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THE ONSET OF THE FAST PHASE IN THE OPTOKINETIC RESPONSE OF THE CRAB, *CARCINUS*

BY G. A. HORRIDGE AND M. BURROWS*
Gatty Marine Laboratory and Department of Natural History, University of St Andrews, Fife, Scotland

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INTRODUCTION

When a crab is held in the centre of a vertically striped drum which is rotated slowly, both eyecups follow the movement in what is called the optokinetic response. Then both eyecups flick back rapidly to start the cycle once more. The whole response is called optokinetic nystagmus.

An important feature of the control of this and all other eye movements in the crab is that experiments have always failed to reveal any part played by proprioceptors. Originally it was found that the characteristic pattern of motor impulses in the oculomotor nerve to the eyecup muscles did not depend on whether the eyecup is free to move, clamped or fixed in an abnormal position. Secondly, when a blind movable eyecup is driven by a seeing eye, forced movements of the latter against a stationary background cause a movement of the blind eyecup *in the opposite direction*, so that the eyecups can be induced to converge or diverge, because the blind eyecup is driven solely by the relative visual stimulus across the other. A third test is to move one eyecup forcibly when both eyes are blind; the other eyecup then makes no movement (Horridge & Sandeman, 1964). In previous papers (Burrows & Horridge, 1968*a*, *b*, *c*) the activity of all the eyecup muscles has been recorded during optokinetic, geotactic and withdrawal responses. Irrespective of whether the eyecup is allowed to move, the appropriate impulse pattern emerges from the brain in at least 20 different individually identifiable motoneurones to each eyecup, and depends only on the visual stimulus when that is taken relative to the seeing eye itself. The fast-phase movement of optokinetic nystagmus is one part of this central programme.

The following experiments are concerned with the question as to what determines the onset of the fast phase and the position which the eyecup reaches at the onset of the fast phase. Although numerous experiments have now been carried out on the crab's optokinetic response, none of them so far bears upon this point, except a preliminary notice of one result presented here (Horridge, 1967), and the finding that one eyecup leads the other by 40–60 msec. in its execution of the fast phase (Barnes, 1968).

METHODS

The movements of the two eyecups were recorded as before. Junction potentials recorded intracellularly from singly innervated tonic muscle fibres were fed to a pulse-shaping circuit which converted each potential to a pulse of constant size. These pulses

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* Present address: Department of Biology, University of Oregon, Eugene, Oregon 97403, U.S.A.

were then fed to a voltage integrator whose output was plotted on a pen recorder. Circuits were incorporated in the systems which recorded the eyecup movement and the muscle frequency so that shocks could be applied to the antennule when the eyecup reached a given position, or when the frequency of junction potentials reached a given level.

RESULTS

The normal fast phase

The central determination of fast phase

One experiment makes it quite clear that the fast phase of optokinetic nystagmus is centrally determined like the rest of the pattern of efferent impulses. Both eyecups are cemented in their sockets and one eye is blinded by coating the cornea with black paint. Intracellular records are taken from tonic fibres of either muscle 20a or muscle 21 of the blind eyecup while a striped drum around the crab is moved steadily through a few degrees and then stopped. The response in these muscles of the blind eyecup shows a series of slow phases, each marked by a progressive increase in frequency and terminated by a fast phase (Fig. 1). Although the drum is now stationary, this iterated output continues for several slow phases, and eventually the tonic frequency settles down to some new value that represents the posture which the eyecup would adopt if free to move. The number of fast phases performed depends only on the amplitude and speed of the movement of the drum and represents the total excursion which the blind eyecup would have taken if free and under open-loop conditions, i.e. with the visual feedback cut by clamping the seeing eyecup. Each fast phase corresponds to about 12° movement of a free eyecup and with slow drum movement a forward gain

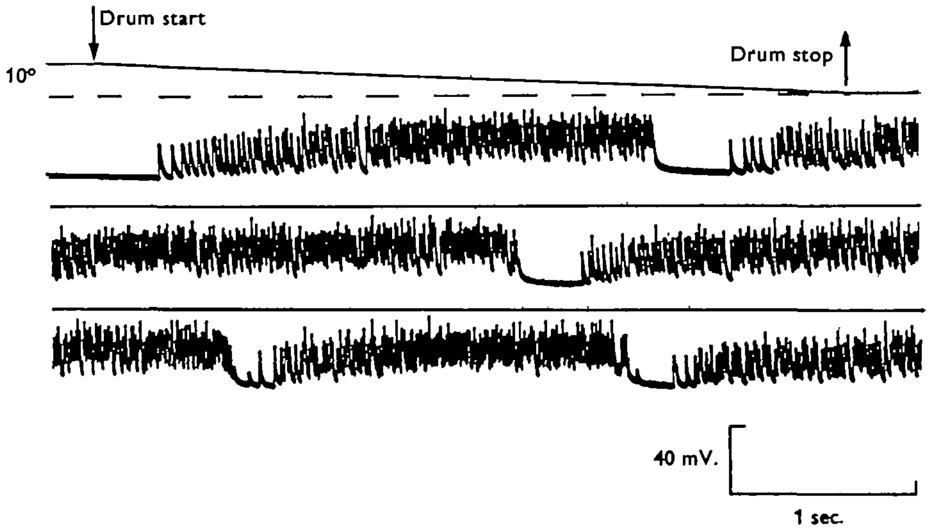

Fig. 1. A movement of the striped drum toward the mid line (continuous line) is presented to a fixed seeing right eye of a crab and then from the arrow at the end of the first line the drum is held stationary. Intracellular activity is recorded from muscle 21 of the contralateral blinded and clamped eyecup. With the seeing eye clamped there is no negative feedback caused by its own movement, and the nystagmus responses continue long after the drum has stopped.

of 10 is typical (Horridge & Sandeman, 1964). Therefore a slow drum movement through 6° would typically give rise to 6° x 10/12° = 5 fast phases, similar to Fig. 1.

