The Ocellar Component of Flight Equilibrium Control in Dragonflies

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Summary. This paper describes the dynamics of light-evoked head reflexes in the dragonfly *Hemicordulia tau* under light conditions which were selected to optimally address the ocelli.

1. The responses occur only during flight.

2. Stimulation by a light positioned to address the median ocellus evokes a head movement around the pitch axis. The threshold is in the order of 10^7 photons $\cdot$ cm^{-2} $\cdot$ s^{-1}. With increasing intensity, the responses become progressively faster but do not increase in amplitude.

3. Stimulation by lights positioned to address the lateral ocelli evokes head movements around the roll axis with a similar threshold and similar dynamics as in the pitch responses. The responses are strongest when two sources at either side of the animal are switched in alternation.

4. No evidence is found for interactions between the lateral and the median inputs.

5. During sustained illumination from the median source, the head is tilted towards it indefinitely, and increasing the intensity causes only a small additional change of head position. Decreasing the intensity causes a large movement of the head away from the source, and then the system readapts rapidly and the head returns to the on-position (high pass filtering). If increment pulses are superimposed on a steady background, the magnitude of their effect is a function of both their duration and amplitude.

6. If the median source is modulated by a square wave of a frequency above the high pass cut-off, the amplitudes of the responses are proportional to modulation depths and independent of average intensity over 4 log units.

7. At intensities below 10^{11} photons cm^{-2} s^{-1}, the spectral sensitivity has a maximum in the green, exceeding the UV-sensitivity by a factor of 5; at higher intensities the responses become more sensitive to UV than to green (reverse Purkinje shift). It is suggested that the reverse Purkinje shift is a functional adaptation to optimize the detectability of the contrast between sky and ground both in dim light and in direct sunlight.

8. The dynamics of the behavioural responses can be largely accounted for by known properties of the neuronal elements of ocellar systems.

«Des expériences semblables à celles que j'ai faites sur les yeux à rézeau, m'ont prouvé que les petits yeux des Abeilles, les yeux lisses leur servent aussi à se conduire.»

R.A.F. de Réaumur (1741)

Introduction

The maintenance of stability during locomotion depends on the presence of equilibrium organs, and the demands on their performance increase with the complexity of the tasks involved. Aerodynamic flight is one of the most complex modes of locomotion, and while many sensory systems participate in the stabilization of flight in insects, specialized gravity receptors do not occur (Wilson 1970). The direction of the centre of overall illumination, however, is usually close to the vertical direction, and it has been shown that flying dragonflies (Mittelstaedt 1950), locusts (Goodman 1965) and crickets (Tomioka and Yamaguchi 1980) exhibit dorsal light responses, turning their backs towards that centre.

These responses could be mediated by two types of visual systems, namely the compound eyes and the ocelli. Ocelli are present in sets of 3 in many pterygote adult insects, and their involvement in flight behaviour has been repeatedly discussed (e.g., Réaumur 1741; Link 1909; Homann 1924a; Kalmus 1945; Bayramoglu-Ergene 1964). As recently demonstrated in detail by Wilson (1978a), the ocelli are particularly

suited to mediate dorsal light responses during flight because (a) their visual fields are wide and their optical axes are aligned such that during balanced flight, half of each field is filled by ground and the other half by sky, and (b) as a result of their underfocussed optics, information on fine details within the visual fields is not received. In consequence, appropriately weighted information about the direction of overall illumination is present in the ocelli at the level of the first synapses, and the question arises whether this information is actually utilized for the control of flight equilibrium.

As shown by Mittelstaedt (1950) and Goodman (1965), the ocelli in dragonflies and locusts participate in the control of flight equilibrium, but under the experimental conditions chosen in those studies their role is secondary in comparison to the role of the compound eyes. The ocellar component of dragonfly dorsal light responses can be observed in isolation, however, if stationary and pulse-modulated stimulus sources of small angular dimensions and moderate intensities are used (Stange and Howard 1979). Under such conditions, the number of compound eye facets stimulated is too small to mediate a dorsal light response (Goodman 1965), while the ocelli are stimulated optimally by fast changes of intensity (Autrum and Metschl 1963). It has been demonstrated (Stange and Howard 1979) that the dorsal light responses observed under those conditions are solely attributable to the ocelli: in response to illumination or shading of the median ocellus, flying dragonflies rotate their heads around the pitch axis, moving the apex towards the light source or away from the shade, and stimulation of either lateral ocellus evokes corresponding movements around the roll axis. Ocelli can therefore directly initiate coordinated behaviour, and the purpose of the present paper is to describe details of these responses in order to complement the available anatomical and physiological data (rev. Goodman 1970, 1975; Laughlin 1980), and to examine the consistency of that description.

Materials and Methods

Animals. Adult dragonflies of the species *Hemicordulia tau* (Anisoptera, Corduliidae) were caught locally. They were kept in total darkness and high humidity at 12–15 °C and used within 5 days of capture. The observations reported below were obtained from a total of 124 animals.

Preparation. Animals were waxed to a holder and mounted in a wind tunnel (Fig. 1). In order to facilitate observations of head movements, a 1 mm^2 spot of white paint was applied to the apex of the head; otherwise the animals were left intact.

The wind tunnel consisted of a 20 cm length of 12 × 12 cm square perspex tubing, open at one end and equipped with a suction fan at the other; the head of the animal was located 5 cm from the entrance. In this arrangement, the air flow around the animal was laminar. The wind speed was adjusted to 4 m/s.

Recordings. To observe the responses, an Ikegami CTC 6000 CCTV camera equipped with a 7262 A vidicon tube was connected to a 105 mm macro-Nikkor objective with 100 mm bellows and aligned as indicated in Fig. 1. Infrared illumination detectable by the camera but not by the animal was provided by light from a 30 W tungsten lamp filtered through 2 Kodak Wratten gelatine filters No. 78 (IR cut on filters; 50% transmission at 800 nm, <0.1% transmission below 735 nm). The light was directed towards the animal at an oblique angle from behind (Fig. 1) in order to minimize stimulation of the ocelli by any residual light in the visible range. Possible effects of this light on the animals were tested by changing its intensity by a factor of 10, and no responses were observed. The sensitivity of the camera was sufficient to obtain a recognizable image of the spot on the animal's head down to an objective aperture of f/11.

Stimulation. In the majority of the experiments, stimuli were provided by a set of three Siemens LD 57C light emitting diodes ($\lambda p = 560$ nm, $\Delta\lambda = 25$ nm), arranged such as to address the three ocelli separately (cf. Stange and Howard 1979). The LEDs were driven by programmable current sources allowing calibrated variation of intensity over a range of 10^3; in addition, filters could be fitted to the LEDs to reduce light fluxes further where necessary. For the measurements of spectral thresholds (Fig. 9), a standard setup was used consisting of a 150 W xenon arc lamp, a set of ND and interference filters, a shutter and a light guide. For the substitution experiment (Fig. 10), stimulation in the near UV was provided by a similar arrangement, using a 15 W tungsten lamp and a combination of Schott glass filters UG1 and BG12 ($\lambda p = 370$ nm, $\Delta\lambda = 20$ nm); stimulation in the green was provided by a LED as described above. The light sources were calibrated using an International Light IL 700 Research Radiometer and calibrated detectors.

