EYE MOVEMENTS IN *DAPHNIA PULEX* (DE GEER)

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SUMMARY

1. The various types of eye movement exhibited by the cyclopean eye of *Daphnia pulex* were studied using high speed motion photography.

2. This rudimentary eye, which consists of only 22 ommatidia, can move through approximately 150° in the sagittal plane and 60° in the horizontal plane.

3. Four classes of eye movement were found: (1) a high speed tremor at 16 Hz with an amplitude of 3–4°, which resembles physiological nystagmus, (2) a slow rhythmic scanning movement at 4 Hz, and 5–6° amplitude, (3) large fast eye movements similar to saccadic eye movements and (4) opto-kinetic nystagmus produced by moving striped patterns.

4. Where the fast tremor occurred concurrently with the slow rhythmic scan, a Fourier analysis revealed that the former was the fourth harmonic of the latter.

INTRODUCTION

The classification of different patterns of eye movement and the description of their functional significance have resulted mainly from observations of simple camera-type eyes of vertebrates. However, the compound and simple eyes of many invertebrates are also movable, and detailed studies of several species have recently been published. For example, Gregory, Moray & Ross (1964), Moray (1973) and Downing (1973) have shown that the single ommatidium which constitutes the lateral eye of the marine Copepod *Copilia* is scanned back and forth in the focal plane of its anterior lens. Land (1969) has shown that the antero-median eyes of the jumping spiders *Phidippus johnsoni* and *Metaphidipus aeneolus* produce several different patterns of eye movement, some of which are related to the identification of certain environmental stimuli. Also Horridge & Burrows (1968 *a, b, c*) have described optokinetic nystagmus, saccadic and compensatory eye movements in the compound sessile eye of the crab *Carcinus*.

It has long been known that many members of the Cladoceran order have movable eyes. *Daphnia* in particular has been shown to produce large eye movements especially in the sagittal plane, and indeed Scheffer, Robert & Medioni (1958) have used this response very effectively to determine the spectral luminosity curve for *Daphnia pulex* (De Geer). Early investigations revealed that the Daphnid eye appears to maintain a fixed direction with respect to a light beam (Radl, 1910; Ewald, 1913), and von Frisch & Kupelwieser (1913) demonstrated that this 'fixation' is an important element in the dorsal light reaction, and therefore possibly involved in the normal orientation

behaviour of the organism. The purpose of this investigation was to determine the gr optical properties of the cyclopean compound eye of *Daphnia pulex* and to describe their full range of eye movements. Informal observations have revealed that many different patterns of eye movements are produced, and an attempt has been made to specify the stimulus conditions which elicit specific movements so that inferences can be made about their functional significance.

MATERIAL AND METHODS

A culture of *Daphnia pulex* (De Geer) was kept in swamp water maintained at room temperature, and fed occasionally with a timothy hay broth. For histology, seven large females 2–3 mm long were fixed in Bouin's solution, dehydrated in ethyl alcohol, and embedded in paraffin wax. Serial coronal sections were cut at 5 μm intervals from the head region of four *Daphnia*, while 10 μm serial sagittal sections were cut from the remaining 3 specimens. All sections were then mounted, stained with haematoxylin and eosin, made into permanent slides and examined under a binocular compound microscope. Measurements of the various parameters of the cyclopean compound eye, such as radius or curvature of ommatidial lenses, rhabdom size, etc., were made with the aid of a micrometer scale attachment mounted in one of the oculars of the microscope.

Records of eye movements were obtained by filming the cyclopean eye through one eyepiece of a binocular dissecting microscope, with an Araflex 16 mm single lens reflex movie camera using Kodak Tri X film. The film was shot at either 25 or 50 frames per second. A frame by frame determination of eye position was made with the aid of a 16 mm projector fitted with a single frame advancement mechanism and frame counter. The procedure involved making an initial tracing of the outline of the eye, carapace, and prominent landmarks such as the one or two ommatidial lenses reflecting light, together with the frame limits of the first frame. This designated the arbitrary zero position of the eye. Then in subsequent frames the angular position of the eye was determined by superimposing the tracing of the eye onto the projected image of the eye and measuring the angular displacement between the traced and projected frame lines. Generally sections of film where no body movement occurred were used, but slight movement could be compensated for by making a new tracing of the changed position.

Informal observations had revealed that *Daphnia* exhibit a variety of different eye movements. Consequently an attempt was made to describe the specific stimulus conditions which give rise to particular types of eye movement. The stimulus conditions that were used in formal experiments were as follows:

(1) *Diffuse white light.* Under this condition the substage illumination of the microscope was passed through a diffusing screen immediately below the slide containing the preparation. This in effect produced a 'ganzfeld' for the *Daphnia*, and provided an opportunity to observe spontaneous eye movements when very few visual contours were present in the visual field.