In this experiment both eyecups are clamped and most of the response appears *after* the drum has stopped. There is a great deal of other evidence that the visual system contains subsystems of long-time constant which infer movement from the mismatch between the present and a previous visual input. Much of this evidence has been gathered under the name of optokinetic memory (Horridge, 1966). After a movement, or inferred movement, the blind or clamped eyecup can continue to respond for up to a minute, because the response is not cut off by its own movement, which would invoke a relative visual input in the opposite direction.

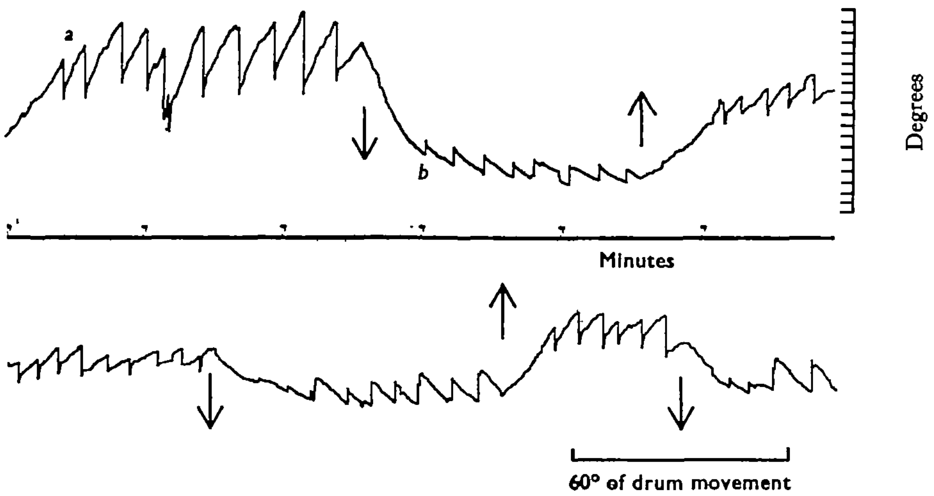

Fig. 2. Nystagmus in different parts of the range of movement. The extent of the slow phase is small in this example, and movements in opposite directions do not overlap. When the drum direction is restored after being reversed, the new position of onset of the fast phase is not necessarily the same as previously. Note the progressive change in the point of onset for the first few fast phases in either direction (*a* and *b*). The second line is the continuation of the first, and the vertical scale is the same.

The relation between fast phases in the two directions

The eyecups follow the slow rotation of a striped drum and then rapidly flick back to their original position, so that a nystagmus occurs over a range of 3–15°. This range is flexible, is variable from crab to crab and the absolute position of the traverse relative to the carapace differs between crabs. When the drum movement is reversed, the eyecups follow the drum far beyond the point where the fast phases formerly ended, establishing a new traverse, with slow and fast phases well to the left or right of their former range and not necessarily overlapping with it (Fig. 2). A curious feature is that after the drum has been reversed the first fast phase occurs at an earlier position and the next few slow phases advance the eyecup progressively further across the orbit. The position of onset of subsequent fast phases is then typically constant to 1°. As the crab habituates to a continuous rotating drum the excursions in nystagmus become smaller and the range over which the excursion occurs in one direction approaches more closely that in the other direction.

Motor impulse frequencies at fast phase

A fast phase toward the mid line is preceded by a high-frequency burst of impulses in muscle 21 and a slow phase in the same direction is accompanied by the progressive increase in impulse frequency to this muscle as the eye traverses the orbit. Exactly the same type of motor output is recorded when the eyecup is clamped so that intracellular recordings can be made from the muscles (Burrows & Horridge, 1968*a*).

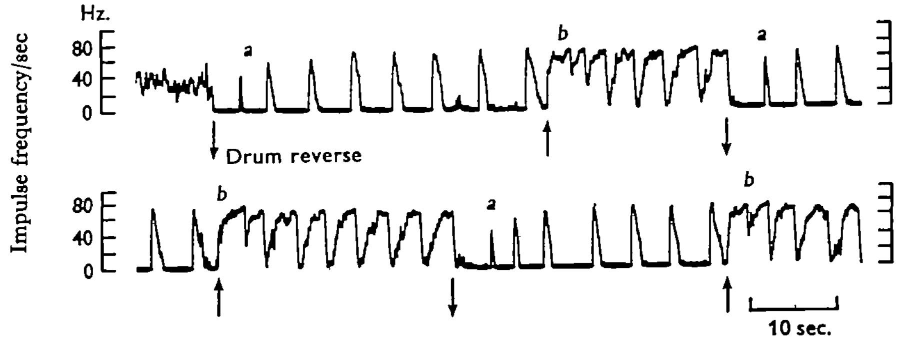

Fig. 3. A pen record of the frequency of junction potentials recorded from a single tonic fibre of muscle 21 of the right eyecup. This muscle shows a gradual increase in frequency during a slow phase toward the mid line and a short burst during a fast-phase movement in the same direction. The arrows show when the drum movement is reversed. Downward arrows show the start of a drum movement away from the mid line.

If the drum is reversed while moving toward the mid line during intracellular recording from a tonic fibre of muscle 21, the bursts of impulses preceding the first two or three fast phases toward the mid line reach a lower frequency and have fewer impulses than later fast phases in the steady state (Fig. 3*a*). This is the result which the recordings of eye movement would suggest if muscle 21 provides the principal motive force for the fast phase. When the drum is reversed the frequency of motor impulses to muscle 21 rises sharply to the maximum value at the first slow phase toward the mid line (Fig. 3*b*). Subsequent slow phases are marked by a progressively slower initial rate of rise of the discharge until the steady state is achieved. In the frequency profiles this is shown by a failure of the integrator to return to zero at the initial fast phases. If the motoneurone impulses to muscle 21 were to account entirely for the slow-phase movements, a gradual increase to maximum frequency would be expected after a drum reversal as the eyecup moved progressively across the orbit in successive slow phases (Fig. 1 *a*, *b*). This does not happen, and therefore changes in the output to other muscles must be involved while the central programme to muscle 21 remains constant. This provides a further example of the general statement that single eyecup muscles do not entirely govern single responses, but that many muscles act in unison (Burrows & Horridge, 1968*a*).

