = yawing.

The dragonfly head can be moved in three planes intersecting at a point just behind the head, by muscles which act on the cervical sclerites (cf. GORB, 1993). The planes are described as yawing (horizontal rotations about a vertical Z axis), pitching (upwards movements about a horizontal X axis), and rolling (rotations about a longitudinal Y axis) (Fig. 1). The pseudopupils were photographed in the eyes of living specimens which were then preserved in 2% formaldehyde. Thick horizontal sections of preserved heads were made with a razor blade for microscopic observations on the orientation of ommatidia.
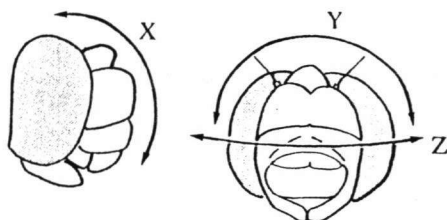
RESULTS

OCCURRENCE OF HEAD-COCKING

All libellulid and gomphid species examined in the field made frequent, fast, spontaneous head-cocks while perched. Some were seen to be made in response to natural targets such as conspecifics, other insects, birds and in one case apparently to vehicles on a nearby road, but in many the target was not identified (Fig. 2).

No head movement, except those accompanying grooming or feeding, was observed in the following species, all examined while perched vertically: *Anax imperator, Aeshna grandis, A. mixta, Cordulegaster boltonii*. Nor were head-cocks seen in any of the following zygopteran species, observed while perched during periods when they were feeding: *Calopteryx splendens, C. haemorrhoidalis, Enallgma cyathigerum* and *Ischnura elegans*. It can tentatively be concluded that head-cocking does not occur in anisopteran fliers which perch vertically, such as aeshnids, nor in Zygoptera.

In libellulid species, head-cocking did not appear while prey items were being chewed, or at least until they had been nearly consumed; nor was it seen in females in tan-
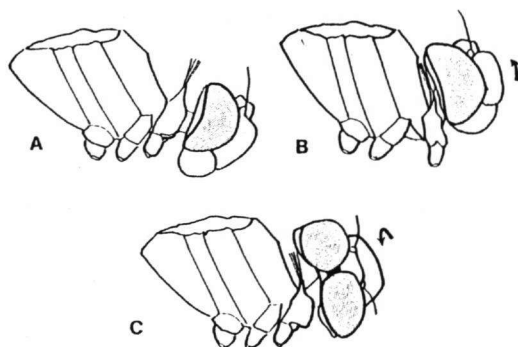

Fig. 2. Diagram to show head positions of a libellulid: (A) in resting position; – (B) pitched upwards; – (C) rolled to the right.

dem though it did occur in tandem males and in males during copulation. No head-
-cocking was seen in tenerals before feeding had started.

FEATURES OF HEAD-COCKING

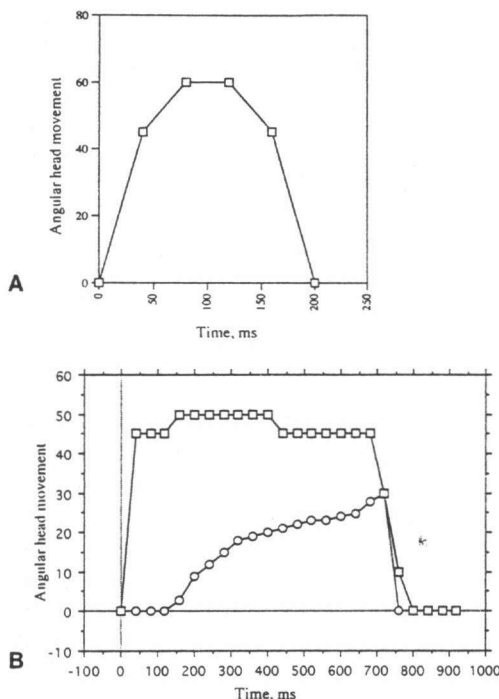The libellulid dragonflies examined perched during the day usually with the long

Fig. 3. Plots of head-cocks in *Orthetrum cancellatum*: (A) a brief head-cock achieved by a rolling movement to the right; – (B) a longer-lasting head-cock brought about by rolling to the right (□——□), the roll position then being held steady while there was a slow pitching upwards (○——○).

axis of the body between 0 and 45° to the horizontal according to the perch site, and with the head and body level in the rolling plane. The angle between the head and thorax showed little change with body position except during head-cocks. Head-cocks involved movement of the head in any or all of the planes of movement. Rolling rotations of the head (Y axis) occurred through up to 80°, upwards pitching (X axis) by a maximum of 50-60°, and yawing (Z axis) to one side or the other by 20-30°. Many recorded head movements combined at least two of these components (Fig. 3), but the video records usually did not permit a more precise resolution of their contributions.