Retrieval and Analysis of Data. In order to obtain numerical representations of the responses, it was necessary to measure the head positions in many individual frames of video information. To permit rapid inspection of the about 10^6 frames of video obtained in the present study, a microcomputer with graphics facilities was progammed to generate a video signal containing a reference grid, stimulus markers and a frame numbering clock. This signal was mixed with the video signal from the camera, and the output was stored on tape for later frame by frame analysis, allowing determination of head positions with an accuracy of $\pm 1.5°$.

The quality of the responses in freshly captured animals is poor as those animals tend to exhibit strong spontaneous head movements, and similar behaviour occurs after strong light adaptation. Therefore, all observations reported here were performed on animals which had been in captivity and absolute darkness for at least 24 h, and the data presented in Figs. 3–8 were obtained from particularly quiet individuals. To further improve the signal-to-noise ratio of the recordings, periodical stimulus patterns were used throughout, and all response waveforms shown are averages of 5 subsequent sweeps. For all results reported, reproducibility was verified by repeating the experiments in at least 5 individuals.

As obtaining measurements through frame by frame analysis is tedious, this procedure was used only where detailed information on the waveforms of the responses was required (Figs. 3–8), and a different technique was used for obtaining the results presented in Figs. 9 and 10. A threshold searching program was implemented in the computer which initially presented a stimulus of randomly selected intensity. After one trial of five repetitions of this stimulus an observer had to make a forced choice whether the animal had responded and to instruct the program accordingly. The program
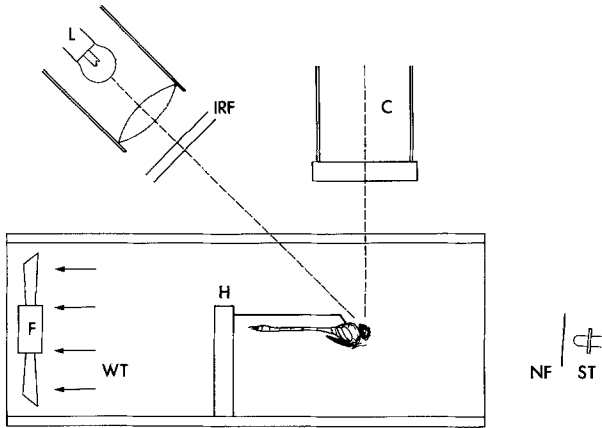
Fig. 1. Schematic side view of experimental setup. *WT* wind tunnel; *F* fan; *H* holder for animal; *L* light source for IR illumination; *IRF* infrared filters; *C* video camera; *ST* stimulus source; *NF* ND filter. Only the median stimulus source is shown; the two lateral sources are aligned along the pitch axis of the head, above and below plane of the drawing. Wind tunnel blackened except for windows for light from the various sources and for observation
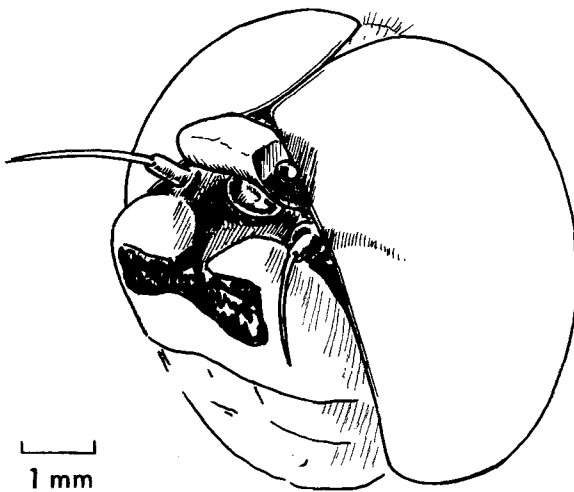

1 mm

Fig. 2. View of the head of *Hemicordulia tau,* illustrating the disposition of the ocelli

then kept changing stimulus intensities systematically (superimposed with a random component in order to keep the observer unaware of the stimulus in the next presentation), and would eventually converge towards a threshold value. The threshold was considered to be established when one intensity had been found to be above threshold in 5 out of 5 trials, and when the same condition had been found to apply to another intensity below threshold. The validity of this procedure was tested by employing a total of 5 observers, 3 of whom were unaware of the purpose of the experiments; there were no noticeable inconsistencies between the results obtained by different observers.

Results

General

The optical axis of the large median ocellus of *Hemicordulia* is aligned with the longitudinal axis of the head (roll axis), and the less conspicuous lateral ocelli are aligned with the transverse axis (pitch axis) (Fig. 2). The field of view of the median ocellus extends laterally over approximately $\pm 80°$, and in the dorsoventral plane it is restricted to $\pm 30°$ by the vertex above and the frons below. As suggested by Stavenga et al. (1979), those structures act as a set of visors, shielding the median ocellus against direct sunlight from above and against reflections from water surfaces from below. The fields of view of the lateral ocelli are less restricted, caudally by the compound eyes, and ventrally by the frons.

As in other Anisoptera (Mittelstaedt 1950), the head of *Hemicordulia* has the shape of an incomplete sphere with a deep indentation at the back; it is pivoted to the neck close to its centre. The head joint, allows rotational movements of the head around all three axes, and when viewed from above (Fig. 1), the magnitude of rotations around the pitch and roll axes can easily be determined from the translational displacements of the apex of the head in the plane of view. Illumination from the front evokes rotation around the pitch axis such that the apex of the head is tilted forward, and illumination from either side causes analogous roll movements.

The head reflexes are observable under the present experimental conditions only if the animals are in flight. In this mode of behaviour, the legs are folded back under the thorax, and both head and abdomen are lifted from their relaxed resting positions. The head exhibits a continuous jitter, indicating sustained activity of the neck muscles. This behaviour is not necessarily accompanied by active wing beat. It is readily evoked by wind of speeds around $4 \text{ m} \cdot \text{s}^{-1}$, and sometimes it is maintained continuously for up to 1 h. In still air, short bursts of flight activity can be evoked by breaking contact of the legs with an object (tarsal reflexes), or they occur spontaneously. The head reflexes can be evoked whenever an animal is in flight, and the presence of wind is not necessary.

Time Course and Intensity Dependence of Responses to 100% Contrast

The data presented in Fig. 3a were obtained by periodically switching the median stimulus source on and off and recording head movements around the pitch axis; for the results in Fig. 3b the two lateral light sources were activated in alternation (right on and left off and vice versa), and movements around the roll axis were recorded.