The governing and the governed eye

When recording simultaneously the movements of both eyecups for the first time, Barnes (1968) found that the fast phase occurs earlier in the eyecup which is making its slow phase towards the mid line, while the other eyecup follows with a latency of

40–60 msec. (Fig. 4). When the visual input is to a single eye, that side does not readily make fast phases *toward* the mid line but acts normally when the fast phases are away from the mid line. Thus the system behaves as if the fast phase starts at the eye which sees a drum movement toward the mid line and as if this eye governs the fast phase of both eyecups. The eye seeing the drum movement away from the mid line and making its fast phase toward the mid line is called the *governed* eye.

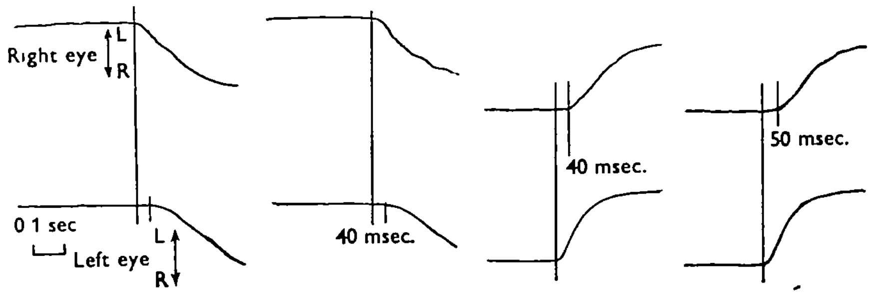

Fig. 4. Simultaneous records from the two sides showing the latency in the onset of the fast phase of a governed eyecup. An eyecup making a fast phase towards its own side leads by 40–60 msec.

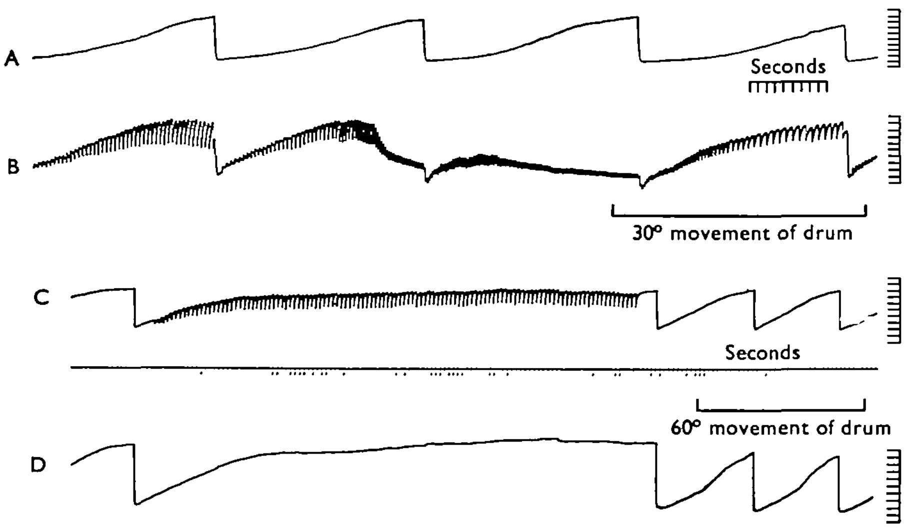

Fig. 5. Simultaneous records from right (A and C) and left (B and D) seeing eyecups. In the upper pair (A and B) the retraction reflex elicited from the *governed* eye (the left) had no influence on the timing of the fast phase, or any aspect of the response of the other eye. In the lower pair (C and D) the retraction reflexes elicited from the *governing* eye (the right), delayed the fast phase, reduced the height of the next slow phase a little, but in this example did not reduce the response of the governed eyecup.

Influence of reflex eyecup withdrawal on the fast phase

A single shock applied to the carapace around an eye socket, or to an antennule, causes a short-lived withdrawal of the eyecup. The size of this withdrawal can be controlled conveniently by the amplitude and duration of the shock. The central mechanism of reflex withdrawal probably involves no more than a single synapse of afferent nerve endings (Sandeman, 1967) upon the two large motoneurones to the muscles of the eyecup (Burrows, 1967; Burrows & Horridge, 1968*c*).

When the governed eye is induced to withdraw repeatedly during optokinetic response there is no effect on the onset of the fast phase in either eye. The governed eye can be driven almost to complete retraction without effect and therefore the fast phase is controlled entirely by the governing eye, which is not influenced in this case (Fig. 5A, 6A).

