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OCULOMOTOR REACTIONS IN THE CUTTLEFISH, *SEPIA OFFICINALIS*

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INTRODUCTION

The eyes of *Sepia* and other cephalopods are extremely well developed and bear a, for invertebrates, unique resemblance to the eyes of vertebrates, as well in structure as in dimensions. Moreover, vision seems to be a dominant factor in the behaviour of the animal, e.g. in prey catching (Messenger, 1968). Before the attack, converging movements of the eyes have been observed, resulting in fixation of the prey on the posterior part of the retina (Messenger, 1968). Nystagmic eye movements, evoked by rotation of the animal, have been described by Dijkgraaf (1961, 1963). Optokinetic nystagmus, elicited by environmental rotation, has also been observed (Messenger, 1968; A. Packard, personal communication). In view of the presence of an intricate set of external eye muscles (see Tompsett, 1939) the occurrence of eye movements is not surprising, and these can indeed be easily observed in the free-swimming animal. However, until now, direct registration and measurement of eye movements in a cephalopod had not been realized. An indirect approach to the problem has been made by the analysis of motion picture frames (Messenger, 1968; A. Packard, personal communication). A more precise analysis of eye movements in *Sepia* seems of considerable comparative physiological interest.

In the present study direct, continuous recording of eye position in *Sepia* was achieved by means of a scleral search coil technique. The main purpose of the investigation was the measurement of eye movements elicited by environmental rotation (optokinetic nystagmus) and by passive rotation of the animal.

MATERIALS AND METHODS

Adult *Sepia officinalis*, caught in the Bay of Naples and stored in tanks with circulating sea water, were used. Specimens with a dorsal mantle length between 10 and 15 cm. could be accommodated in the experimental apparatus.

Eye movements were measured using Robinson's (1963) scleral coil method, which is based on magnetic induction. Briefly, an a.c. magnetic field was generated in the eye region by passing an a.c. current (10 kHz) through two solenoids, placed in front of and behind the animal, respectively. The direction of the field was parallel to the longitudinal axis of the animal. A small induction coil was fixed to the eye; depending upon its orientation with respect to the stationary magnetic field a varying a.c. potential was induced; by suitable amplification and detection this signal was transformed in an analogue voltage, proportional to the angular position of the eye. While

in mammals the induction coil can easily be attached to the eyeball, either directly or mounted on a contact lens, the situation in cephalopods is more complicated, since the cornea is merely a transparent part of the skin and not a part of the eyeball.

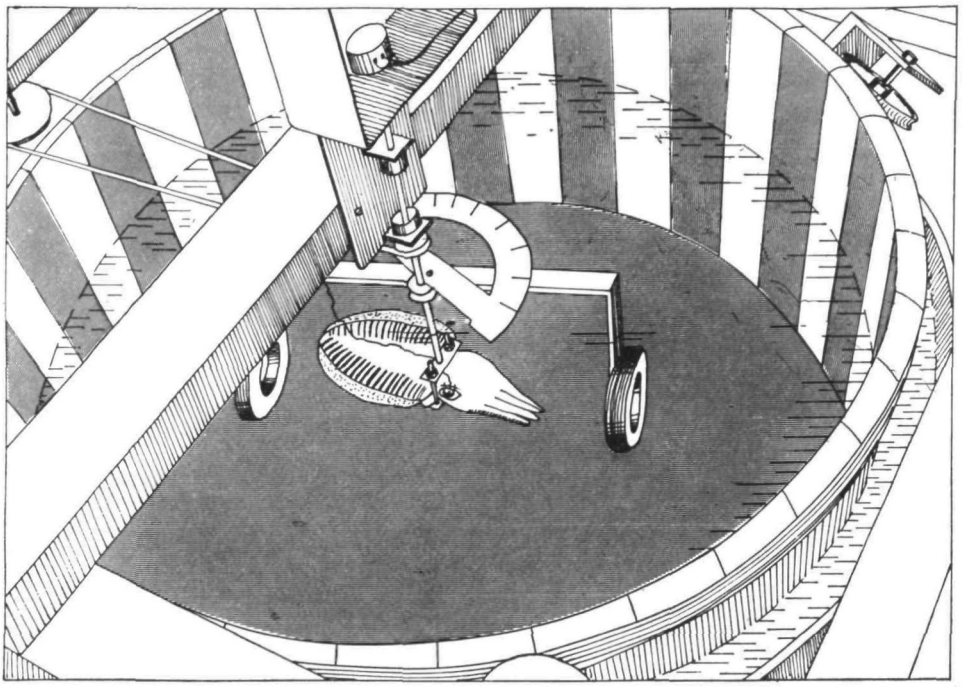

Fig. 1. A view of *Sepia* mounted in the experimental apparatus. The restraining collar and the axis of rotation are clearly visible.

Animals were anaesthetized in 0·5% urethane in sea water and then transferred to a shallow vessel containing circulating aerated sea water with 0·25% urethane. In this way they remained lightly anaesthetized but continued to respire. A healthy animal could be kept for over half an hour in this condition, with prompt recovery upon transfer to normal sea water. A more profound anaesthesia quickly caused irreversible respiratory arrest and death. The skin and orbital membrane were opened with longitudinal incisions above the right eye. The search coil, consisting of ten windings of insulated copper wire (diameter 0·05 mm.) and having a diameter of 16 mm., was now introduced in the space between cornea and iris and fixed to the sclera of the eyeball by means of two fine sutures of atraumatic surgical silk. Orbital membrane and skin were closed by sutures and the connecting wires of the coil were fixed to the back of the animal. The anaesthesia was not profound enough to prevent defensive reactions, in particular, grasping reactions of the arms and jet action evoking backward movement. However, these reactions were as a rule not sufficiently organized and determined to prevent the successful completion of the operation. Ink ejection did not occur in this situation.