For the case of the pitch responses (Fig. 3a), the amplitude of head deflection approaches a maximum value once the light intensity exceeds the threshold by more than 1 log unit: at higher intensities, the
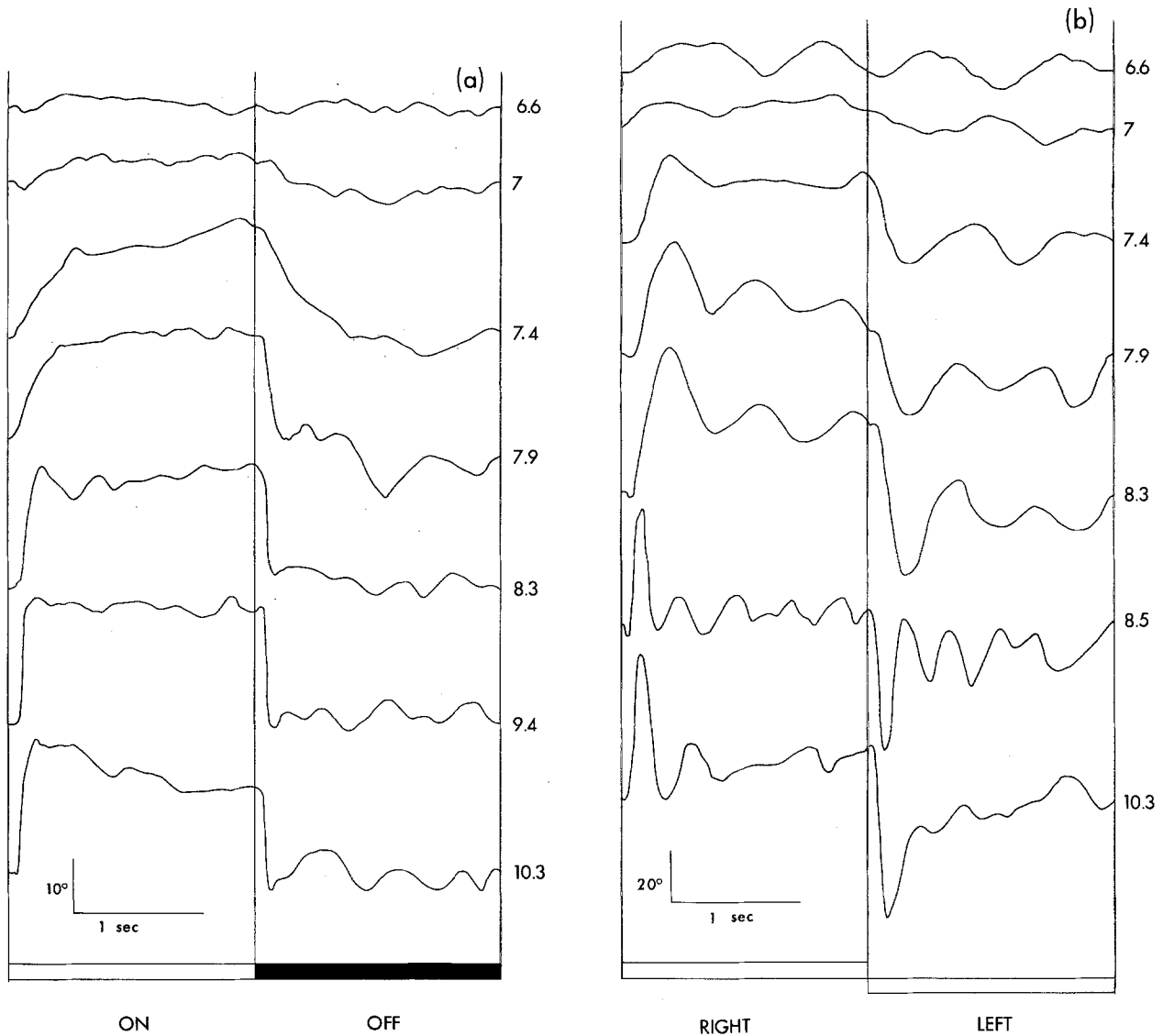
Fig. 3. a Changes in head position around pitch axis in response to activating the median light source at the indicated intensities (log photon · cm^{-2} · s^{-1}). Upward deflection: rotation towards light source. b Changes in head position around roll axis in response to switching lateral sources. Upward deflection: rotation to the right

responses become progressively faster without further increases in amplitude. Even for the highest intensities, no clear head movements are detectable for the first 50 ms after stimulus onset. After this latency period the head moves to its on-position at an intensity-dependent rate: at intensities above 10^9 photons·cm^{-2}·s^{-1} the movements are very fast (about 500 degrees/s), and essentially completed within 40 ms after response onset. After termination of the stimulus, the movement back to the off-position occurs in a similar fashion. The responses are predominantly tonic, and in continuous light the on-position is maintained indefinitely, and is the same at all intensities tested.

This description of the essential response parameters can be generalized: detailed measurements on 4 other animals and direct observations on 23 animals showed very similar responses. In particular, the thresholds were consistently in the range around 10^7 photons·cm^{-2}·s^{-1} (± 0.5 log units), provided that the animals were dark adapted.

For the roll responses (Fig. 3b), thresholds were in the same range, and also the increase of response speed with intensity followed a similar pattern. Other parameters of the roll responses are too inconsistent however, both between individuals and at different moments in the same animal, to permit generalization. For example, the pronounced increase in re-

sponse speed following a marginal increase of intensity from 8.3 to 8.5 (Fig. 3b) is fortuitous: it coincided with a brief interruption of the experiment in order to change filters attached to the light sources. In one other example, the responses slowed down under the same conditions, and in other cases the waveforms of the responses changed spontaneously. The responses in Fig. 3b are predominantly phasic and oscillations occur after the initial peaks, but this cannot be generalized either, as demonstrated by the two other examples contained in Fig. 4.

Interaction Between Inputs

The roll responses are strongest when the two lateral stimuli are activated in alternation (Stange and Howard 1979), and it was for this reason that this stimulus configuration was used for the measurements in Fig. 3b. In order to further specify the interaction between the two lateral inputs, animals were subjected to stimulus conditions where delays of varying durations were inserted between the termination of illumination from one side and the onset of illumination from the other.

Two examples of the resulting responses are presented in Fig. 4a and b. They show that the off-response from one side interacts with the on-response from the other side: in example (a) the dark period between switching off one source and switching on the other must not exceed 200 ms to give a clear response, i.e. the off-response from one side facilitates the on-response from the other; in example (b) the effects appear to be simply additive. As in the responses of Fig. 3b, there was considerable variability between individuals, and spontaneous changes could occur in the same individual.

To test whether the pitch responses are influenced by inputs to the lateral system, both lateral sources together and the median source were switched in various combinations (e.g. in alternation, simultaneously, median source switched and both laterals continuously on, etc.). In no case were the pitch movements different from those expected for the stimulus patterns applied to the median source alone.

Consequently it is concluded that the pitch responses are conveyed solely by the median ocellus. For this reason, and also because the roll responses are less consistent, the further details of the system as described in the following sections are obtained exclusively from observations of pitch responses.