(2) *A moving spot of light.* During preliminary observations it was noted that large saccadic eye movements could be produced by moving a light across the visual field of *Daphnia*. Consequently under this condition the substage microscope light was
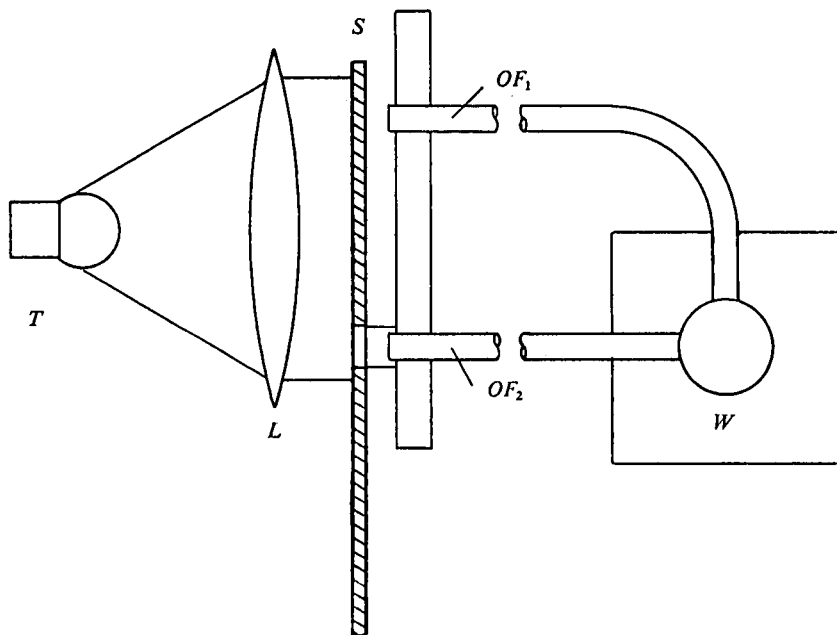
Fig. 1. Apparatus for presenting stimuli in two alternate positions in *Daphnia*'s visual field. Light from a tungsten light source (6 V automobile headlamp) was collimated by a short focal length lens *L*, and directed on to two flexible fibre optic cables OF_1 and OF_2. *Daphnia* were positioned on their side in the bottom of a well *W*. The two optic fibres were inserted 90° apart through the plexiglass block so that their ends came in close proximity to the wall of the well. A sliding shutter *S* made it possible to illuminate either OF_1 or OF_2 alternately.

focused to form an intense spot 2 mm in diameter on the ground glass screen immediately below the *Daphnia*. This spot was then moved back and forth across the visual field of the *Daphnia* by manipulating the microscope mirror.

(3) *A light spot flashed alternately between two positions.* This stimulus arrangement was used to observe eye movements generated by change in position without continuous movement through the intervening space. To produce such stimuli the simple optical device illustrated in Fig. 1 was constructed. *Daphnia* were positioned on their sides facing midway between the two light spots and then pinned to a thin layer of wax in the bottom of the well. Thus the two spots of light, which subtended approximately 15° of visual angle, could be alternated between 2 positions 90° apart in the sagittal plane of the *Daphnia*.

(4) *Moving striped patterns with velocity and spatial frequency varied.* Optokinetic nystagmus was investigated by placing *Daphnia* in a fixed position in the centre of a cylinder around which various patterns of stripes were rotated. Fig. 2 shows a schematic diagram of the apparatus used to make these observations. The apparatus, which was driven by a Cole–Parmer constant torque, variable speed drive unit, produced a visual field of moving vertical stripes which extended approximately 180° in the horizontal plane and 70° in the vertical plane.

Several different stimulus cylinders were constructed which produced: (*a*) *Black and white (clear) stripes* subtending visual angles to the *Daphnia* of 45°, 22·5°, 15°, 10°, and 5°; (*b*) *a single chromatic stripe* 22·5° in visual angle, produced by inserting
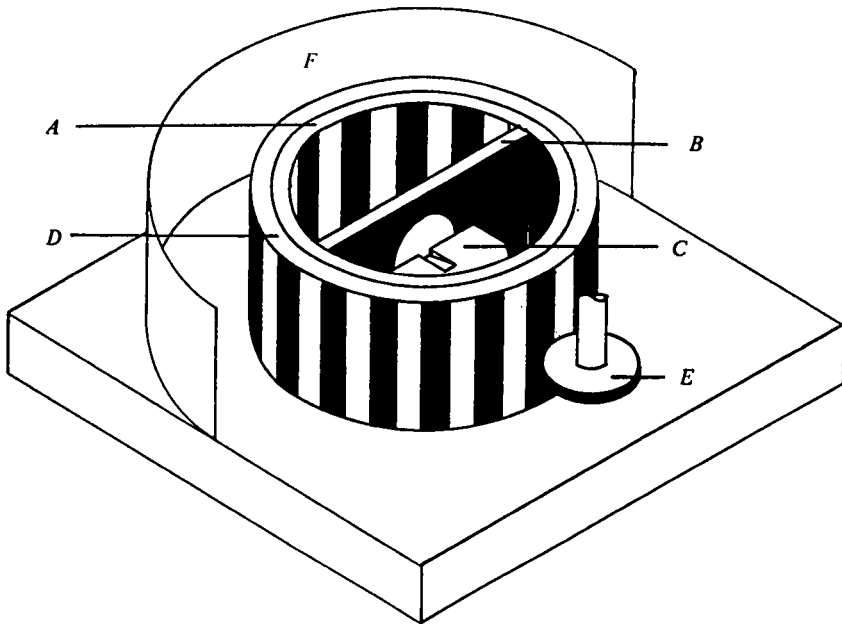
Fig. 2. Apparatus for presenting moving grating patterns to *Daphnia* to elicit optokinetic nystagmus. A plexiglass cylinder *A*, was divided into two hemicylinders by a plexiglass partition *B*. *Daphnia* were gently wedged into a sawcut in the upper surface of block *C* so that they faced the other hemicylinder which was filled with water. Various stimulus patterns were attached to marginally larger plexiglass cylinders *D*, which could be rotated in either direction by a friction drive wheel *E*. A constant torque variable speed drive unit connected to the drive wheel permitted velocity adjustments over a wide range of values. A diffusing screen *F* back illuminated by a 100 W tungsten bulb produced an evenly illuminated background against which the various patterns of stripe were viewed by the *Daphnia*.