The animal was fixed in the following way. A tight collar, consisting of two vertical bars separated by a distance of 17 mm. and held together by horizontal bars, was mounted around the neck. The vertical bars just fitted between the dorsal shield and

the back of the cartilaginous skull. Subsequently the animal was mounted in the centre of a round tank filled with sea water (without urethane) (Fig. 1). The collar was connected to a vertical axis that could be either locked in a fixed position or left free. If the axis was locked, the animal was effectively immobilized, though slight displacements of head and body remained possible. If the axis was unlocked, the animal was free to rotate; by means of a precision potentiometer mounted on the same axis, the (active) rotation of the animal could be recorded. (The inertia and friction of the freely rotating support system were small in comparison to that of the animal in the water.) A third possibility was, to drive the same shaft by means of a motor and gearing system. In this way passive rotation of the animal was induced and recorded by the same potentiometer. Angular velocities of 0·29 up to 29°/sec. were used. The coils that generated the magnetic field were mounted on the same axis, so that the field would rotate with the animal. The different connecting cables provided enough freedom for at least two complete revolutions. By rotating the field coil assembly over a known angle with respect to the animal the measuring system could easily be calibrated.

Around the animal, a cylindric drum (diameter 57 cm.) was suspended. This drum could be rotated at angular speeds, variable between 0·036 and 36°/sec. (in 10 steps), in either direction. The drum had a white surface, on which vertical black strips could be mounted. The standard pattern consisted of alternating white and black bars, each subtending 10°. The eyes of the animal were about 6 cm. below the water surface. The stripe pattern extended from 10 cm. above the water down to the (black) bottom of the tank 25 cm. below the surface. The water was aerated. Most animals tolerated this experimental situation quite well for many hours.

Recovery from anaesthesia was almost instantaneous, and often followed by backward grasping reactions of the arms, directed at the collar, and evasive jet action. This activity usually subsided soon, and the animal would remain quiet, showing the regular striped pattern of pigmentation. The operated eye usually had a normal aspect, in particular the iris and pupil were normal and functionally active. No attention was paid by the animal to the wounds and sutures; the operation could be survived for many days. Ink expulsion, which would of course terminate the experiment, was fortunately rare.

RESULTS

Optokinetic reactions

Optokinetic reactions could usually be obtained as soon as a few minutes after placing the operated animal in the apparatus. However, at least half an hour was always allowed before making any permanent recordings. As a rule the stimulus pattern consisted of alternating black and white bars, each subtending 10°.

Optokinetic nystagmus was usually elicited by a large range of drum velocities (Fig. 2). In most animals, positive reactions, that is a regular nystagmus consisting of a slow phase in the direction of the drum movement and a fast phase in the opposite direction, was evoked by speeds in the range from 35°/sec. down to 0·35°/sec. In a somewhat smaller number of animals unambiguous nystagmus was recorded even at drum speeds as low as 0·035°/sec., that is, one complete revolution in nearly 3 hr. The shape of the nystagmus is quite characteristic and similar in all animals. The slow

phase consists of smooth following at a rather constant velocity. The fast phase has a sharp beginning but a very gradual end. The amplitude of the movements is rather constant once a 'steady state' has been reached; it is as a rule larger at high slow-phase velocities than at low ones, and rarely exceeds a width of 10°.