Dark Adaptation After Increment Flashes

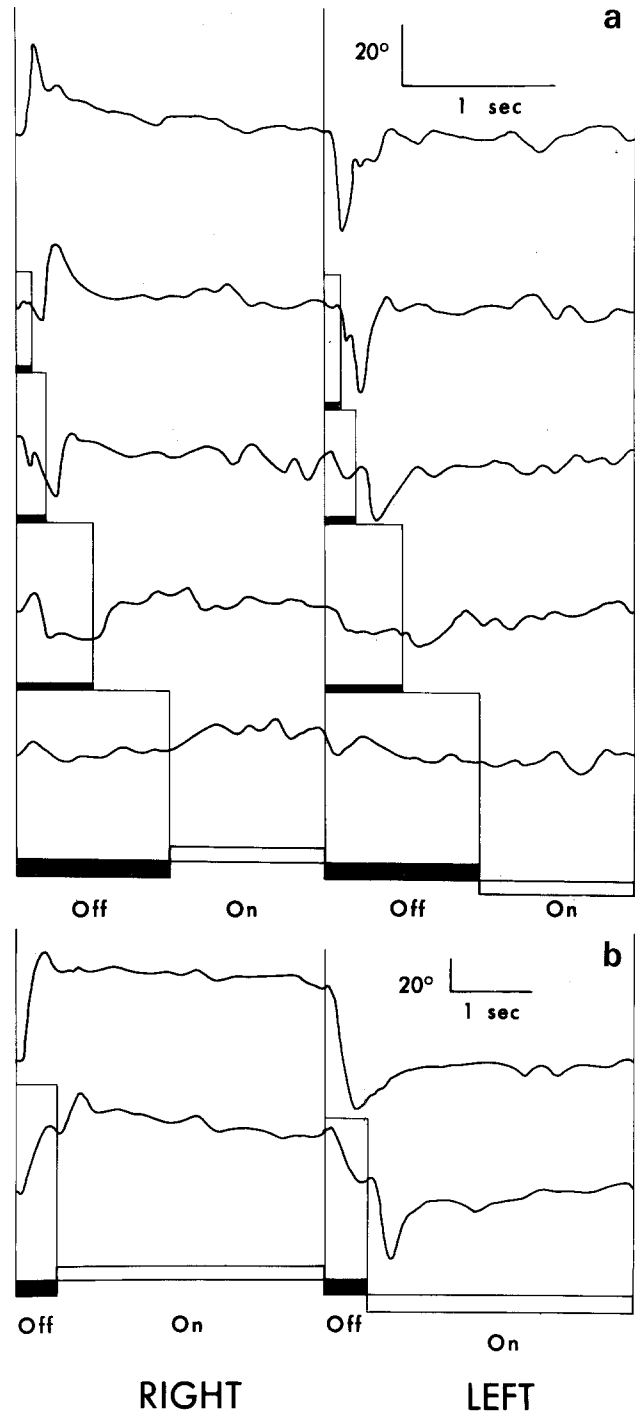The amplitude of the pitch responses saturates at an intensity of 1 log unit above threshold (Fig. 3a), and

Fig. 4 a, b. Effect of inserting delays between switching off one lateral light source and switching on the contralateral one for the examples of two animals (**a, b**). Measurements taken at an intensity of 10^9 photons·cm^{-2}·s^{-1}

the responses are predominantly tonic. At first sight this suggests that, in the presence of any significant sustained background, the system would saturate and therefore be incapable of signalling changes in intensity. This shortcoming would mean that the system
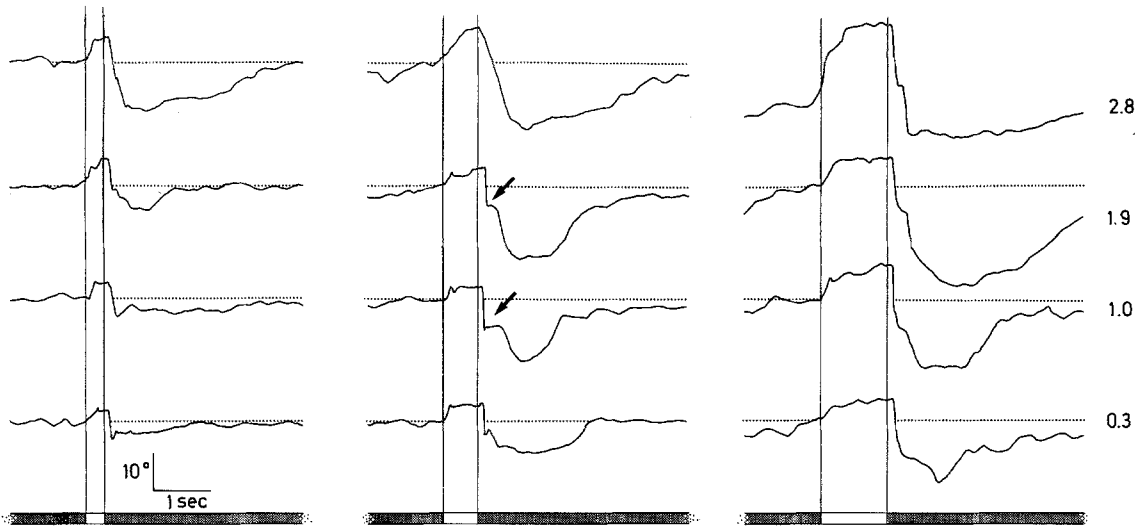
Fig. 5. Responses to superimposing increment flashes of varying intensity (I) and duration on a steady background (I_o) of 10^{10} photons $\cdot \text{cm}^{-2} \cdot \text{s}^{-1}$. Figures indicate logs of I/I_o. Dotted lines: method of quantifying aftereffects. For arrows see text
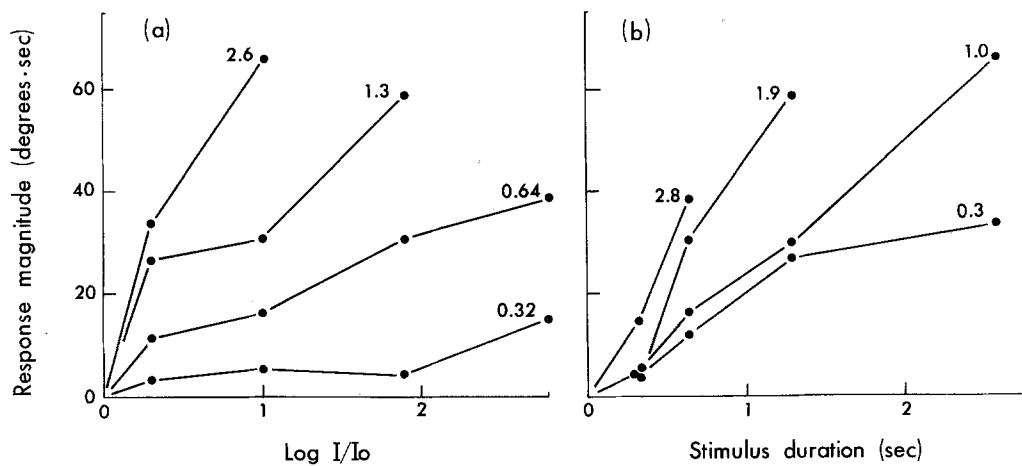

Fig. 6a, b. Magnitude of aftereffect, plotted as a function of **a** intensity and **b** duration of increment flashes. Figures inside the graphs represent **a** durations and **b** logs of I/I_0

could only control flight attitude in a natural environment at intensities just above the absolute threshold level, which is equivalent to the light conditions during an overcast moonless night.