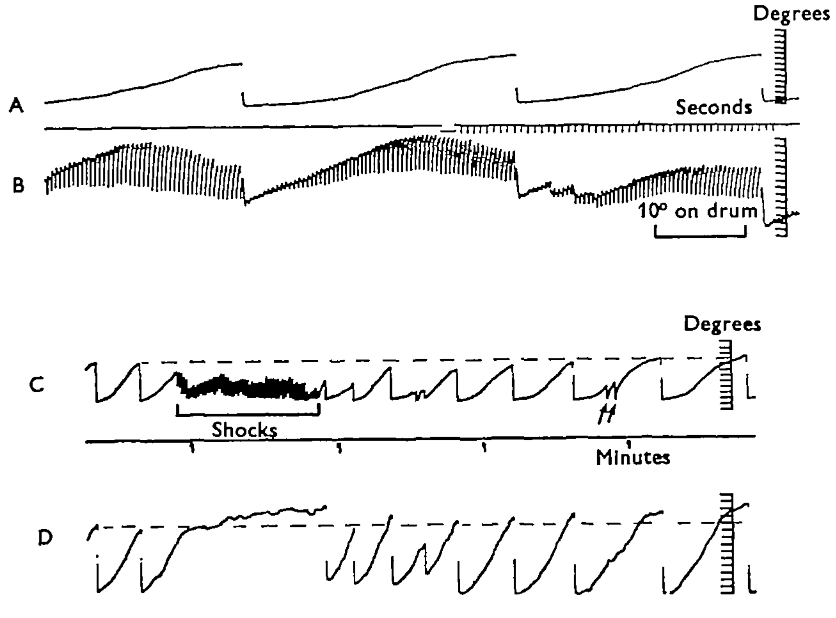

Fig. 6. Simultaneous records of the right (A and C, governing) and left (B and D, governed) eyecups respectively, showing effects of shocks on subsequent fast phases. Small spontaneous retractions are marked by arrows. Shocks to the governing eye cause a delay in the fast phase and the onset of the fast phase thereafter occurs earlier. There is recovery by about the eighth fast phase after the shocks.

When the governing eye is caused to withdraw in the same way there is a suppression of the fast phase for as long as stimulation is continued and both eyes are affected. To prevent the fast phases for many minutes the shocks have to be applied at about 1 Hz. (Fig. 5C), since a single reflex or spontaneous withdrawal of the eyecup is ineffective (Fig. 6C).

Following a period of shocks to the region of a *governing* eye the fast phase often occurred sooner than normal (Fig. 6D). This change in behaviour had the effect of shortening the slow forward phase of nystagmus and led directly to a new type of experiment.

Plasticity of the observed response

The onset of the fast phase

The eyecup movement of a naïve crab showing a regular nystagmus is recorded by a photocell and a circuit is incorporated so that shocks at 1 Hz., are delivered to the region of the *governing* eyecup whenever it passes and remains beyond a certain point. This point is arranged to lie in the path of a slow phase toward the mid line about 1°

before the normal onset of the fast phase. Under the influence of the drum the eyecup moves toward the mid line and inevitably gives itself a series of shocks. These cause withdrawal, which carries the eyecup *away* from the shock. The experiment is therefore arranged so that the unconditioned response is an adaptive one. The eyecup is free to move but receives shocks only for the period that the optokinetic response carried it past the critical point. The eyecup extends again and the continuing movement of the drum again forces it beyond the point where it is shocked. It retracts again and after a further variable period of irregular movements the fast phase occurs earlier, but at first not necessarily consistently earlier (Fig. 7). Thus some slow phases avoid the shock altogether, but eventually the eyecup may exceed the critical point and be shocked again. After further minutes, in which an occasional shock may be received, the movement of the eyecup settles down to a new routine, with the fast phase consistently earlier and so avoiding the shock completely. This is a long-term change which may persist for 1 hr. and lasts many times the length of the period of shocks. The whole sequence is shown in Fig. 7.

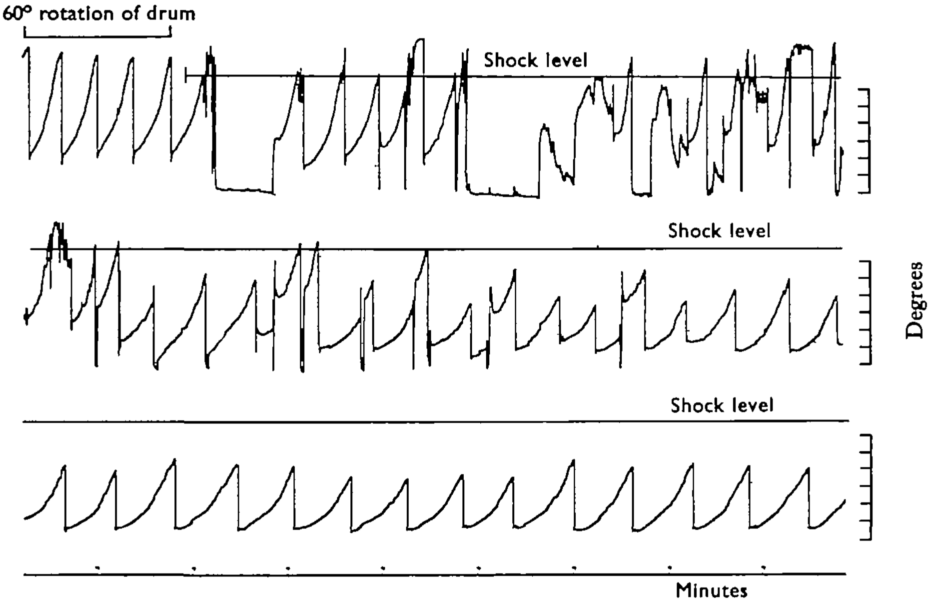

Fig. 7. The effect of shocks in moving the point of onset of the fast phase away from the mid line. This is a continuous record from the right eyecup, with the fast phase away from the mid line. The horizontal line, about 1° before the normal onset of the fast phase, shows the point beyond which shocks were given at 2 Hz. In the first line there are two long-lasting retractions of the eyecup; in the second the onset of the fast phase occurs at various points, but by the third line it has become stabilized at a new point.

When the movement of both eyecups is recorded during a similar experiment the movement of the governed side is also modified, but only because it is obliged to make a fast phase whenever the governing eye does. The consequence is that the governed eye moves less far from the mid line and may terminate its fast phase nearer to the mid line than previously. Effects are, however, irregular because several factors act indirectly upon the movement of the governed eyecup.

Spontaneous retraction of the eyecup can be followed by an earlier onset of the fast phase, but only in naïve animals (Fig. 8). Animals which have received shocks become insusceptible to further change, presumably because all the available plasticity has already been exhausted.

The limit of plasticity is soon reached if the task is made progressively harder. A change in position of onset of the fast phase by 2° or 3° is readily accomplished; a change by 5° is rarely achievable. When the preparation is given too severe a task it may for a time succeed in avoiding the shock, but the eyecup soon takes up a position where shocks are avoided and from which fast phases do not occur (Fig. 13). Alternatively it may take up a position in which shocks are received continually. The response is reminiscent of postural learning in the headless cockroach or locust when the experiment is arranged so that the leg has to be lifted too high (Horridge, 1962). There is the same temporary improvement followed by a lapse in which the preparation gives itself a long series of shocks.