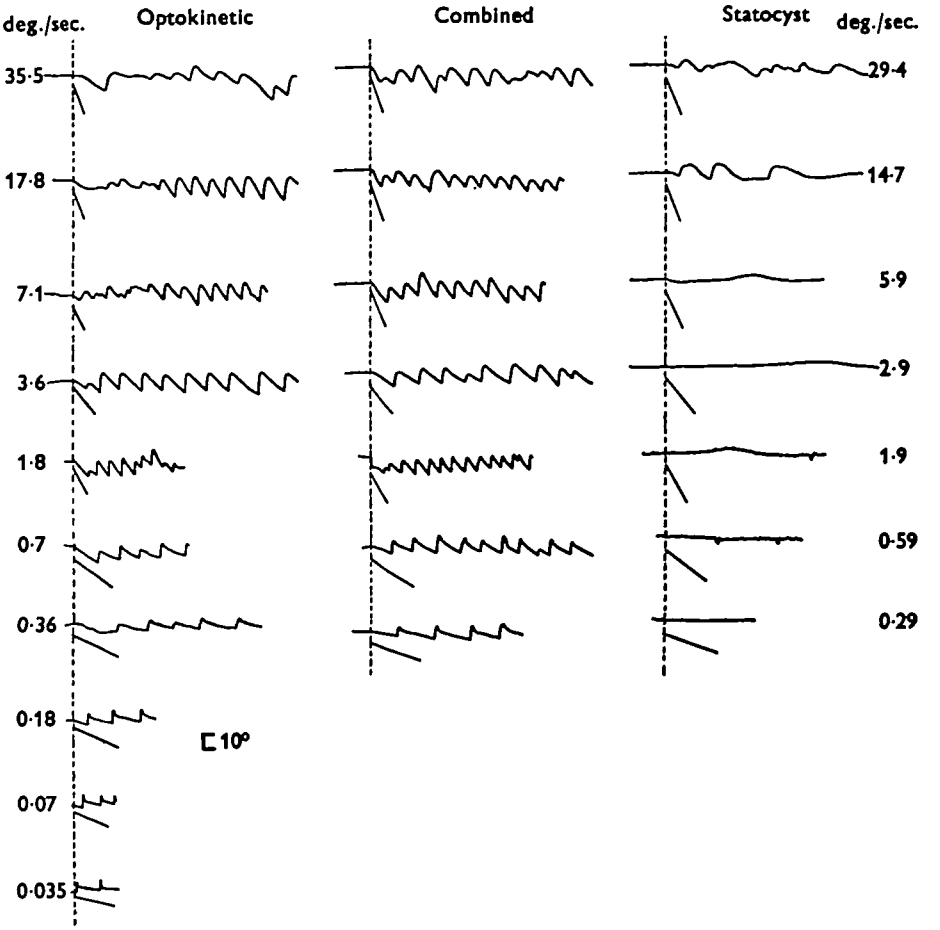

Fig. 2. Examples of eye movements elicited by drum rotation to the right (left row); passive rotation of the animal to the left in the dark (right row) and in the light (middle row). All recordings are from the same experiment. Drum velocities (for left row) are indicated at the left, animal velocities (middle and right row) at the right. The interrupted vertical line marks the onset of rotation in each case. The solid lines below each curve represent the actual relative movement between the animal and its surroundings. Vertical calibration, 10°. The calibration of horizontal time axis varies for the different velocities. Downward movement of the eye-movement trace indicates posterior rotation of the right eye.

Slow and fast phases seem to be well balanced, which results in a long-term stability of the space angle covered by the nystagmus. At low stimulus velocities the start of a slow phase is often too fast (Fig. 2); the eye then gradually slows down to its steady slow phase velocity.

Only movement of the right eye was recorded, but upon visual inspection both eyes always appeared to move conjugately.

There is no evidence for any fatigue or habituation; an animal that shows good optokinetic reactions will continue to do so even during several hours of uninterrupted drum rotation, without any systematic change in the reactions.

As a routine, reactions to all drum speeds were tested in both directions of rotation. Clockwise rotation of the drum or animal as seen from above will be defined as a right rotation and vice versa; the direction of the nystagmus will be defined by the direction of the slow phase. As a rule, the reactions to right and left rotation were equal in magnitude, though opposite in sign.

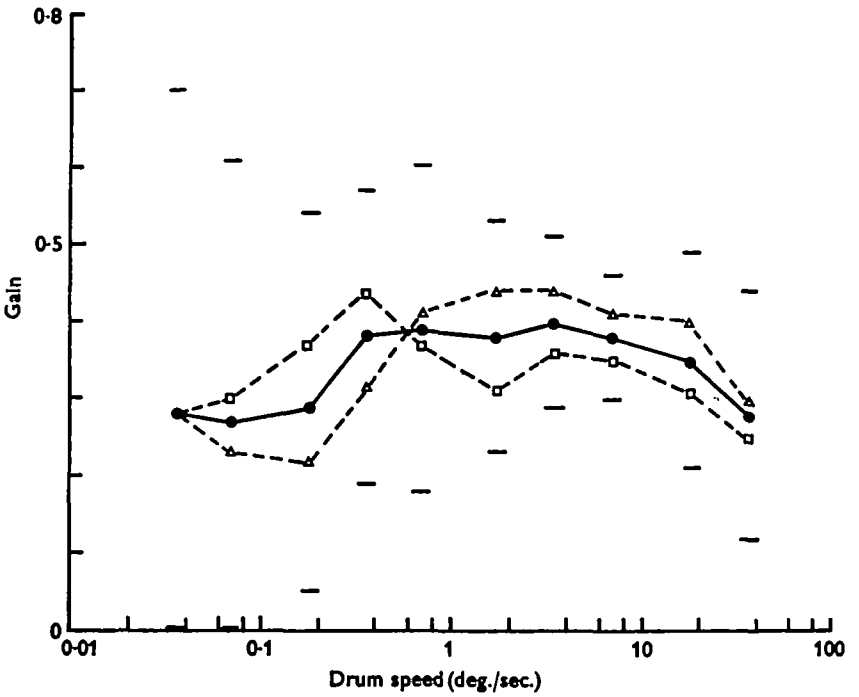

Fig. 3. Gain (eye speed/drum speed) of the slow phase of optokinetic nystagmus for different velocities of the drum. □: drum rotation to the left; △: drum rotation to the right; ●: average of these two, with standard deviations indicated by horizontal bars.

In a number of cases the animal as a whole was left free to rotate around the fixation axis of the collar. Though the animal was quite capable of turning its body around this axis (these movements will be discussed later), it was found that such body movements were never used to follow the drum. The optokinetic reactions were only achieved by movements of the eyes in the orbits (Fig. 8, lowest graph). Of course, this finding cannot be extrapolated beyond the limitations of the experimental situation. A free-swimming animal in the same tank followed the drum movement mainly by swimming in circles around the periphery of the vessel.

For an evaluation of the effectiveness of the slow-phase tracking mechanism, which should ideally prevent or at least highly limit the shift of the patterns projected upon the retina, the ratio eye speed/drum speed was determined for the slow phase at all drum speeds used. This ratio will be designated as the *gain* of the system; ideally it should approach a value of 1·0. The results are plotted in Fig. 3. As indicated by the

horizontal bars, the spread between different animals is considerable. A few conclusions are obvious: (*a*) Gain remains as a rule considerably below 1 and even below 0·5, resulting in a large amount of 'slipping' of the image over the retina. The compensation is therefore rather poor. (*b*) Gain is actually remarkably constant over a speed range varying by a factor 1000. The tendency towards a slightly lower gain at the highest and lowest drum velocities is probably genuine, but quite small in proportion to the variation in speed. (*c*) Differences in gain during reactions to rotation to the right and to the left are small and not systematic.

Reactions to passive rotation in darkness

The animal was passively rotated in the water by means of the collar. Angular velocity was stepwise increased from zero to a steady value (between 29° and 0·29°/sec.) by starting the motor. Actually, this acceleration did of course take a certain time determined by the power/mass ratio and the elastic properties of the driving system. No attempt was made to measure the actual accelerations; a steady state was reached in any case within a second. To study the effect of rotation (which is thought to stimulate the crista of the statocyst) in isolation, without optokinetic complication, these reactions were studied in complete darkness.