To examine this point, animals were adapted to a constant background, upon which increment flashes were superimposed. The flashes were varied in intensity and duration, and the resulting responses are shown in Fig. 5. Indeed, the onset of the additional illumination causes only a small change of head position, even for increments of 2 log units. After returning to the background, however, a pronounced transient aftereffect occurs. The magnitude of this aftereffect increases both with intensity and duration of the stimulus, and it consists of two components with different time courses, namely a fast response similar to the off-responses shown in Fig. 3a, and a slow

transient. The biphasic nature of the effect is particularly evident for stimuli of intermediate durations and amplitudes, as indicated by arrows. In response to the strongest increment stimuli, the head returns to the dark position, and the response does not fully readapt to the background within the 5 s chosen as interstimulus intervals.

With changes of stimuli, the off-transient changes both in duration and amplitude. In order to account for both parameters, the area between the waveform and the position after readaptation (approximated by averaging over the last 500 ms before stimulus onset) was chosen as a measure for the magnitude of the aftereffect (cf. dotted lines in Fig. 5). The cases in which the interstimulus interval was too short for readaptation were not analysed.

The values thus determined are plotted in Fig. 6

as functions of both stimulus intensity and duration. Within the limitations of experimental accuracy, the magnitude of the aftereffect is proportional to both the duration and the logarithm of intensity.

The results presented in this section imply that it is adequate for conceptual purposes to characterize the pitch movements as 'shading reflexes' and to interpret the constancy of head positions at any sustained illumination above threshold as a baseline rather than as saturation: increasing intensity from a sustained background has little effect, decreasing it has a strong effect. This effect is of a transient nature, however, and within a few seconds the system readapts to the reduced intensity and returns to the baseline. Therefore the system contains a high pass filter component, and the frequency range in which intensity changes are signalled optimally has a lower limit determined by the time constant of that filter (about 1 s) and an upper limit set by the latency (about 50 ms).

Responses to Varying Contrasts

To measure response amplitudes as a function of small intensity changes within the optimum frequency range, light of a preset background intensity was modulated by a 1 Hz symmetrical square wave, and several modulation depths were tested. Furthermore, to obtain information about the effect of background intensity on the response-versus-contrast function, the same measurements were taken at 3 background intensities in steps of 2 log units.

The waveforms of responses thus obtained are shown in Fig. 7, and the data points in Fig. 8 represent the response magnitudes for each waveform (average difference between on-position and off-position). It turns out that clearly recognizable responses occur at modulation depths of 0.33 and above, that the response amplitudes are approximately proportional to modulation depths, and that the dynamic range of the responses extends up to 100% modulation, i.e. no saturation occurs. The effect of varying the background intensity by a factor of 10^4 is small: the magnitudes of the responses to a given modulation depth and also the thresholds do not change drastically with background intensity ($\Delta I/I$ = constant; Weber-Fechner law).

Spectral Sensitivity

To measure the wavelength dependence of absolute threshold, pitch responses were evoked by 1 s light flashes from the monochromator/light guide setup at a repetition rate of 0.5 Hz.
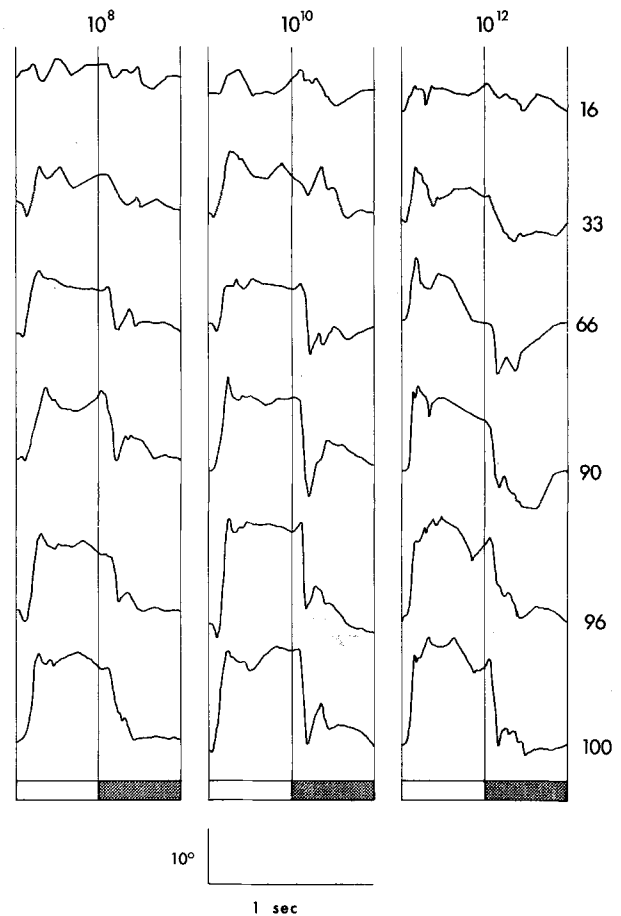

Fig. 7. Responses to modulated light as a function of modulation depth and average intensity. Figures at the right: modulation depths in %; top figures: average intensities in photons $cm^{-2} \cdot s^{-1}$

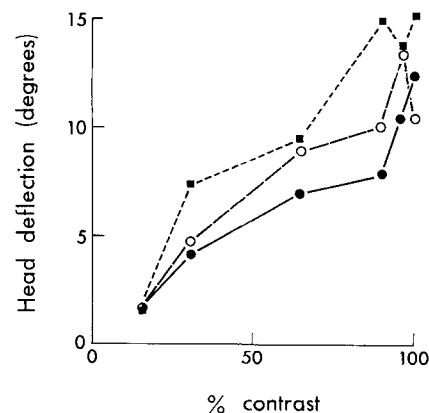Fig. 8. Same data as in Fig. 6, response magnitude as a function of modulation depth. ●——● 10^8, o----o 10^{10}, ■----■ 10^{12} photons $\cdot cm^{-2} \cdot s^{-1}$ of average intensity