O. cancellatum, O. coerulescens and *L. quadrimaculata* commonly perched with the forelegs held up in the flight position and in these species head-cocks were sometimes accompanied by lateral turning movements of the prothorax on the synthorax. The raising of the forelegs appears to be a mechanism to allow a greater degree of head movement to occur. Sometimes dragonflies rotated about a vertical axis on the perch by moving their legs, and this provided a further means of amplifying the head movements in the yawing plane.

Spontaneous head-cocks were variable in duration lasting from 80 to exceptionally > 1000 ms, measured from the start of a head movement until the return to the

rest position. In *O. cancellatum* they had a mean total duration of 350 ± 36 ms (s.e.; 32 movements from 4 individuals; max 800 ms). In contrast evoked head-cocks in response to stones which were thrown or swung past perched insects were typically brief with a mean duration of 182±11 ms (s.e.; 46 movements from 4 individuals), significantly shorter than spontaneous head-cocks (paired t-test: Df, 31; p = 0.0002), and they were often completed when the stone was still approaching the dragonfly.

Head-cocks can be divided into three stages: firstly, a fast saccade-like rolling and/or pitching movement causing the acute zones of the eyes to face towards the target, usually completed in <40 ms; secondly, a period of no movement or of slow, smooth turning, assumed to be target tracking, which might be brief but sometimes lasted for up to several hundred ms and might include a yaw component; and thirdly a fast return to the rest position, completed in 40-80 ms (Fig. 3). The majority of head-cocks involved mainly fast up and return movements, the prolonged mid--stage appearing less commonly, perhaps when the target was distant or slowly moving.

Spontaneous head-cocks commonly occurred 10-20 times per minute, although sometimes there were only 1-2 per minute and the mean frequencies for different species ranged from 8 to 18 min^{-1} (Tab. I). The values probably reflect the variable abundance of visual targets in the vicinity and are unlikely to depend on intrinsic species differences, although the possibility of some spontaneous head-cocks occurring without a stimulus cannot be ruled out.

Table I

The mean frequencies of spontaneous head-cocks observed in the field – [S.E. = standard error; N = No. of insects observed]

Species	Mean frequency (min^{-1})	S.E.	N
Onychogomphus uncatus	17.0	–	1
Libellula fulva	18.0	5.5	3
L. quadrimaculata	8.0	1.94	5
Orthetrum brunneum	16.0	–	1
O. cancellatum	8.33	1.72	6
O. coerulescens	11.56	1.41	9
Sympetrum striolatum	9.44	3.12	9

'Investigatory' flights are defined as those in which the dragonfly took off and flew towards a target, and then quickly returned to the same perch. In contrast 'alarm' flights are those in which take-offs were followed by the departure of the insect. In most dragonflies only a small proportion of head-cocks, and sometimes none, was followed by a take-off. For example one *O. uncatus*, perched close to the river, head-cocked to each of 40 stones thrown at 3 s intervals or swung at 0.5 s^{-1} in its vicinity, but never took off. An actively feeding *S. striolatum* head-cocked in response to 47% of all swung stones (n=112) and took off in response to 10% (11) of them. However an immature *O. cancellatum* (a male lacking pruinescence) head-cocked and then took off to investigate each of 20 stones thrown at 5-second intervals, re-settling on the same perch in < 3 s, although in no case did it attempt to seize the stone. Such take-offs which led to investigatory flights were normally
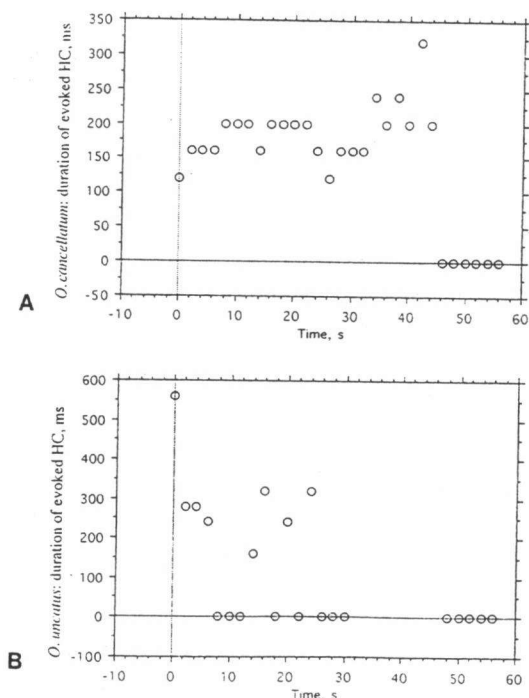
Fig. 4. Plots of successive head-cocks in (A) *O. cancellatum* and (B) *O. uncatus* in response to a stone being swung 15 cm in front of the head once every two seconds. – [Each head--cock is represented by one point. Zero readings indicate the absence of a head-cock].