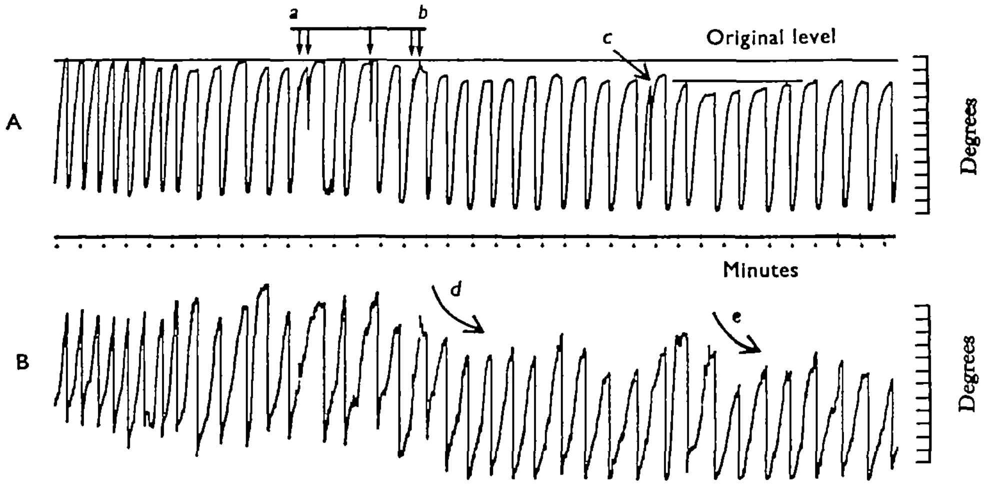

Fig. 8. Mechanical stimulation of the hairs in the orbit and spontaneous retraction hastens the onset of the fast phase. The upper record (A) is of the right seeing eye, the second (B) is of the left, also seeing, eye recorded simultaneously. Mechanical stimulation of the edge of the socket, as shown by the line *ab*, causes the earlier onset of the fast phase. The horizontal ruled line shows the original position of the fast phase. Spontaneous retraction at *c* also causes earlier onset of subsequent fast phases. The fast phase of the left eye is governed by that on the right, and the change caused by stimulation *or* retraction is reflected on the other side, as shown by the curved arrows at *d* and *e*.

Shocks applied to a governed eye are not so effective. This is principally because the governed eye is moving away from the mid line in its slow forward phase and when it receives a shock it withdraws into the region where further shocks are received. To conduct experiments, therefore, shocks must be switched off while the eyecup is withdrawn, and only switched on while the eyecup is moving towards the critical point. Even by working in this way, only one preparation out of half a dozen tested gave any indication of an earlier onset of the fast phase (Fig. 9). Plasticity in this direction is not within the animal's repertoire, and is unnecessary if the onset of the fast phase of both eyes is governed by one eye.

Early onset induced by a mechanical stimulus

Mechanically stimulating the hairs on the medial edge of the eye socket, or even the hairs on the governing eyecup itself, also causes an earlier onset of the fast phase (Figs. 8, 10). Experiments are not easy to carry out without causing reflex eyecup withdrawal, which itself has the same effect. A suitable stimulator is a short piece of flexible wire mounted on a micromanipulator, which can be moved down to irritate the edge of the eye socket or nearby carapace. There is no evidence that the crab distinguishes between different regions around the eyecup or socket; any stimulus located near the edge is adequate.

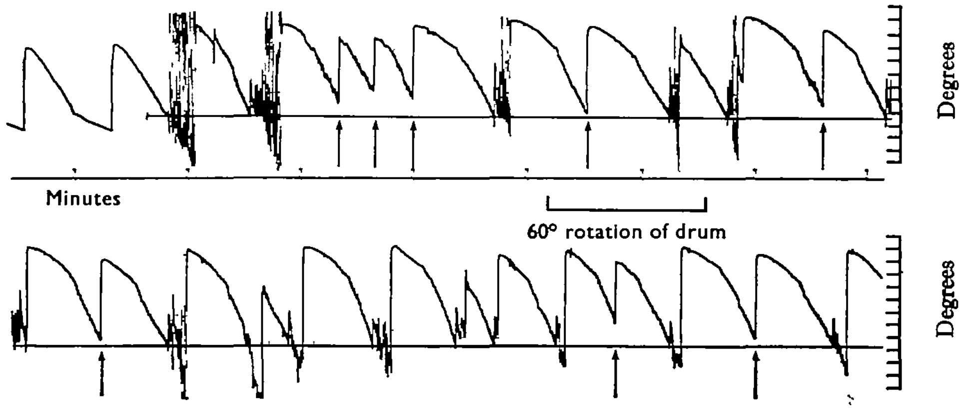

Fig. 9. A record of the only experiment to show an adaptive change when the slow phase of the right eye was away from the mid line (downwards on the trace). The horizontal line shows the position beyond which shocks were given. Following two periods of about 15 sec., during which the eye orbit was shocked while the eyecup was over the line, there were three early fast phases (arrows). There followed other early fast phases interspersed with periods of shocks, but there was a progressive loss of this early adaptive change, as shown in the second line. In the continuation of the record after that shown here, there were no more fast phases without shocks.