Thresholds were determined at 14 wavelengths ranging from 340 to 620 nm by means of the threshold searching procedure described in the methods section; complete sets of data could be obtained from 5 individuals. As the absolute sensitivities varied be-
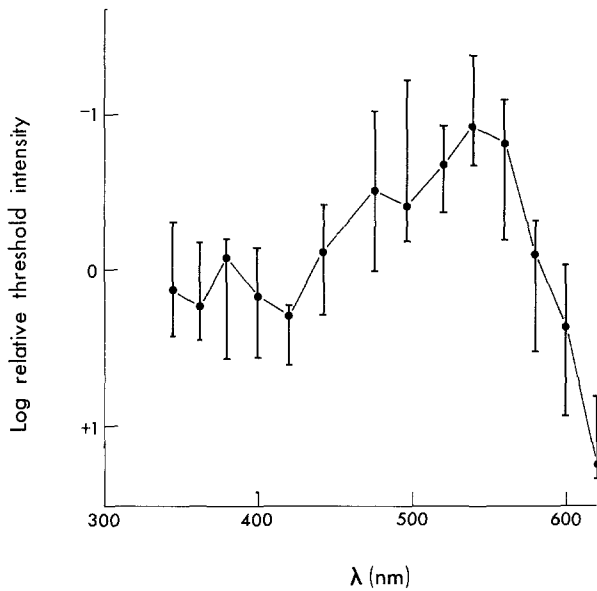
Fig. 9. Spectral sensitivity of pitch responses at threshold. Data · points and error bars: medians and ranges from measurements on 5 animals
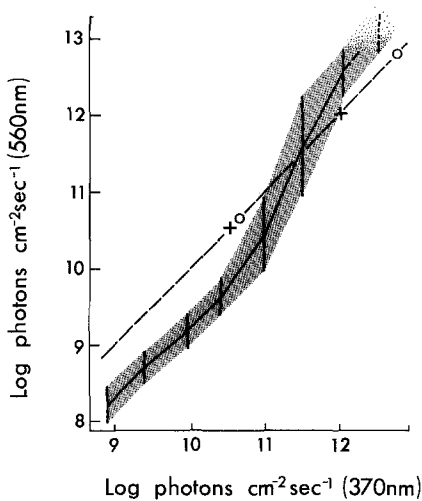

Fig. 10. Changes in UV/green sensitivity ratios with intensity. Each bar indicates range of green intensities which were confused with respective UV intensity. Dashed line corresponds to a UV/green sensitivity ratio of 1; solid line drawn through mid-points of bars. Crosses: range of crossovers for a total of 8 animals. Circles: crossover points reported for single cell recordings in dragonfly ocellar receptors (Chappell and DeVoe 1975)

tween individuals, it was necessary to normalize the data for each, and the average of the logs of the 14 threshold intensities was used as the reference value for normalization. The results are presented in Fig. 9, showing maximum sensitivity around 540 nm, indications of a minimum around 420 nm and a secondary peak in the UV.

It has been reported in the literature that the spectral sensitivity of the ocelli can depend on the thresh-

old criterion chosen: Chappell and DeVoe (1975) observed that the green/UV sensitivity ratios are reversed in the threshold range of receptor potentials in dragonfly ocelli, and also the spectral sensitivities of ocellar ERGs in moths depend on intensity (Eaton 1976). To test for similar effects in *Hemicordulia*, a 'silent substitution' experiment was performed by presenting UV and green stimuli repeatedly in alternation, each for 1 s. At a given UV intensity, the green intensity was varied by the threshold search routine until two values were determined which clearly evoked opposite changes in head position, meaning that they were more and less effective respectively than the UV intensity tested. This procedure was repeated for a range of UV intensities, and the observed behaviour is illustrated in Fig. 10. At low intensities, the sensitivity to green is higher than the UV sensitivity, and it is possible to determine equivalent green and UV intensities with high accuracy: a change of green intensity of 0.4 log units is sufficient to clearly reverse the direction of the responses. For an intermediate intensity range, however, the determination of equivalent intensities becomes less accurate: at a UV intensity of 3×10^{11} photons·cm^{-2}·s^{-1} the green intensity had to be varied by 1.2 log units to evoke clearly recognizable and opposite responses. At the highest intensities tested, the accuracy of the measurements increases again, and now the UV sensitivity exceeds the green sensitivity.

Identical experiments were conducted in a total of 8 animals. In all cases, the green sensitivity exceeded the UV sensitivity at low intensities by approximately 0.7 log units, the same amount as in Fig. 9. Also the reversal in relative sensitivities occurred consistently, but the absolute intensity at which the crossover occurred varied between individuals over the range indicated in Fig. 10.

Discussion

Absolute Sensitivity

In Fig. 11, the data from Fig. 3a are replotted together with published data on ocellar receptors and second order neurons. Within the limitations of comparing data obtained by different methods in different species, it is clear that healthy behavioural responses occur at intensities several log units below the lowest intensities at which slow potentials in receptors and second order cells become detectable. In this intensity range, the presence of light is signalled by discrete events (bumps) which are presumably caused by the arrival of single photons (Wilson 1978c). Therefore, it appears that the sensitivity of the present behaviour-
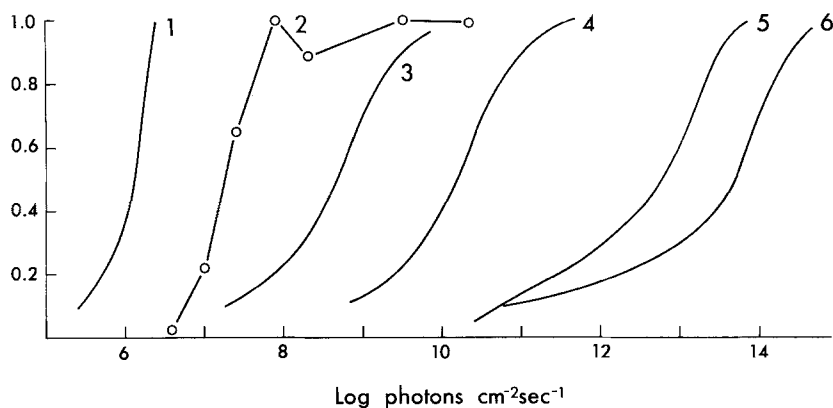
Log photons cm⁻²sec⁻¹

Fig. 11. Sensitivity of behavioural responses in comparison to sensitivities of ocellar receptors and second order neurons. *1* Responses of locust ocellar L-neurons: discrete events/100 ms (from Wilson 1978c). *2* Behavioural responses in *Hemicordulia:* normalized average differences between on- and off-positions of the waveforms in Fig. 3a. *3* Responses of locust ocellar L-neurons: normalized voltages of slow potentials (from Wilson 1978a). *4* Responses of dragonfly ocellar L-neurons: normalized voltages of slow potentials (from Chappell and Dowling 1972). *5, 6* Responses of dragonfly ocellar receptors in the UV and green, respectively: normalized voltages of slow potentials (from Chappell and DeVoe 1975). Note: Curve 4 is positioned 2 log units below the receptor curves, as reported by the authors

al responses approaches the absolute limit set by the ability of the sensory organ to detect single photons, and it becomes interesting to make an estimate of the quantum efficiency of the system. A pronounced response occurs at an intensity of 2.5×10^7 photons $\cdot$ cm$^{-2} \cdot$ s^{-1} (7.4 in Fig. 3a) and becomes clearly recognizable within 200 ms after stimulus onset. Given a corneal area of 2×10^{-3} cm^2 and 10^3 receptors in the median ocellus of *Hemicordulia,* this corresponds to the arrival of 10^4 photons at the cornea, or 10 photons per receptor. This quantum efficiency is not remarkably high, particularly in view of the strong convergence between receptors and second order cells.