a two layers thick strip of yellow filter transmitting wavelengths centred around 590 nm (Edmonds No. 815) between the ends of a blue filter (Edmonds No. 855) transmitting wavelengths centred around 445 nm (with this arrangement the blue and yellow regions of the pattern transmitted approximately equal intensities of light); (*c*) *a single polarized stripe*, also 22·5° in visual angle, produced by inserting a section of Polaroid filter with the *e*-vector rotated 90° from the Polaroid filter making up the remainder of the cylinder. Angular velocity of these stimuli were varied over the range of 5–720° sec⁻¹ in either a clockwise or anticlockwise direction.

<center>RESULTS</center>

<center>*The cyclopean compound eye*</center>

The histological observations indicate that the *Daphnia* eye consists of a cyclopean compound structure containing 22 ommatidia arranged with their axes approximately 38° apart around the surface of a nearly hemispherical structure. The mean radius of curvature of ommatidial corneal lenses was 16·5 μm while the mean thickness of the lenses was 41 μm.

Twenty-two bundles of optic nerve fibres each containing 8 axons, presumably from the same ommatidium, leave the eye and terminate in the first optic ganglion
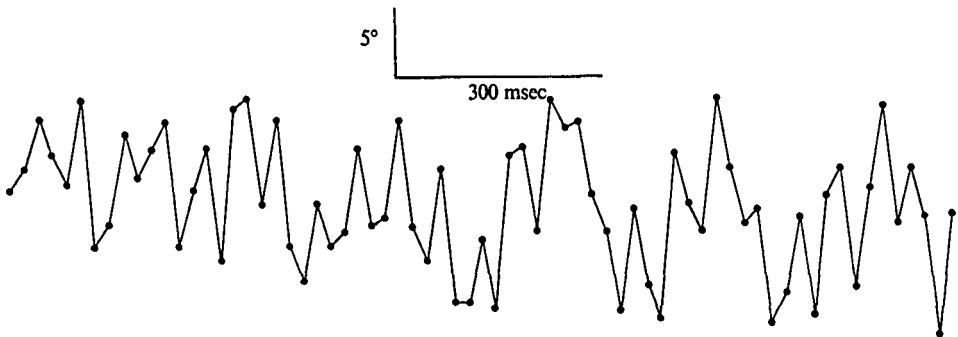
Fig. 3. An example of the fast tremor eye movement of *Daphnia*. This type of eye movement occurred in an evenly illuminated visual field containing a minimum of contours. Each point represents the *Daphnia's* eye position on a single frame of movie film, the dorsal direction is up and ventral down. A Fourier analysis of this data is presented in Fig. 5, where it can be seen that the fast tremor has a frequency of 17 Hz, and that it is superimposed on a slower wave which has a frequency of 4·25 Hz.

of the brain. This structure consists of the familiar rind of cell bodies enclosing a dense neuropile in the interior. Two pairs of eye muscles insert on either side of the anterior loop of the digestive tract and radiate out to attach to the eye hemisphere at roughly 90° intervals.

These observations are in general agreement with those of Rohlich (1967), Güldner & Wolff (1970) and Wolff & Güldner (1970), who have provided a much more detailed analysis of the anatomy and ultrastructure of the cyclopean eye of *Daphnia*.

Eye movements

Under diffuse light conditions, two types of eye movement were observed: (1) *a fast tremor*, somewhat irregular but with a frequency of approximately 18 Hz, and an amplitude of 3–4°, and (2) *rhythmic scanning movements* at 4 Hz with an amplitude of 5°–6°. Typical examples of the tremor and scanning are illustrated in Figs. 3 and 4 respectively, both records originating from the same *Daphnia*. A casual inspection of Fig. 3 indicates that the fast tremor may be superimposed over the slower rhythmic scanning pattern. To investigate this further, Fourier analyses of the data comprising these two records were performed and the relative power spectra are presented in Fig. 5 for the data portrayed in Fig. 3, and in Fig. 6 for the data contained in Fig. 4. These analyses clearly indicate that the slower scanning eye movement is present in both records, with a frequency of 4·25 Hz in Fig. 3 and 3·5 Hz in Fig. 4. It should also be noted in Fig. 5 that the fast tremor at 17 Hz is the fourth harmonic of the slow scanning movement at 4·25 Hz.