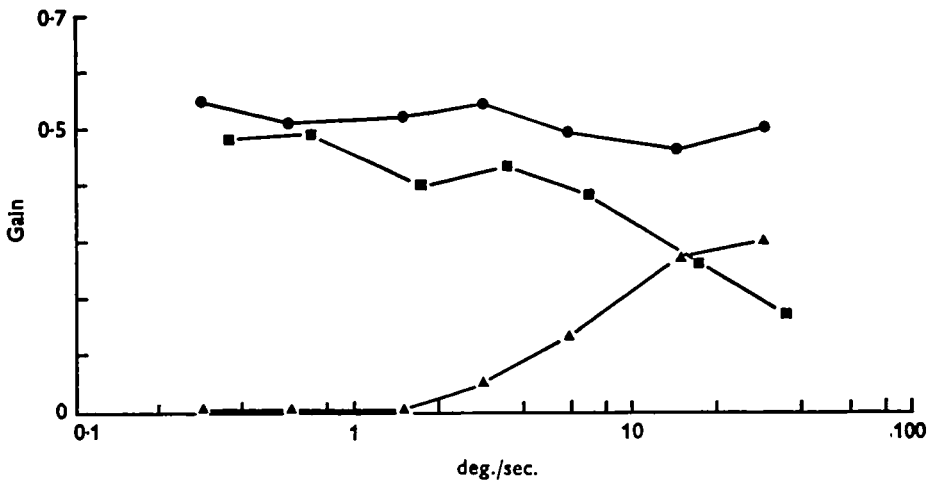

Fig. 4. Velocity gain for optokinetic stimulation alone (■), statocyst stimulation alone (▲), and for stimulation of both systems together (●). Maximal slow-phase velocities that were reached have been used for the reactions to statocyst stimulation (▲). Vertical axis: Gain. Horizontal axis: Relative speed between animal and environment.

A nystagmic reaction, consisting of slow and fast phase, was always found at the higher rotation velocities. The direction of the slow phase was always opposite to that of the rotation of the animal, as would be expected.

Good reactions were usually found after onset of rotation at 29·4°/sec. and 14·7°/sec.; at 5·9°/sec. reactions were much smaller. At still lower velocities reactions were absent (Fig. 2, right row). Moreover, reactions always declined quickly and died out completely during steady rotation. At high angular velocities reactions lasted longer than at lower ones. Once the reaction had disappeared a sudden arrest of the rotation would

evoke an after-nystagmus which was quite similar to the first reaction, but of opposite direction (Fig. 5). In general, the shape of vestibular nystagmus was much less regular than that of optokinetic nystagmus. Especially the slow phase velocity was quite variable. The fast phase looked similar to that in optokinetic nystagmus.

Combined optokinetic and statocyst stimulation

By passively rotating the animal with the lights on and the (stationary) striped drum present, both inputs were activated at the same time. The result was a nystagmus that showed considerable improvements over either form of stimulation apart, especially at the higher velocities; the gain is higher and the maximal velocity of the slow phase is reached much sooner after onset of the rotation. Examples are shown in Fig. 2 (middle row). The improved gain is illustrated in Fig. 4 (maximal velocities

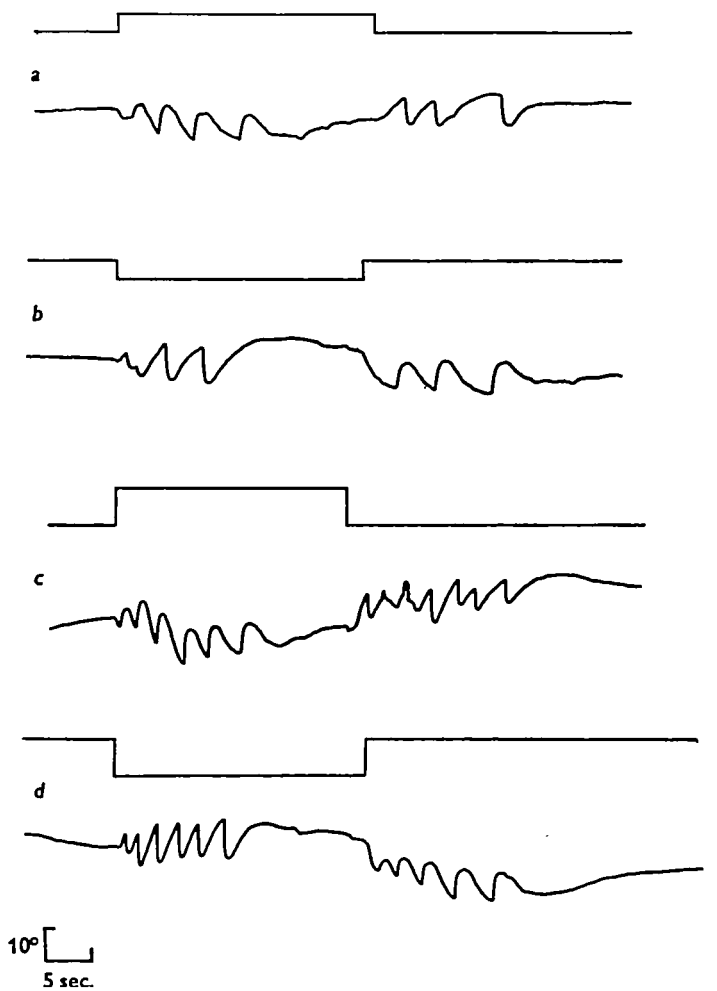

Fig. 5. Nystagmus and after-nystagmus at onset and arrest of passive rotation in the dark, as marked above the traces. (*a*) 14·7°/sec. to the left; (*b*) 14·7°/sec.to the right; (*c*) 29·4°/sec. to the left; (*d*) 29·4°/sec. to the right. Calibration: vertical, 10°; horizontal, 5 sec.

were used to determine the gain in the case of stimulation of the statocyst alone). Of course, this combined stimulus is the closest approach to what the animal might experience in its normal surroundings. In this situation, no after-nystagmus was ever seen after arrest of the rotation.