made in the direction to which the head had been cocked, flight being initiated before the head had returned to its rest position.

Repeated swings of a stone in front of a perched dragonfly sometimes evoked head--cocking responses which gradually waned in frequency, perhaps representing habituation of the response (Fig. 4). However the difficulty of presenting a target identically in consecutive swings makes this conclusion uncertain. LAND (1971) found that spiders quickly habituated to repeated excitation of one region of a lateral eye, but remained responsive to excitation of nearby regions.

Observations and photographs of the eyes in living *O. cancellatum* have shown that in the forward-looking region either side of the frons the pseudopupil is about 1.3 mm long and 0.43 mm wide. Horizontal sections of preserved heads of *O. cancellatum* and *S. striolatum*, made at the level of the ventral margin of the frons where the eyes are separated by 3.5 mm, allowed the positions and orientation of ommatidia in this region to be photographed and drawn (Fig. 5). The ommatidia nearest the frons were found to be inclined towards the midline by maximally 4.5° to the long axis of the body, with visual axes converging about 2 cm in front of the head. Over a small distance laterally of about 5 ommatidial diameters the inward tilt declined and disappeared, but the area of convergence extended vertically on either side of the frons for about 1 mm. Ommatidia in the medial part of the eyes on the dorsal surface also have visual axes with a small convergence, but they are probably spaced too closely to be used effectively for stereopsis. Ommatidia in the hind part of the eye are tilted towards the posterior and have fields of vision directed behind the insect.

DISCUSSION

Saccadic behaviour, in which the eyes are rapidly switched to a new part of the environment by body, head, eyestalk, or eye movements, is widespread in both vertebrates and invertebrates (e.g. ROGERS et al., 1993). By keeping the eyes steady, visual discrimination can be enhanced and the target can be fixated by that part of the eyes best adapted for high resolution. During the saccade the brain may cease to analyse visual information (cf. HEISENBERG & WOLF, 1979).

The main conclusion based on observations of dragonflies in the wild is that active, perched libellulids make surprisingly frequent saccade-like head-cocks, often one every few seconds, even though the great majority are not followed by a take-off. When take-off does occur, it is commonly made in the direction to which the head was cocked. Observation of male *S. striolatum* perched on a stick in a cage in the laboratory revealed no head-cocking and I assume that all spontaneous head-cocks in the wild occur in response to moving visual targets even though I failed to detect many of those targets.
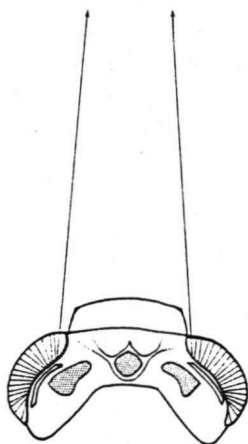

Fig. 5. Diagram of a horizontal section of the head of *O. cancellatum* made at the level of the lower margin of the frons, showing the orientation of the ommatidia. Ommatidia in the anterior part of the eye have visual axes which converge in front of the dragonfly's head.

Head-cocks are divisible into three stages: a fast saccadic roll and/or pitch of the head, a period of variable duration when there may be no movement or a slow turning often including a yaw component, and finally a fast return to the rest position. Only when targets can be presented under more controlled conditions will it be possible to relate the head movements more closely to target position and velocity. When the perched dragonfly keeps its forelegs lifted, head movements in the yawing plane are sometimes amplified by laterally directed turns of the prothorax. Dragonflies may also turn the whole body sideways by moving the legs. Head-cocking appears to be inhibited during prey-chewing at least until most of the food has been consumed, and also during grooming and roosting, and in teneral insects and tandem females.