When moving spots of light were swept across the visual field of *Daphnia*, large saccadic eye movements, such as those shown in Figs. 7 and 8, were produced. The photographs in Fig. 11, Plate 1 illustrate a large saccadic eye movement of the type produced in this experiment. In this case the eye has moved through 70° between these two frames. The maximum range of these saccadic eye movements was approximately 150° in the sagittal plane and 60° on the coronal plane, and mid-saccadic velocities of the eye often reached 330° sec^{-1}. In Fig. 7 the tremor can again be seen at the completion of the saccadic eye movement.
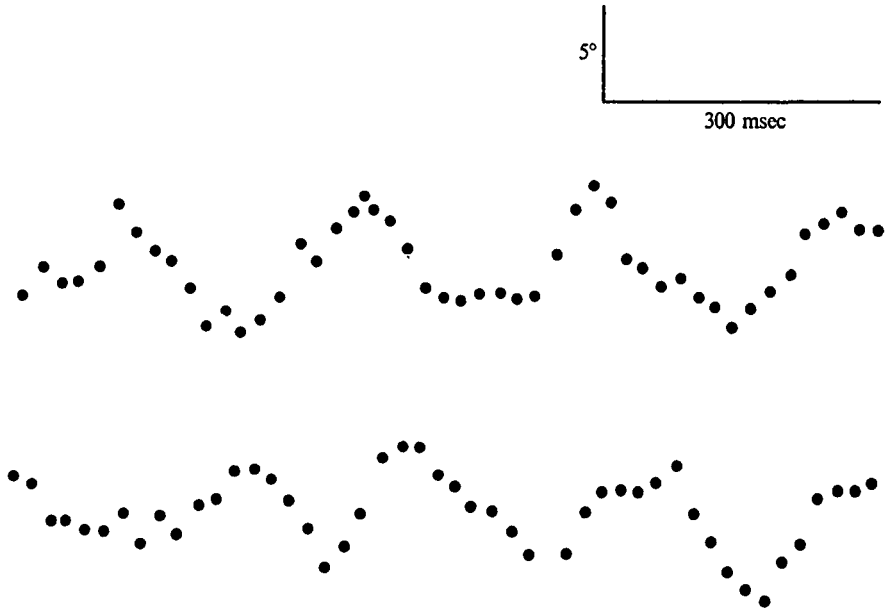
Fig. 4. An example of the rhythmic scanning type of eye movement. This pattern also tends to occur in an evenly illuminated visual field containing few contours. The Fourier analysis for this section of record is illustrated in Fig. 6 where it can be seen that the most power occurs at 3·5 Hz.
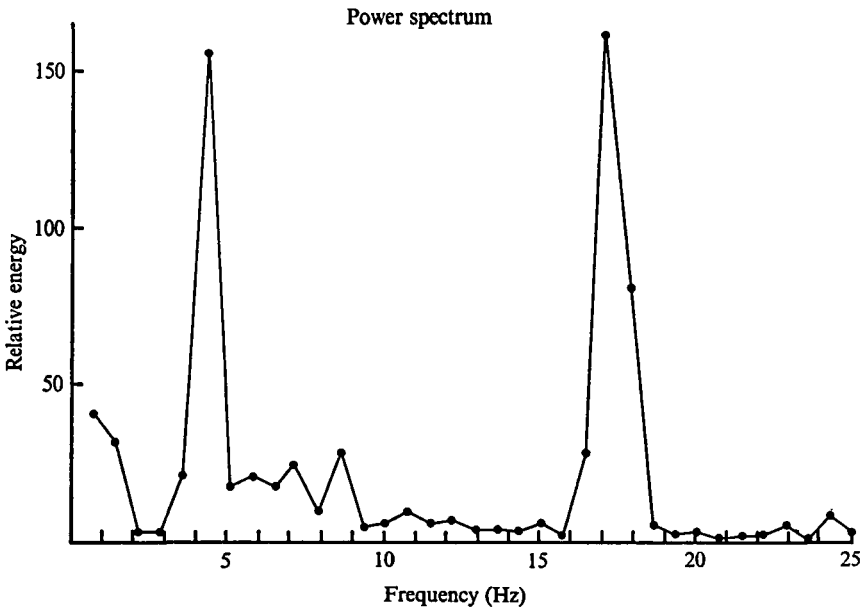
Fig. 5. Fourier analysis of the fast tremor eye movements presented in Fig. 3. An inspection of Fig. 3 indicates that the slow rhythmic scan illustrated in Fig. 4 may also be present. This conclusion is confirmed by the Fourier analysis, which indicates that there is considerable power around 4 Hz. It should also be noted that the frequency of the fast tremor at 17 Hz is the fourth harmonic of the slow rhythmic scan at 4·25 Hz.
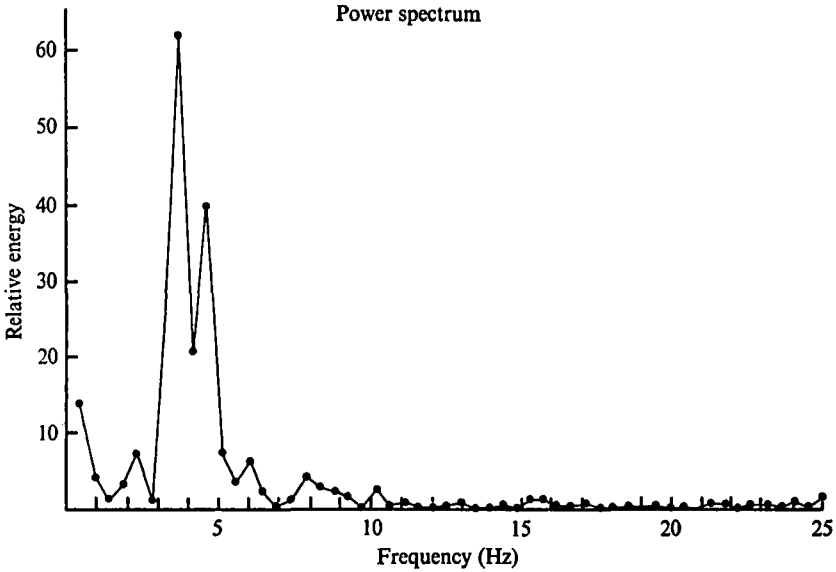
Power spectrum