It should be considered, however, that the ocellar optics are not optimized for focussing light on individual rhabdoms as it is the case in the compound eyes, but they are optimized instead to collect light over as wide an angle as possible. In consequence, the sensitivity of the system is adequate under most natural conditions: Wilson (1978a) estimated that the light emitted by an axial full moon is sufficient to saturate locust ocellar L-neurons. The luminance of the clear moonless night sky is in the order of 5×10^{-8} lm $\cdot$ sr^{-1} $\cdot$ cm^{-2} (Kaye and Laby 1973); by following a procedure analogous to that used by Wilson (1978a), this leads to the estimate that the median ocellus of *Hemicordulia* receives the equivalent of at least 10^8 peak axial photons $\cdot$ cm$^{-2} \cdot$ s^{-1} when exposed to the night sky. At this intensity the behavioural responses are fully functional (Figs. 3a, 7, 11), and the question remains open whether this capacity is actually used by *Hemicordulia,* as the nocturnal habits of this species are not yet known.
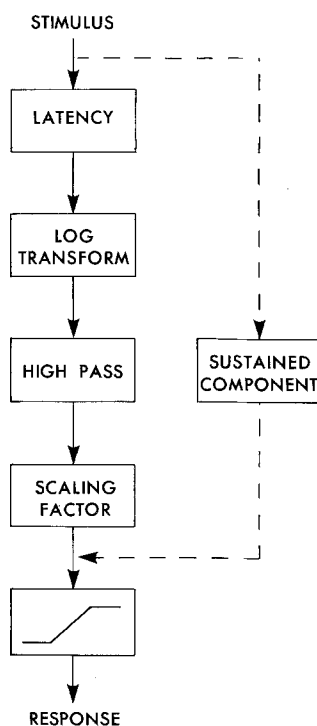
STIMULUS

Fig. 12. Components of pitch responses

Dynamic Behaviour

In order to provide a guideline for comparisons with properties of the neuronal elements of the median ocellar system, the block diagram in Fig. 12 summarizes the essential parameters of the pitch responses.

Latency. Within the intensity range covered, the shortest latencies are in the order of 50 ms (Fig. 3). Cer-

tainly, a fraction of this latency is attributable to synaptic delays: there are at least 3 synapses between receptor and effector (receptor/interneuron(s)/moto-neuron/muscle); the delay at the first synapse, for instance, is 5 ms (Chappell and Dowling 1972). A major fraction of the latency, however, can be ascribed to the receptors: all measurements in Fig. 3 were taken at low intensities, and Chappell and Dowling (1972) measured receptor latencies in the order of 30 ms in the lower range of receptor potentials.

Log Transformation. The magnitude of the aftereffect of increment stimuli is proportional to the log of the stimulus increment (Fig. 6). Also, the response-versus-contrast function changes little with intensity (Fig. 8), indicating adherence to the Weber-Fechner law and hence implying a log transformation.

It is possible that this transformation occurs in the receptors in a similar way as in the compound eyes of flies and dragonflies (Laughlin and Hardie 1978), but it appears that the intensities used in the present experiments are below the range in which the intensity transfer characteristics of the receptors show logarithmic behaviour (Fig. 11). However, the log transformation could be the result of range shifting mechanisms (Laughlin 1980), occurring in higher order elements.

High Pass Filtering. As indicated by the aftereffect, the system contains rate sensitive components which adapt to changes in background, effectively constituting a high pass filter. If only a single component with first order characteristics were present, the expected time course of the readaptation after a disturbance should be simply exponential. However, the observed waveforms (Fig. 5) consist of distinct fast and slow components, similar to the waveforms of the off-responses found in locust ocellar L-neurons (Wilson 1978b), except that they occur within a faster time scale. The time scale of off-responses in dragonfly ocellar second order neurons (Chappell and Dowling 1972) is similar to that observed here, but signs of complex transient behaviour were not found. It appears, therefore, that the high pass filtering occurs essentially at the level of the second order cells; it remains open as to what underlies the more complex component.

Scaling Factor. The system has a defined scaling factor of the dimension [degrees of head movement/change in contrast], and this factor is set such that the possible range of head positions matches the possible range of contrasts (Fig. 8). The scaling factor varies between individuals within the range of 15–30°/100% contrast. The dorsoventral field of view of the

median ocellus extends over approximately $\pm 30°$ above and below the horizontal plane, and for the observations reported here, the median light source was positioned such that it would remain within this field during head movements. Therefore, the present observations reflect the behaviour of the system under essentially open loop conditions. To assess the performance of the system as an equilibrium organ, it is important to estimate the extent to which passive displacements in a natural environment are balanced out by the compensatory reflexes (closed loop gain). Assuming that the angular sensitivity of the median ocellus is constant within its dorsoventral field of view and assuming that the contrast between sky and ground is close to 100%, passive rotation of the animal around the pitch axis will change the received intensity with a proportionality constant of 100% contrast/60°. Given a scaling factor of 15–30°/100% contrast, the lower bound for the closed loop gain becomes 0.25–0.5.

The assumption that the angular sensitivity is uniform applies, if at all, only in dark adapted animals, and the closed loop gain in the light adapted state must be considerably larger than this estimate. The ocelli of both dragonflies and locusts possess pupils which close with light adaptation, but while the field of view of locust ocelli changes very little with closing of the radial pupil (Wilson 1978a), the pupil mechanism in dragonfly ocelli is different: in the light adapted state, a layer of screening pigment covers the ventral half of the proximal surface of the thick ocellar lens, thus attenuating light entering from the dorsal half of the visual field which is normally occupied by sky (von Hess 1920, 1921; Homann 1924b; Lammert 1925; Stavenga et al. 1979). Therefore, a steep gradient of sensitivity exists between the ventral and the dorsal parts of the visual field. In level flight, the borderline between the two parts is aligned with the horizon, and consequently small changes in attitude will cause large changes in received intensity.

Dynamic Range Limitations. There are upper and lower limits of head positions, which are probably determined by the mechanical properties of the head joint and not the preceding neuronal circuitry: also during spontaneous movements, the head does not move past those positions.

Sustained Component. In sustained illumination, the head is kept in the on-position indefinitely, indicating that the high pass filtering system is not perfect. Indeed, a small tonic component is present after a phasic transient in non-spiking dragonfly second order neurons (Chappell and Dowling 1972), and in extracellular recordings from ocellar nerves of both dragonflies and flies, the presence of light suppresses the spontaneous activity for a prolonged period (Rosser 1974; Metschl 1963).

Apart from some details, the system in Fig. 12 is essentially equivalent to the log-transform-subtraction-amplification model inferred from the dynamics

of second order cells in the compound eyes of flies and dragonflies (Laughlin and Hardie 1978). The implications of such a strategy have been discussed in detail (Laughlin 1980); its essential effect is elimination of the background in order to keep the system operative over a wide range of average intensities and to introduce contrast constancy.

Interactions

The considerations outlined so far are based upon the observation that the pitch responses are controlled solely by the median ocellus (Stange and Howard 1979). It is necessary, however, to briefly discuss possible interactions between the three ocelli, interactions with the compound eyes, and interactions with other inputs.