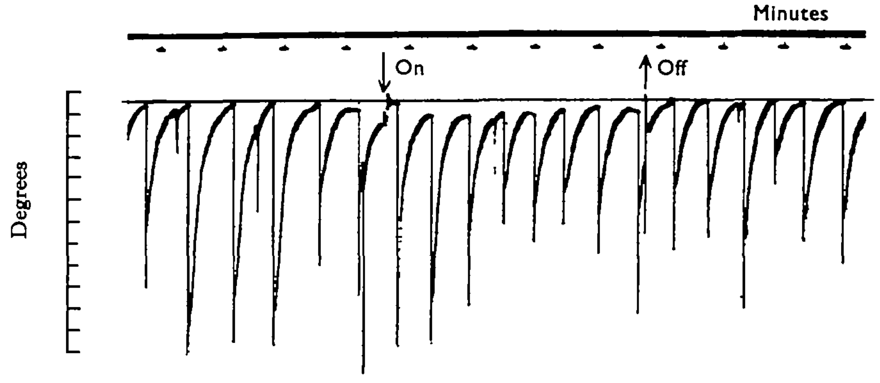

Fig. 10. Movements of a right eyecup with the slow phase toward the mid line. At the first arrow a small piece of Plasticine is placed on the medial edge of the eye so that the hairs on the edge of the socket are now stimulated by the eyecup as it approaches the end of its slow phase movement. Without reflex eyecup withdrawals necessarily occurring, the subsequent slow phases are shortened, until the Plasticine is removed (2nd arrow). There is no flattening of the record at the end of each slow phase and therefore the movement of the eyecup is not impeded mechanically.

This result means that if the eyecup optokinetic response were incorrectly programmed so that the eyecup tended to run into the edge of the socket near the mid line, there is available a mechanism which provides a correction so that the position of onset of the fast phase is moved away from the edge of the socket. If the eyecup hits the outer edge of the socket there will be no effect because the fast return phase of this eye in this direction is governed by the opposite eye.

The plastic change after drum reversal

The traverse of an eyecup in optokinetic nystagmus hardly overlaps for the opposite directions of drum movement (Fig. 2).

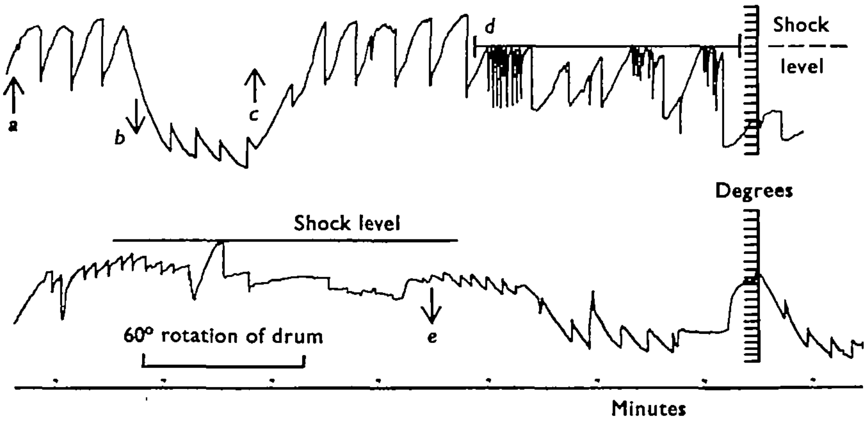

Fig. 11. The position of the onset of the fast phase and the effect of shocks. The record is of the right eyecup; movements to the mid line are upwards; the arrows show the reversals of the drum at *a*, *b*, *c* and *e*. The lower half is a continuation of the upper. The first part, *a–c*, shows nystagmus in opposite directions in different parts of the traverse of the eyecup. The horizontal ruled line *d* shows the point beyond which shocks were given. The shocks cause the onset of the fast phase to be earlier, and nearer the centre of the traverse. After drum reversal at *e* there is a similar but temporary effect upon nystagmus in the other direction.

When shocks are applied so that the onset of the fast phase of a governing eye comes earlier and then the drum is reversed, the fast phase in the opposite direction is not changed in a consistent manner. This is because the eye under observation is now governed by the opposite side, which has not been influenced by the contralateral stimuli. Occasionally, the traverse becomes smaller for about 1 min. and moves closer to the centre of the socket for drum movement in both directions (Fig. 11), but this change is not persistent like that in Figs. 7 and 8.

Plasticity of the central programme

Motor activity

The motoneurone discharges to muscle 21 are mainly responsible for moving the eyecup toward the mid line during a slow forward phase of nystagmus. The fast motoneurone shows an uneven increase in impulse frequency starting midway through the response and reaching a maximum just before the fast return phase. The slow motoneurone, however, shows a steady increase in frequency, starting immediately after the previous fast phase and reaching a peak of 75–100 Hz. just before the next fast phase (Fig. 12).

The seeing eyecups are both clamped and intracellular activity is recorded from a