Fig. 6. Fourier analysis of the slow rhythmic scan presented in Fig. 4, indicating that the major frequency component is at 3·5 Hz.
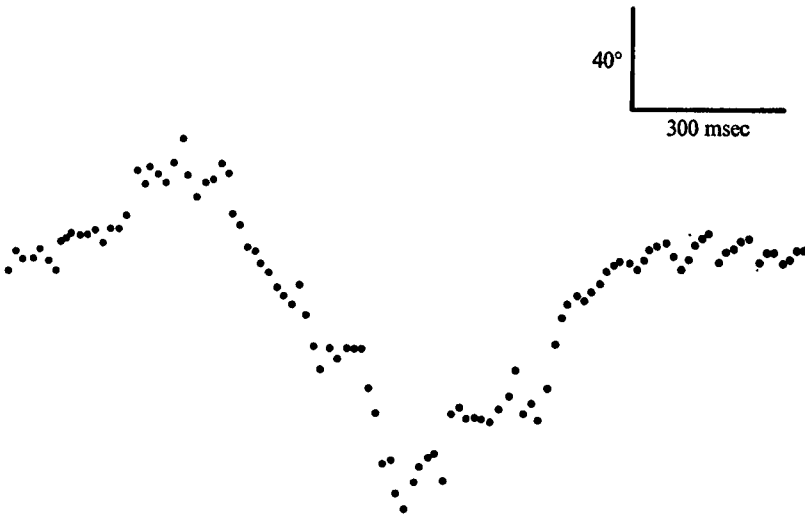

Fig. 7. Large spontaneous saccadic eye movement in the sagittal plane. This movement occurred under diffuse illumination. Note that the fast tremor appears to be superimposed on the saccade and is clearly visible when the eye comes to rest at the end of the record.

Observations taken with the two light spots alternated in positions 90° apart yield essentially the same results as produced under the moving stimulus conditions. An example of the saccadic-like eye movements produced by this condition is shown in Fig. 9.

Optokinetic nystagmus was produced by moving a striped cylinder around *Daphnia*, using the apparatus described above. Although different widths of stripe ranging from 45° to 5° of visual angle were used, stripes of less than 15° failed to elicit any measurable
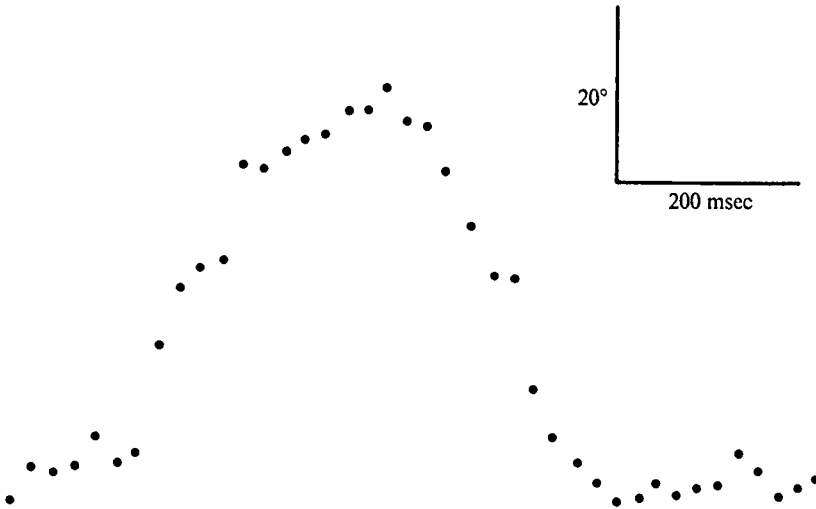
Fig. 8. Saccadic eye movements produced by a moving stimulus. The substage illumination was focused to form a bright spot 2 mm in diameter on a ground glass screen below the *Daphnia*, and in this case was moved dorsally and then ventrally. The eye position can be seen to follow this movement first in a dorsal direction and then in a ventral direction.
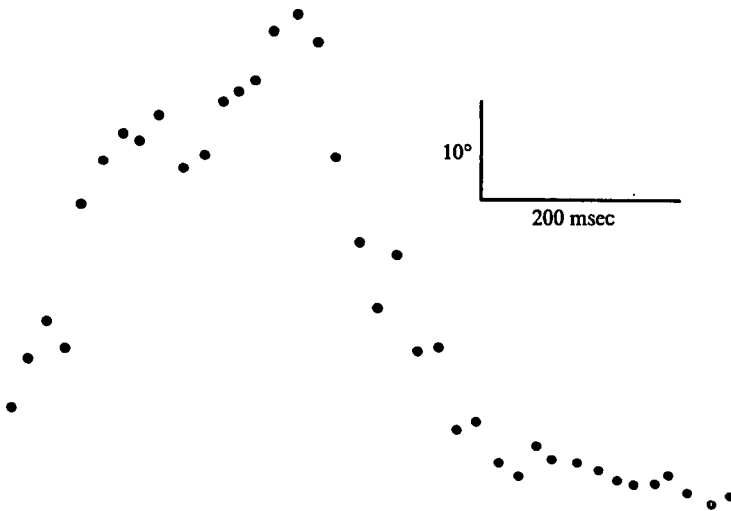
Fig. 9. Saccadic eye movement produced by displacement of a light spot. See text for details.