Monocular optokinetic stimulation

In three animals the left eye was blinded by removing the lens and vitreous body and stitching the eyelids together (Messenger, 1968). One day later optokinetic reactions of the right eye were tested. In three other animals the eyelids of the right

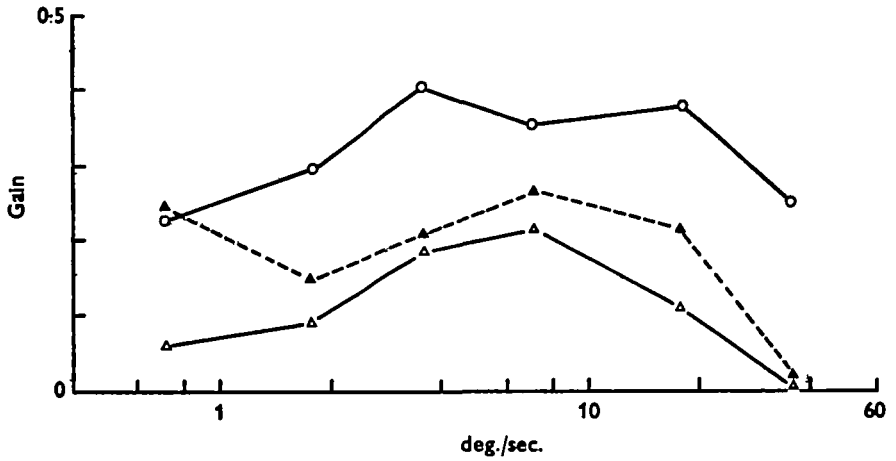

Fig. 6. Gain of monocularly and binocularly evoked optokinetic nystagmus. △: movement of (closed) right eye, stimulation of left (seeing) eye. ○: same with both eyes open. ▲: movement of (open) right eye 24 hr. after blinding of left eye. Averaged results of rotation to left and right side. Vertical axis, gain. Horizontal axis, drum speed.

eye were closed by sutures which could be removed later to restore binocular vision. In this way monocular and binocular reactions could be determined in the same animals. As in all cases, movement of the right eye was measured. As is shown in Fig. 6, gain was considerably down in the monocular situation; at 35°/sec. reactions were even consistently absent. Moreover, monocular reactions were rather inconstant; at one moment the animal would show a regular nystagmus, while a few minutes later or earlier reactions might fail completely. However, in the monocular, as in the binocular, situation reactions remained equal in both directions: drum rotation to the left and to the right was equally effective in evoking a nystagmus, with similar gain. This is in contrast to findings in rabbits (see discussion).

Apparently eye movements remain conjugate when only one eye is open, since the closed right eye is being 'driven' by the seeing left eye.

Variations in optokinetic stimulus patterns

It was intended to test a range of different widths and numbers of black bars mounted against the white background of the drum in order to get some estimate of

contrast requirements of the optokinetic system. However, when in the very first trial all black stripes were removed and the plain white drum was rotated, a similar vigorous nystagmus was elicited as when the stripes were present (Fig. 7). This demonstrates that, at least for this specimen, the 'blank' background contained already enough contrast for movement detection, and that the black bars were actually redundant. Though in a few later experiments reactions were sometimes indeed decreased after removal of the bars, it did not seem fruitful to pursue the study of this problem with the existing arrangement.

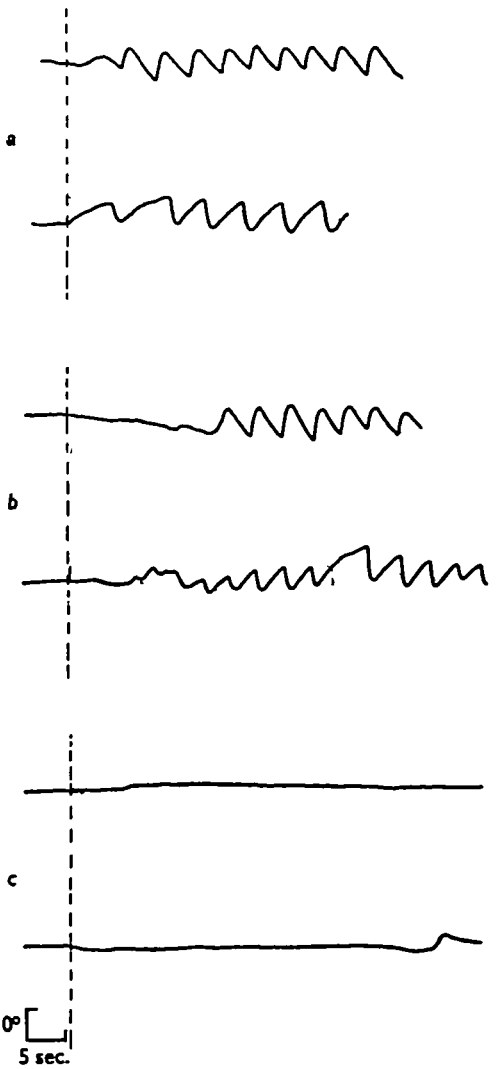

Fig. 7. (*a*) Optokinetic reaction to leftward and rightward rotation (at 7·1°/sec.) of drum with pattern of alternating white and black bars, each subtending 10°. (*b*) Optokinetic reaction after removal of the stripes. The white background apparently contains sufficient contrast to elicit the same reaction as in (*a*). (*c*) Reaction to rotation of drum containing bars as in (*a*), but with a screen masking the left half of the drum; the reaction is completely abolished. (All records from the same experiment). Calibration: vertical, 10°; horizontal, 5 sec.