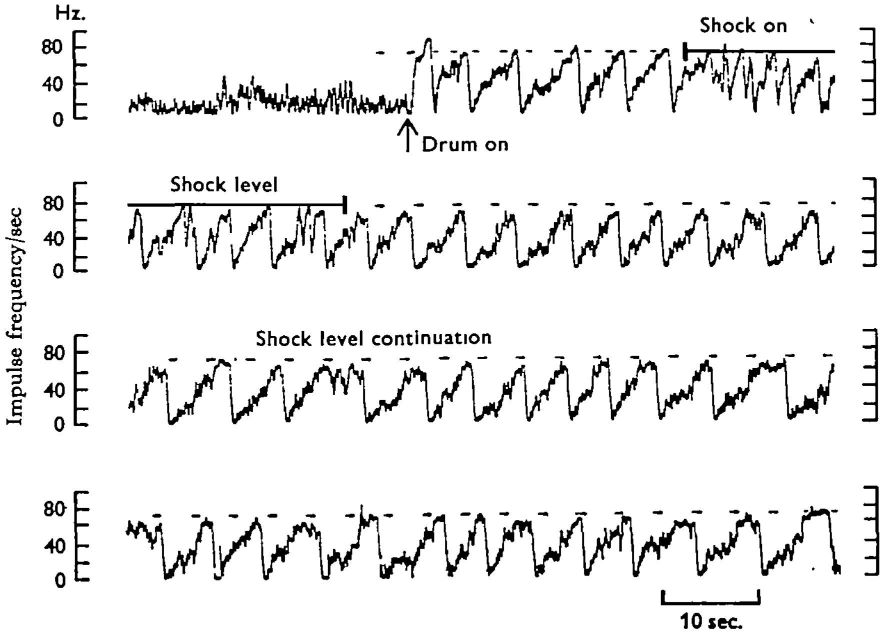

Fig. 12. The effect of shocks on the tonic motor output to a single fibre of muscle 21 of the right eyecup which is responding to a continuous rotation of the drum toward the mid line. The record is of impulse frequency. The drum is started at the arrow, a gradual increase in frequency during each slow phase is followed by a sudden drop at each fast phase. Shocks are applied whenever the frequency exceeds a given level (continuous horizontal line) and cause irregular retractions. The shocks cause the fast phase to occur at a lower frequency and also cause a changed frequency profile during the slow phase. The onset of the fast phase eventually returns to the previous level indicated by the dashed line.

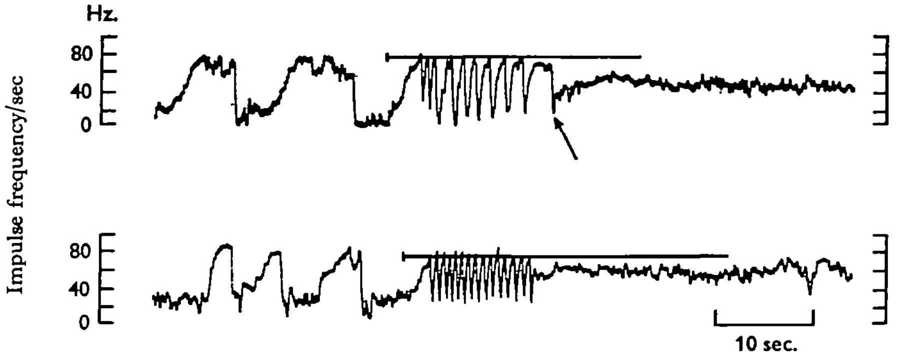

Fig. 13. If the level at which shocks are delivered is set at too low a motor frequency, then retractions occur as before; but after perhaps one fast phase at a lower level (arrow) the motor frequency never reaches a level at which a fast phase can occur. The lower trace is a repeat of the same experiment. Records are of the frequency of slow junction potentials from a single innervated fibre of muscle R21 in response to a continuous rotation of the drum toward the mid line of that eye. The failure of the eyecup movement is therefore due to central causes, not peripheral neuromuscular or mechanical causes.

fibre, innervated by a single slow motoneurone, of muscle 21 of the governing eye. A circuit is incorporated to apply shocks at 1 Hz. to the eye region whenever the frequency of slow junction potentials rises beyond a set threshold level. The shocks cause a withdrawal-response that is recognizable by the motor-impulse pattern although no movement occurs. After a variable period the fast phases occur at a lower tonic frequency than before (Fig. 12). The experiment can be repeated by recording instead the junction potentials caused by a single fast axon, with the same result. If too great a change in frequency is demanded an occasional fast phase may occur earlier, but the frequency eventually remains at a low level so that shocks are avoided and fast phases are impossible (Fig. 13).

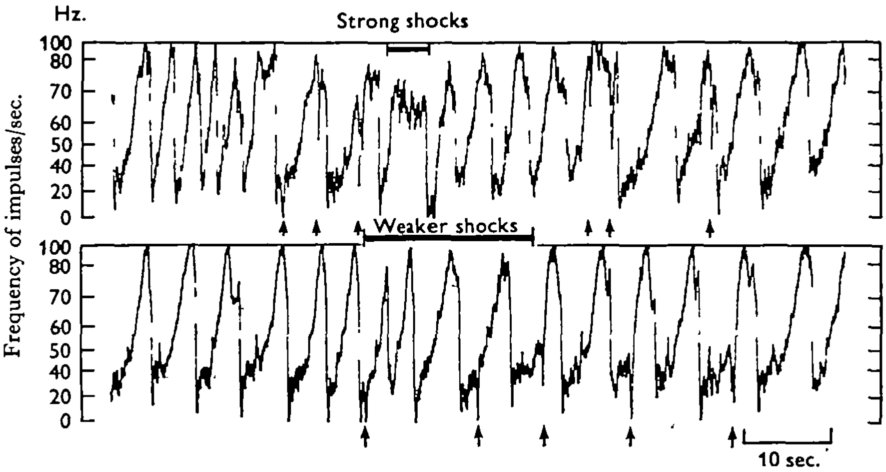

Fig. 14. If shocks are applied indiscriminately (horizontal bar) and not at a set frequency level, then the onset of subsequent fast phases still occurs at a lower frequency. If spontaneous retractions (arrows) occur towards the end of a slow phase, the fast phase sometimes occurs at a lower motor frequency. Records are of the frequency of slow junction potentials from a single innervated fibre of R21 in response to a continuous rotation of the drum toward the mid line for that eye.

Effect of indiscriminate shocks

In this experiment shocks are applied indiscriminately during optokinetic responses so that there is no possible association between the frequency reached and the shocks received (Fig. 14). The fast phases temporarily occur at a lower motor frequency following the periods in which the shocks are received, but in this case soon return to their previous level.

Effect of shocks without drum movement

When the frequency of slow junction potentials of muscle 21 is measured as before in a naïve crab, the fast phase occurs at a definite frequency. When the drum is stopped and then started again after a short period, the onset of the fast phase occurs at the same tonic frequency as before (Fig. 15A). If shocks are applied while the drum is stopped the fast phase occurs at a lower frequency when the drum is restarted (Fig. 15B). The shocks themselves applied to the eye region without the drum moving have only a temporary effect on the frequency of slow junction potentials in muscle 21 (Fig. 15E). The effect is therefore not a general depressant one on the motor output programme to the eyecup.