optokinetic nystagmus. The optimum width of stripe was approximately 22·5°, and the ability of the cyclopean eye to follow different velocities of this stimulus was investigated. At slower velocities (A) of the stimulus, eye velocity does not always match stimulus velocity, but rather the eye appears to track first in the direction of stimulus movement, and then remain stationary for a period of time before returning with a saccadic movement. However, at medium stimulus velocities (B), the slower following or pursuit phase can be clearly differentiated from the fast saccadic returns. Again, at higher velocities eye velocity fails to match stimulus velocity, as can be seen in the latter part of record (C), until it eventually disappears at a stimulus velocity of approximately 220° sec^{-1}.
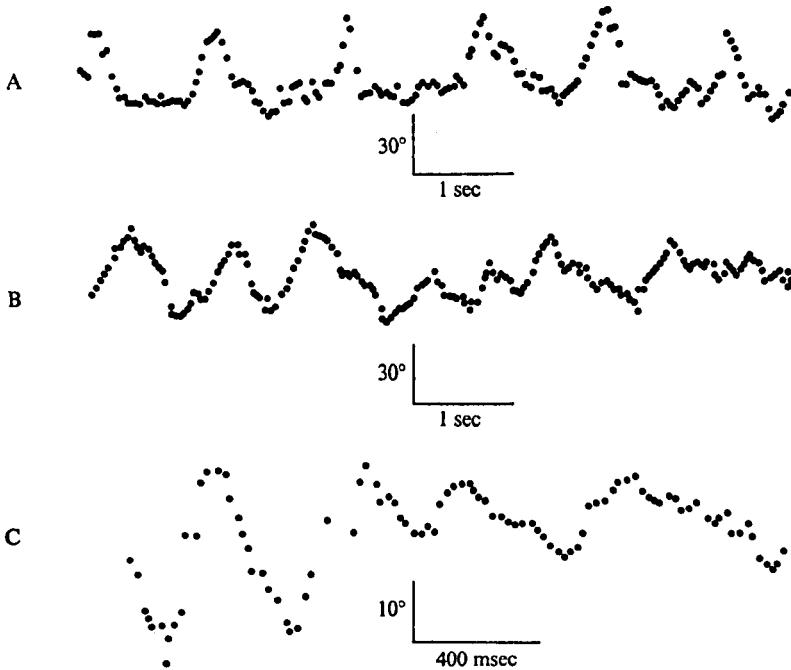
Fig. 10. Optokinetic nystagmus produced by a grating pattern moved at various velocities. The apparatus illustrated in Fig. 2 was used to rotate the grating pattern, consisting of 22·5° black and white stripes, around *Daphnia*. The stimulus velocity was 40° sec⁻¹ in A, 75° sec⁻¹ in B, and 150° sec⁻¹ in C.

Since optokinetic nystagmus provides a useful index of visual resolution it was decided to see if stripes formed by *e*-vector rotation and wavelength differences would also elicit eye following responses. However, it appears that only luminance differences will produce optokinetic nystagmus, since none of these other stimulus patterns produced any discernible response.

DISCUSSION

The results of this series of experiments indicate that *Daphnia* exhibit a variety of different types of eye movements, many of which bear a close resemblance to those described for higher organisms.

(1) *The fast tremor.* This type of eye movement has a frequency in the range of 15–20 Hz and sometimes occurs in conjunction with other types of movement. The fast tremor appears to be similar to physiological nystagmus in man, which has been shown by stabilized image experiments (Ditchburn & Ginsborg, 1952; Iarbus, 1967) to be essential for reducing adaptation and the fading of visual images. It has also been suggested by Autrum (1950) and Mazokhin-Porshnyakov (1969) that the irregular jerky flight patterns produced by many insects with fixed compound eyes might achieve the same effect as eye movements by producing rapid transients in the visual input. Because of the rather coarse visual resolution of the cyclopean eye of *Daphnia* these continual tremoring movements would increase the probability of changing the luminous flux reaching a particular ommatidium. The fact that the amplitude of these

movements in only 3°–4°, whereas ommatidia are spaced approximately 35° apart indicates that the most significant changes in luminous flux might take place at the subommatidial level. Optical calculations made on the basis of measurements of the ommatidial lenses, together with theoretical calculations of the static resolving power of single ommatidia (Mazokhin-Porshnyakov, 1969), indicate that subommatidial resolution will be poor. However, both empirical observations by Burtt & Catton (1954, 1956, 1960) and theoretical considerations by Mazokhin-Porshnyakov (1969) indicate that a compound eye in motion is able to resolve image detail which would go unnoticed in the absence of motion. It would therefore seem likely that the fast tremor type of eye movement found in *Daphnia* could serve two possible functions, one concerned with preventing loss of information through adaptation and the other to increase acuity.