Stimulation of a part of the visual field only

All experiments described so far were performed while the entire moving drum was visible to the animal. In that way the whole horizontal plane of vision, which is the main visual plane in *Sepia*, covering 360° (Messenger 1968) was stimulated.

By placing a black screen between the moving drum and the animal the effect of partial stimulation of the visual field was tested.

It was found that masking of 180° of the drum, in any orientation, prevented the occurrence of optokinetic nystagmus at higher drum velocities (7°/sec. and more), while at lower velocities, reactions were either absent or inconstant and weak (Fig. 7).

The difference of the results when one half of the visual field is blinded (monocular viewing) and when one half of the visual field is occupied by a stationary screen suggested that the reaction of the optokinetic system in the present conditions was determined by the algebraic sum of movement in the entire available visual field.

Reactions to isolated moving objects

As a further test of the possibility of evoking ocular tracking of movements other than in response to the entire surroundings, the effect of moving 'interesting' objects around the animal was tried. Living small crabs, of a type and size that had been immediately attacked by the same animal the day before the experiment, were used for this purpose. They were rotated in front of a white background without black bars, at similar speeds as used for the drum movements. The crabs were loosely tied down and were usually active. In no case did such a crab elicit any optokinetic nystagmus or body rotation. However, even when the crab was brought within the reach of the tentacles or even the arms, no attack or anything like it was evoked. This may indicate that in the circumstances of the experiment the animal was too upset to display its normal aggression, or even to follow visually a prey, which would normally be seized in an instant. Since under normal circumstances a hungry animal immediately directs its attention to similar objects and seems to fixate them at the posterior part of the retina, it seems that the experimental conditions were not favourable for the demonstration of a possibly existing 'fixation type' of optokinetic nystagmus (ter Braak, 1936). The present negative findings cannot be considered as conclusive evidence against such a mechanism in *Sepia*.

Spontaneous eye and body movements

In the situation in which the animal was free to turn around a vertical axis active rotation was often observed (Fig. 8). Eye and body movements were often seen in combination. In many cases eye movements preceded body movements. Eye position was measured relative to body position, body position was measured relative to the tank.

Therefore, absence of eye movement during body rotation would indicate that the eyes were rotating passively with the body, without fixation of the surroundings. This turns out to be rare. Usually body movements are accompanied by vigorous eye movements. The latter often have the characteristics of nystagmus; the slow phase is directed opposite to the direction of body rotation, so that there is a certain amount of compensation of body movements by eye movements.

It can be seen from the examples in Fig. 8 that this nystagmus does especially occur during fast body rotations (angular speeds up to 40°/sec. were recorded). The slow-phase velocity of the nystagmus is rarely above 10°/sec. In view of the irregular and unpredictable character of these movements, no formal analysis was attempted.

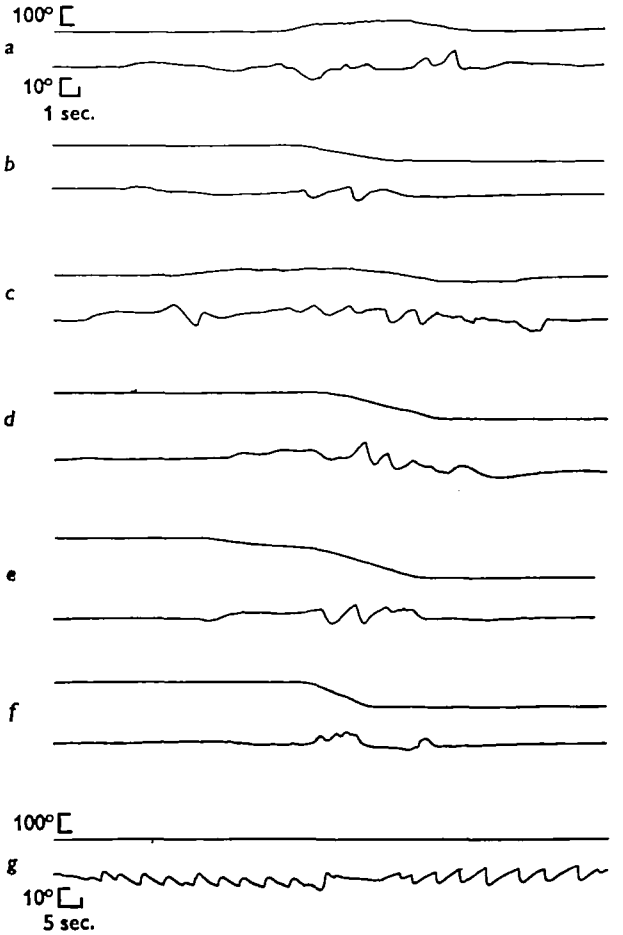

Fig. 8. (*a–f*). Examples of simultaneous active body rotation (upper traces) and eye movements (lower traces). These were spontaneous movements within the stationary striped drum. Calibration (given in (*a*)): vertical, body rotation 100°; eye rotation 10°; horizontal, 1 sec. (*g*) absence of active body rotation during optokinetic nystagmus (drum rotation 3·6°/sec., first rightward, later leftward). Calibration: vertical, body rotation, 100°; eye rotation, 10°; horizontal, 5 sec. Downward displacement of the traces indicates rotation to the right.

Background activity of the eye

Coarse eye movements, often occurring in conjunction with (attempted) body movements, such as described above, were usually relatively rare, with long quiet intervals in between. During the latter the eye seemed to be quite stable when ordinary sensitivity of the measuring system was used (full scale deflexion for *ca.* 20° deviation from the mid-position). No spontaneous nystagmus was ever seen. In Fig. 9 spontaneous activity levels in three animals are illustrated, recorded at ten times the usual

sensitivity. In Fig. 9*a*, the slow drift is caused by eye movements, but the fast tremor is at the level of the noise of the measuring system. In *b* and *c* slightly higher activity levels are shown. At the present level of resolution, no microsaccades are revealed.