Interactions Between the Ocelli. The observations that the pitch responses are mediated by the median ocellus, that the lateral ocelli cooperate in mediating the roll responses and that the lateral system has no effect on the pitch responses are consistent with the stimulus configurations which can occur during flight and with the anatomical disposition of the three ocelli.

Consequently, we would expect to find indications from anatomical and physiological data that the median and lateral ocellar pathways are independent of each other, and that there are strong interactions between both lateral pathways. However, anatomical data on dragonflies (Chappell et al. 1978) and physiological data on locusts (Patterson and Goodman 1974) suggest that the median and lateral ocellar pathways interact strongly, while there is only limited evidence for interactions in the two lateral pathways. It is not known why interactions between lateral and median inputs did not become evident in the present experiments, but it is interesting to note that some units in the locust ventral cord are inhibited by illumination of one lateral ocellus and excited by illumination of the other; a stimulus configuration in which the lateral ocelli are stimulated in alternation has yet to be tested electrophysiologically.

Interactions Between Ocelli and Compound Eyes. The present stimulus conditions were selected such that stimulation of the compound eyes alone does not evoke responses (cf. Stange and Howard 1979). However, the possibility cannot be excluded that the present results are influenced by compound eye inputs: the obvious approach of obscuring the compound eyes by paint is problematic as the additional weight impairs the function of the delicate head joint of the dragonfly (cf. also Mittelstaedt 1950). It is apparent anyway that both visual systems interact (e.g. Kondo

1978; Guy et al. 1979; Hu and Stark 1980), and further behavioural experiments are required to sort out details about those interactions.

Interactions with Other Inputs. As described above, head movements in response to light occur only during flight, and flight is evoked by wind, tarsal reflexes and intrinsic factors. 'Flight' does not necessarily mean that active wing beat is present, and it is worth mentioning that dragonflies often glide with stationary wings. In every way these observations are consistent with the account of interactions between flight behaviour and visually controlled head movements in crickets, as it was given by Tomioka and Yamaguchi (1980): it appears that activation of the flight mechanism is required to gate inputs from the ocellar system. The possible general importance of gating systems has recently been discussed by Sandeman (1980), and for the specific case of dragonfly ocelli, a neuron has been described by Kondo (1978) which provides efferent control of ocellar inputs in response to stimulation of the wing mechanosensory system. It is interesting that this efferent system synapses with the lateral ocellar neuropile, suggesting that gating occurs right at the periphery. For the case of locusts, Simmons (1980) described a neuron which responds to stimulation of the median ocellus, provided that wind is present, and which controls the pitch attitude of the wings during flight.

Reverse Purkinje Shift

The observation that the spectral sensitivity changes with intensity presents a violation of the principle of univariance (Naka and Rushton 1966). This implies that two (or more) photopigments must occur in dragonfly ocelli, either in the same set of receptors or in different sets, and it implies that information from the two pigments is processed in different ways. As shown by Chappell and DeVoe (1975), the phenomenon cannot be explained by simple models involving either interactions between photopigments in the same cell or electrical coupling between cells with different spectral sensitivities. Therefore, the possibility arises that the phenomenon reflects a specific functional adaptation and not some peculiarity of photochemistry.

As pointed out by Wilson (1978a), the fact that ocellar receptors are generally most sensitive in the UV suggests a functional adaptation for discrimination between sky and ground because the contrast between sky and ground is small in the green and large in the UV (Fig. 17 of reference). Indeed, the contrast in the UV is always large, because the reflectance of the ground in the UV is negligible. The con-
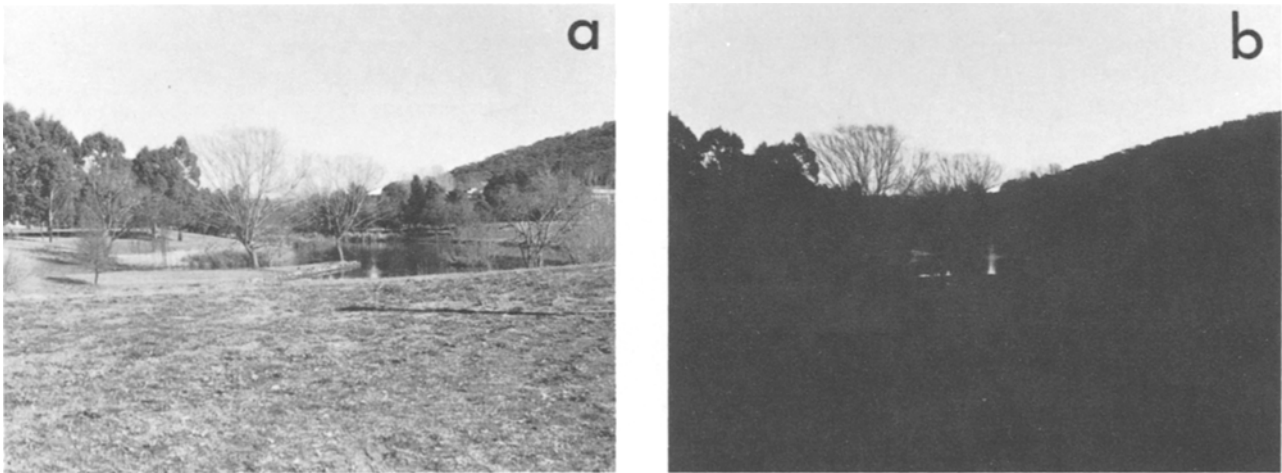
Fig. 13 a, b. Wide angle views of typical habitat of *Hemicordulia,* taken through a Schott VG14 green filter. In **a**, elevation of the sun is 35° (noon), and in **b** it is 0° (sunset). Pictures were taken on a cloudless day with the camera facing southwest

trast in the green, however, is not always small and depends on the conditions of illumination: the light received by a patch of ground consists of two components, namely the contribution of direct sunlight and the contribution of diffuse skylight. Direct sunlight will be dominant during a clear day and when the elevation of the sun is high. A scene viewed in the green will then show little contrast between ground and sky (Fig. 13a), because the reflection of direct sunlight from the ground is high enough (reflectance = 0.2 for vegetation, Wyszecki and Stiles 1967) to yield a luminance similar to that of the sky. A patch of ground which is shadowed, however, will be illuminated only by skylight, and therefore the contrast against the sky will be high.

The whole of the earth's surface is shadowed before sunrise and after sunset, and now the disadvantage of viewing through a green filter becomes smaller since the ground is much darker (Fig. 13b). In addition, the colour temperature of illumination changes when the sun is below the horizon, and longer wavelengths become predominant (cf. Menzel and Knaut 1973). In dim light, noise becomes a limiting factor for the performance of the receptors, and the signal-to-noise ratio will be best if the sensitivity maximum is matched to the wavelength range of maximum radiation. It appears therefore, that the reverse Purkinje shift is an adaptation to optimize the performance of the system both at low intensities, where UV photons are scarce both in relative and absolute terms, and in direct sunlight, where the contrast between ground and sky is a maximum in the UV.

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