(2) *Rhythmic scanning movements.* This pattern of movement, which consists of slow sinusoidal oscillations of the eye at approximately 4 Hz with an amplitude of 5–6°, tends to occur more frequently when *Daphnia* are placed in a diffusely lit environment with a minimum of contours. On some occasions the scanning occurs in the absence of any obvious tremor. The possible function this type of eye movement could be performing is not altogether clear. However, Moray (1973) has argued that the relatively slow scan found in *Copilia denticulata* increases the amount of information that can be transmitted about the visual field. If this is generally true, then the scanning movements of *Daphnia* might possibly be concerned with a search for visual detail. This interpretation is consistent with the fact that this type of movement seems to occur more often in a diffusely illuminated field than in one containing many visual contours. Land (1969) has reported that similar scanning movements are produced by the antero-medial eyes of jumping spiders, but in this case the characteristics of the scan are clearly determined by the stimulus configuration presented to the spider. In fact, it appears that the scanning movements in jumping spiders are intimately associated with object identification.

An interesting relationship was observed between the frequencies of the fast tremor and the rhythmic scanning movements when they occurred concurrently. A Fourier analysis of these data reveals that the tremor frequency was in fact the fourth harmonic of the rhythmic scan, which suggests that a single neural time base might be responsible for generating both patterns of movement. Many different neuronal models can be generated to provide the sort of neural economy suggested by these eye movements but it would be premature to specify these at this stage in the absence of any electrophysiological data.

(3) *Saccadic eye movements.* These fast and often very large eye movements have been observed to extend to a remarkable 150° in the sagittal plane. Experiments with moving spots of light and spots changed in position indicate that stimulus displacement is a sufficient condition to produce this type of movement. However, *Daphnia* placed in a fixed position in a stationary visual field in which several contours are present will also exhibit spontaneous saccadic eye movements. In vertebrate species possessing a fovea the function of saccadic eye movements is clear, that is they bring the image of an object of interest to the organism onto the region of most acute vision (Walls, 1967). Also, other types of areal specialization, such as the colour fields in certain avian retinae, would require the appropriate alignment of the eyes with

ccadic-like movements. However, there is no evidence available at present to suggest areal specialization in the compound eye of *Daphnia*, although subsequent studies of the microstructure of ommatidia in different locations on the eye might reveal such differentiation. In fact, since the ommatidia are approximately equally spaced around the nearly hemispherical structure of the eye, it seems unlikely that saccadic movements can be functioning to extend the visual field of the organism, because the visual field is essentially limited by parts of the *Daphnia*'s own anatomy. In animals possessing non-foveate eyes, such as most species of fish, Walls (1967) has suggested that eye movements serve the function of compensating for both voluntary and involuntary body movements. Several attempts were made to film free-swimming *Daphnia* while they were confined to a very thin transparent tank in the hope of being able to correlate eye movements with self-induced changes in position. However, with the equipment available it was not possible to produce film in which both eye and body position could be clearly determined.

(4) *Optokinetic nystagmus.* The series of experiments in which various striped patterns were moved through the visual field of *Daphnia* confirm that its visual resolution is poor, since stripes of less than 15° visual angle and velocities of movement faster than 220° sec^{-1} do not elicit an optokinetic response. As in other species, optokinetic nystagmus in *Daphnia* is characterized by a slower pursuit phase, where the eye matches the angular velocity of the moving stripes in order to stabilize its visual world, and a faster return or saccadic phase.

It might be argued that rotation of the striped pattern could produce flickering illumination at the *Daphnia*'s eye. If each individual flash evoked an eye movement, it is possible this could be mistaken for optokinetic nystagmus. However there are several facts which make this interpretation of the data unlikely. In the first instance, the apparatus and stimuli were designed so that the mean luminance of the striped hemicylinder viewed by *Daphnia* remained constant during movement of the patterns. Secondly, under optimum conditions of stimulus velocity and spatial frequency the eye movements could be clearly differentiated into a following phase, where the eye matched the direction and angular velocity of the stripes, and a faster reset, or return, saccadic phase. Finally, the frequency of eye movements did not increase in frequency with increased stimulus velocity as would be predicted from the flicker hypothesis.

An analysis of the colour dances of *Daphnia* by Baylor & Smith (1957) and the determination of their spectral luminosity curve by Scheffer *et al.* (1958) indicates that these organisms possess at least a primitive form of colour vision. *Daphnia* also orient orthogonally to the *e*-vector of plane polarized light (Baylor & Smith, 1953; Hazen & Baylor, 1962), and electron microscopy studies (Eguchi & Waterman, 1966) have revealed that rhabdom microvilli are oriented only in two planes 90° apart. This indicates that the *Daphnia* visual system is specialized for differentiating the *e*-vector of incident light. Consequently, stripes constituted of wavelength differences and *e*-vector differences were used, but under no conditions were optokinetic responses produced by these stimuli. Thus, it would seem that optokinetic nystagmus can only be produced by moving patterns of luminance differences within the visual field.