Some actively feeding, immature *O. cancellatum* had particularly low flight thresholds, taking off after every evoked head-cock, whereas mature dragonflies head-cocked as frequently but seldom took off. Though dragonflies respond to many visual targets by head-cocking, a central mechanism probably determines the threshold of a subsequent take-off, causing it to be low in immature and hungry insects but higher in those which are mature and well-fed. That sexually active males responded to artificial targets with head-cocks as readily as immature insects but were never then seen to take off to investigate them, suggests either that experience, or possibly an innate response to conspecifics, can improve the discrimina-
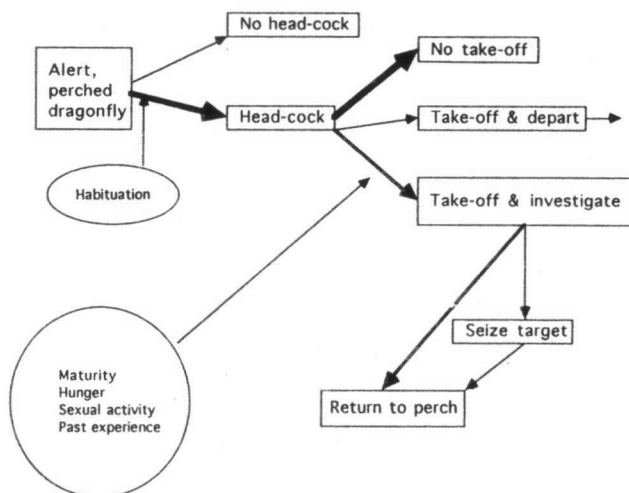
Fig. 6. Flow diagram showing the possible effects of various factors, shown within circles, which may influence the head-cocking and the take-off thresholds. – [Arrow thickness gives a qualitative impression of the frequencies of occurrence].

tion of visual targets. A tentative scheme is presented in Figure 6 in which several factors are shown to act on the take-off threshold.

In smooth tracking, slow and continuous adjustments of eye (or insect) position keep the acute zones aimed at a moving target (e.g. LAND & COLLETT, 1974; COLLETT & LAND, 1975; LAND, 1992) and they over-ride optomotor responses which would otherwise tend to stabilise the eyes' (and insects') position in space (EGELHAAF, 1987). The slow movements of the dragonfly head which sometimes followed the initial fast saccade are assumed to represent visual tracking. That such activity occurred much more commonly during spontaneous head-cocks than in those evoked by artificial targets suggests that the dragonfly could quickly identify stones as targets of no interest, a conclusion also supported by the brevity of most evoked head-cocks.

Head-cocking in a perched dragonfly may serve three possible functions. Firstly it may aim either the dorso-frontal or forward-looking acute zones of the eyes towards the target, thereby enhancing target discrimination. Secondly it may provide information about the target's distance from the dragonfly. Anisopterans in flight can probably estimate the distance of prey, mates or landing sites by motion parallax information as in some other insects (SRINIVASAN et al., 1989; SOBEL, 1990), although stereopsis may also play a part at short distances. Perched dragonflies, however, cannot use motion parallax and probably depend on stereoscopic vision for distance estimation, as do some of their larvae and many other ambush predators (COLLETT, 1987). The frons of S. *striolatum* and O. *cancellatum* separates the forward-looking regions of the eyes by about 3.5 mm, slightly more than the separation of the eyes of some Calopterygidae. Forward-looking ommatidia near the medial margins of the two eyes have visual axes which are aimed inwards by up to about 4.5° and converge about 2 cm in front of the head. Ommatidia placed slightly more laterally have axes which converge further in front. These

may permit some stereoscopic vision to occur, allowing the distance of a target to be estimated. Information about target size and distance are two of the factors which may be used to determine whether take-off should occur, but dragonflies may also learn to recognise the appearance or characteristic movements of potential mates or prey. These mechanisms may combine to reduce the likelihood of pursuing inappropriate targets such as birds or aeroplanes – or thrown stones. A third function of head-cocks may be to determine the direction of take-off through the asymmetrical excitation of neck proprioceptors (MITTELSTAEDT, 1957).

The species of *Aeshna* observed together with *Cordulegaster* were not seen to make head-cocks when perched. This may be because such species are 'fliers' (CORBET, 1962), being continually on the wing when feeding and usually also when sexually active. The absence of head-cocking in the Zygoptera examined, however, is more surprising since *Calopteryx* spp. and other Zygoptera frequently detect passing prey while perched and take off in pursuit. If head-cocking never occurs in these species, it may be because their eyes do not have well developed acute zones, adequate information about target direction and identity being provided by any region of the eyes.

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