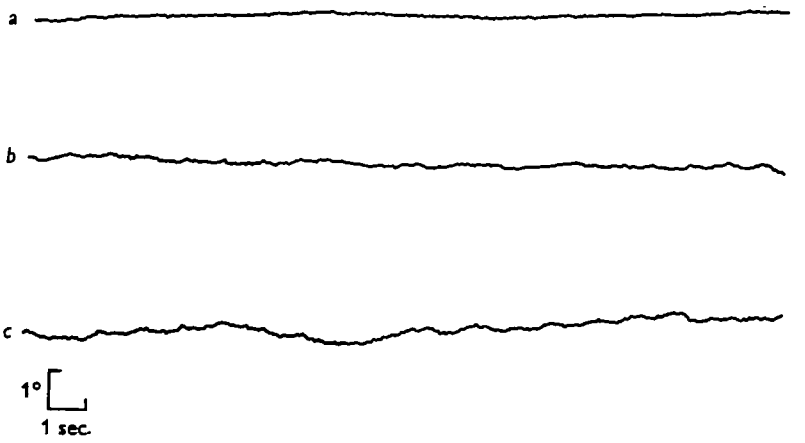

Fig. 9. Examples of background activity of the eye in three different animals. Calibration: vertical, 1°; horizontal, 1 sec.

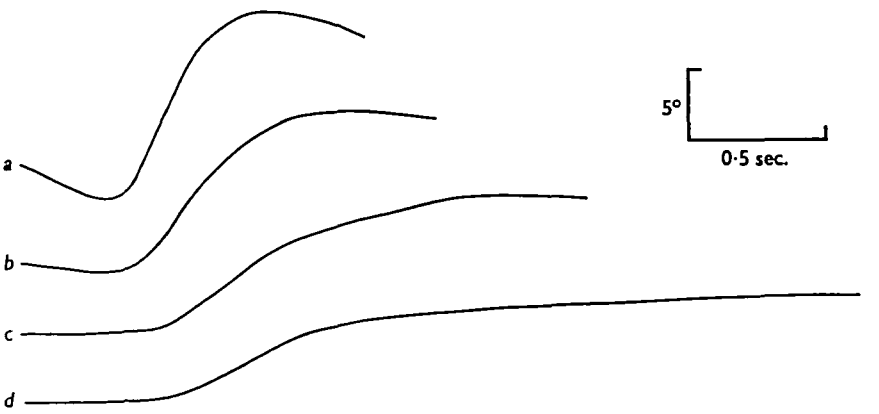

Fig. 10. Examples of saccades in the same animal at different drum velocities: (*a*) 35·5°/sec; (*b*) 7·1°/sec; (*c*) 0·7°/sec.; (*d*) 0·07°/sec. Calibration: vertical, 5°; horizontal, 0·5 sec.

Shape of fast phase

The general shape of the fast phase (saccade) is rather constant: a sudden beginning of the movement with strong acceleration to a maximal speed, which is followed by a very gradual transition to the next slow phase. A closer study of the shape of the fast phase revealed that its parameters vary strongly with the velocity of the slow phase. A few representative saccades, occurring at different drum velocities, are shown in Fig. 10. It turns out that at lower slow-phase speeds the saccades have a smaller amplitude, longer duration and lower maximal velocity. By comparing these parameters in a larger number of saccades it was found that maximal velocity and duration are not functions of the amplitude alone, but also of slow-phase velocity. In Fig. 11

it can be seen that the average length, duration and maximal speed of saccades all vary with the slow-phase eye speed during which they occur. Even at high velocities duration of saccades is around 0·5 sec., which is about five times slower than in the rabbit.

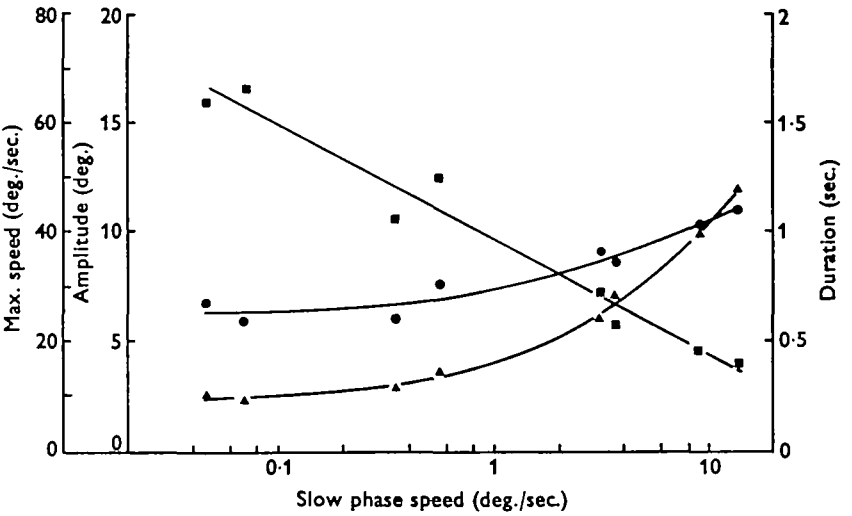

Fig. 11. Amplitude (●), duration (■) and maximal velocity (▲) of fast phase, as a function of slow-phase velocity (horizontal scale). Every point represents the average value from 10 saccades.

DISCUSSION

In the present experiments eye movements in *Sepia* have been recorded by a direct method which allows some quantitative conclusions. The confirmation of an optokinetic response in *Sepia* is in itself not surprising, since optokinetic reactions are almost universally found in animals with movable eyes.