When the surface of water is still, then underwater animals possess an 'areal window' (Walls, 1967) in their visual field, which is an optical effect produced by the total reflexions of rays that strike the surface at angles greater than the critical angle

of incidence. In the natural habitat of *Daphnia* this would provide a visual field which consisted of a bright circular window centred above the organism, surrounded by a darker field constituted of reflexions from the bottom of the swamp or pond. Goodman (1965) has suggested that locusts regulate their flight attitude by orienting their heads so that the horizon is horizontal and the upper half of their visual field is brighter than the lower half, then reflexly align their bodies with their heads. As von Frisch & Kuplewieser (1913) and Harris (1953) have suggested, such an 'areal window' could possibly provide a similar orientational landmark for *Daphnia*, wherein any departure from their maintained orientation would result in a reflex change in eye position followed by compensatory movements of their setae to regain their appropriate orientation.

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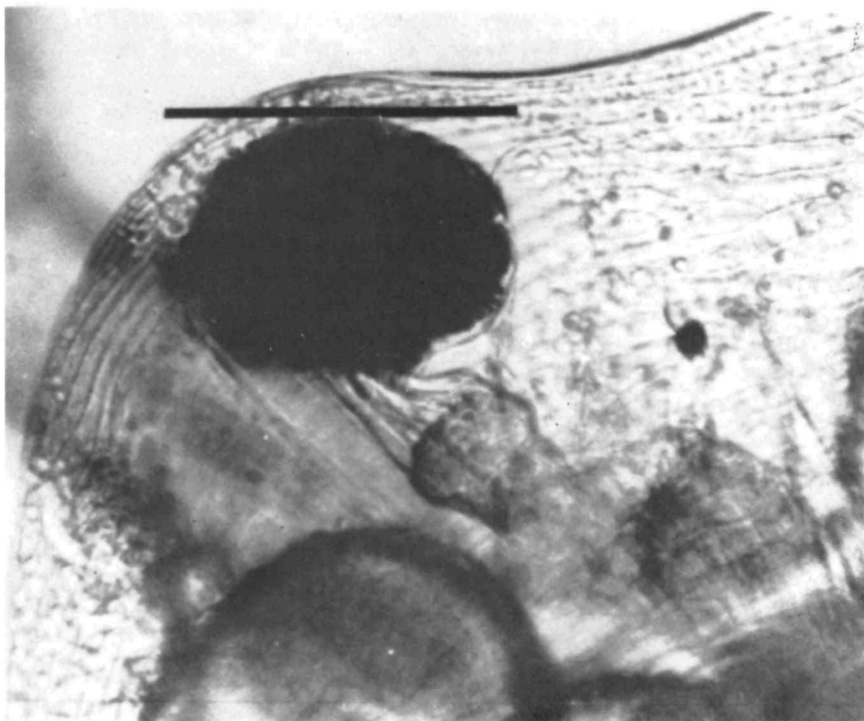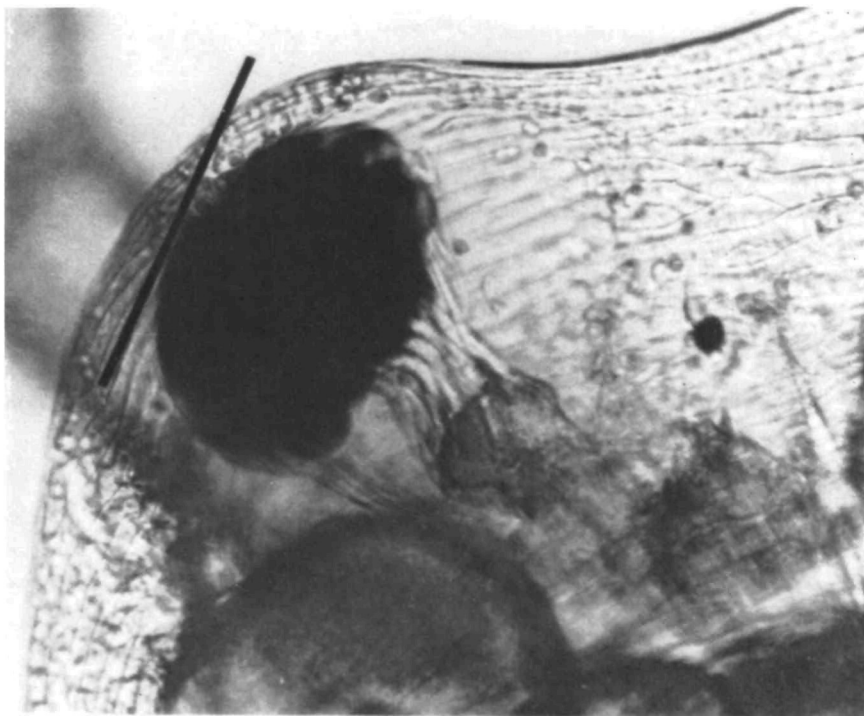
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EXPLANATION OF PLATE

Photographs of cyclopean compound eye of *Daphnia pulex* showing a ventral saccadic eye movement of 70°. Some of the 22 bundles of optic nerve fibres can be seen leaving the eye and converging on the first optic ganglion of the brain. Two of the four eye muscles can also be seen to be attached to dorsal-lateral and ventro-lateral positions of the eye and to insert close to the forward loop of the gut.