In accordance with findings in the crab (Horridge & Sandeman, 1964) and the rabbit (ter Braak, 1936; Collewijn, 1969) optokinetic reactions could be demonstrated even to very low angular stimulus velocities (0·035°/sec.). By subjecting the animals to a sudden change in angular velocity in the dark a transient nystagmus was evoked. It is supposed that such accelerations stimulate the crista of the statocyst, which is thought to have a similar function to the semicircular canals in vertebrates (Dijkgraaf, 1961, 1963). The crista would thus mediate the dynamic reactions to (passive) postural changes, while the (loaded) macula would serve the static regulations, such as the pupil horizontal in varying body positions.

It was shown that by combined stimulation of visual and statocyst systems the best reaction is obtained. It was often seen that a fast drum rotation would evoke a poor or late optokinetic response, while passive body rotation at the same speed would give a good reaction. Apparently, the optokinetic system was able to maintain a steady response once the necessary acceleration had been achieved with the help of the statocyst input. The contribution of the statocyst is mainly the fast response to a sudden acceleration, while steady responses to high or low constant velocities are only mediated visually.

The gain of the system varies only little over a speed range of three decades and was in the present experiments usually below 0·5. The performance of the system as a position feedback is therefore quite poor and clearly inferior to that in rabbits (Collewijn, 1969), at least in the conditions of the experiment. Possibly it is better in the natural situation.

The threshold of contrast level for the optokinetic input was apparently too low to be determined by the arrangement used, which might indicate that the system is well adapted to the low-contrast visual environment under water. Ter Braak (1936) was the first to distinguish two types of optokinetic eye movements, namely the 'stare' type, caused by a general movement of the retinal image, such as found in rabbits, and the 'fixation' type, caused by the foveal tracking of isolated objects to which the attention is directed. The latter type has been demonstrated so far only in species with clear foveal vision such as man and monkey. In *Sepia* the retina contains a horizontal equatorial strip where rhabdomes are more closely packed, especially in its anterior and posterior ends (Young, 1963). Behavioural evidence indicates that the image of a prey is moved to the posterior end of this strip, which may thus be a specialized area of vision (Messenger, 1968). It is highly interesting that rabbits also possess an equatorial specialized retinal area, the visual streak. Nevertheless, no fixation movements have ever been demonstrated in the rabbit; only compensatory eye movements of vestibular, proprioceptive and optokinetic origin are seen. On the other hand, *Sepia* normally has spontaneous eye movements, and might therefore possess a fixation mechanism. In the present experiments this could not be demonstrated. Boulet (1958), in a series of experiments of quite different design, found eye-movement reactions of *Sepia* to isolated targets moving at speeds from 7 min. to 51°/sec. In his experiments the animal was moving free in a tank.

The results of blinding one eye and of masking half of the moving drum demonstrate that the information from both eyes is well integrated. A stationary image in one eye clearly cancels the movement seen in the other eye, since optokinetic nystagmus does not occur. If it were to occur, the stationary image would of course start to move, which would reverse the stimulus. This is only true if the eyes always move conjugately, and not independently. In *Sepia* this seems to be indeed the case, as is also indicated by the driving of a blind eye by a seeing one. (This may be different in *Octopus*.)

It is important to note that in the monocular situation optokinetic reactions were depressed, but equal in both directions. This is in sharp contrast to the rabbit, where each eye is much more sensitive to forward drum movement than to backward movement. In the monocular rabbit, nystagmus in the preferred direction is as large as in the binocular situation, but reactions to backward drum rotation are very poor (Collewijn, 1969). Though contrast requirements for *Sepia* are very small, the information apparently has to come from both eyes in order to evoke a maximal reaction. The eye movements occurring in combination with body movements are deserving of further study. According to Dijkgraaf (1959, 1961) 'nystagmus' is observed during active movement in *Octopus* even after bilateral section of the optic tract and removal of both statocysts. This would indicate a primary central origin of these movements. This raises the old queston whether optokinetic or vestibular reactions are overruled during active movements. Dijkgraaf's (1953) discussion of this point is very pertinent here, since in our case the animal had only one degree of freedom: horizontal rotation.

It is therefore unlikely that the actual rotation of the animal would agree with its intended movement; this rotation might therefore be considered to be effectively passive. The observed nystagmus might thus be largely determined by statocyst and optokinetic input. In studying the fast phase it should be realized that the mechanical properties of the *Sepia* eye are very different from those of the mammalian eye. Intraocular pressure is very low and the eye is a flaccid sac, rather than a tense ball. Also, the orbital tissues lack firmness and do not provide a smooth socket. Therefore, the visco-elasticity of the system may result in heavy overdamping. The sluggishness of the saccades is therefore not surprising.

The dependence of the shape of the saccades upon the slow-phase velocity is a rather surprising finding, which should be further studied. The present findings clearly indicate that the saccade is not a constant entity in which the amplitude is the only independent variable, as has been found in voluntary saccades in man (Robinson, 1964) and monkey (Fuchs, 1967). Koike (1958) has reported a similar dependence upon the slow phase of saccades in nystagmus in rabbits. If his finding can be verified, it might indicate either species differences in the oculomotor system, or a fundamental difference between 'voluntary' and nystagmic saccades.

SUMMARY

1. Eye position in *Sepia* was measured in restrained animals, using a scleral search coil technique.

2. Optokinetic nystagmus was elicited by drum rotations from 0·035 up to 35°/sec.

3. Passive rotation of *Sepia* in darkness evoked a transient nystagmus, followed by after-nystagmus at arrest.

4. Combination of these two stimuli yielded the best results, but the ratio eye velocity/surroundings velocity was usually not better than 0·5.

5. Eye movements were conjugate and a closed eye could be driven by a seeing eye. Monocular reactions were smaller than binocular ones, but equal in both directions.

6. Fixation movements could not be demonstrated in the present conditions.

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