Another effect of shock, most noticeable in the recording of frequency with a pen recorder, is a modification of the rate of change of impulse frequency. In a naïve animal the rate of rise of frequency falls off during the slow forward phase. After treatment with shocks the frequency rises at first slowly and then more quickly. The same effect can be found in records of eyecup movement; for example, in Fig. 6 this change in the acceleration of the eye affects both eyecups, after shocks to the governing eye.

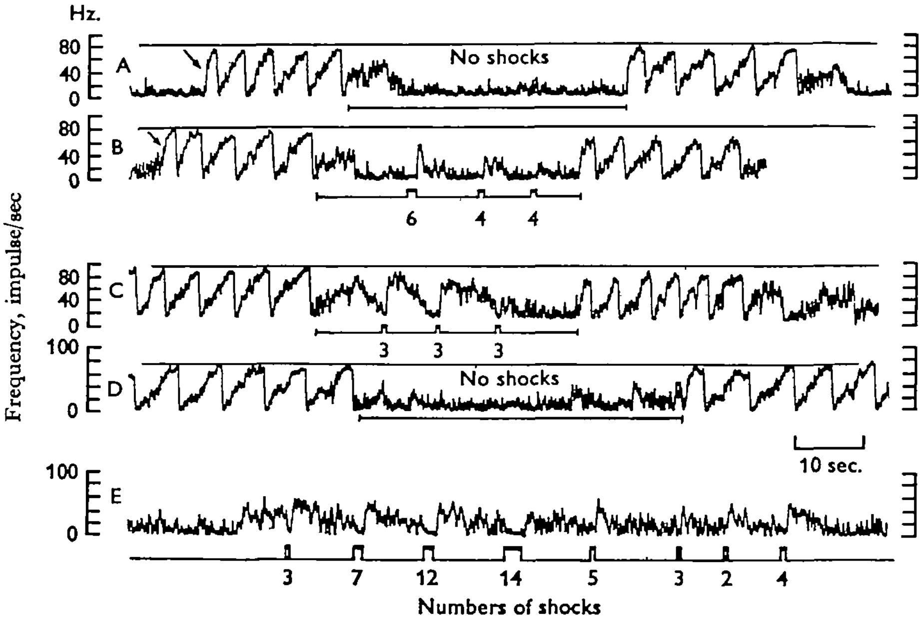

Fig. 15. The frequency of the tonic motor output to muscle 21. A, D: Frequency at which fast phases occur remains the same after a short period in which the drum is stationary. B, C: if during a stationary period the shocks are applied at 10 Hz., causing retractions, the subsequent fast phases occur at lower tonic frequencies. E, Effect of shocks on the tonic output while the drum is stationary, showing no long-term fall in frequency. Each record was separated by a 2 min. period during which the drum was stationary. All records are from the same fibre of muscle 21 in response to a continuous rotation of the drum toward the mid line for that eye.

DISCUSSION

The concept of a governing and governed eye is essential to the interpretation of these experiments. The eye over which the visual movement stimulus sweeps from lateral to medial, that is, the eye which is moving in a slow forward phase of nystagmus toward the mid line, undergoes its fast phase 40–60 msec. before the other eye. If the visual stimulus moves from medial to lateral across a single eye, the frequency of nystagmus movements of both eyes is drastically reduced. Shocks to the region around an eye which is moving toward the mid line in a slow forward phase delay the onset of the fast phase of both eyes while shocks to the other eye are without effect. Therefore the eye which is moving toward the mid line in the slow forward phase is the *governing* eye; the other the *governed* eye.

The topic of interest is the plastic change in the onset of the fast phase which occurs after a stimulus on or near the eyecup. The experiments in which frequency is measured prove that (*a*) movement of the eyecup is unnecessary, (*b*) the onset of the fast phase occurs earlier in the centrally determined programme of motor impulses. Therefore the earlier experiments with a moving eyecup are not to be explained by assuming that increased tonic activity in muscle 19a, responsible for holding the eyecup in its socket, tends to pull the eyecup away from the mid line.

The plastic change is not learning

The experiments demonstrate that any shock causing eyecup withdrawal, a spontaneous withdrawal, or a mechanical stimulus likely to cause eyecup withdrawal leads to an earlier onset of the fast phase. Admittedly the long-term plastic change is adaptive because it prevents the eyecup bumping into the edge of the socket if the central programme of motor impulses is allowed to carry it too far, but there is no element of association. The shocks can be applied at any point irrespective of eyecup position; if the eyecup is clamped the plastic change still takes place as measured by the motor output to muscle 21. The shocks can be applied while the drum is stationary and both eyes are clamped in their sockets, but still the onset is earlier when the drum starts once more.

The output of motor impulses to tonic and phasic components of the nine muscles of the eyecup form a complex but internally self-consistent programme which emerges from the brain irrespective of movement of the eyecup. This programme is an appropriate combination of impulse frequencies for every position of the crab in space (Burrows & Horridge, 1968*b*) and for every possible history of the visual input (Horridge & Sandeman, 1964; Burrows & Horridge, 1968*a*). Given this indifference to proprioception, the problem of interest is how the position of the traverse is controlled so that the eyecup moves across the middle of the socket without touching the edge and yet with a maximum scan.

The experiments show that the central programme has written into it a flexible phrase which is the relation between tonic frequency to muscle 21 and the onset of the fast phase. Any disturbance makes it undergo a fast phase sooner when the eyecup is moving toward the mid line.

In its proper anatomical situation this modifiable behaviour is adaptive. The eye which is moving toward the mid line governs the onset of the fast phases of both eyes. There is no need for a similar change in the other direction. The system therefore fits together logically as the consequence of there being two separately movable, visually stabilized eyes that are operated by a suitable central programme for each stimulus situation.

SUMMARY

1. The onset of the fast phase in the optokinetic response is a part of a centrally determined programme.

2. An eyecup moving in a slow phase toward the mid line *governs* the onset of the fast phase for both eyes and leads by 40–60 msec.

3. Repeated reflex withdrawal of a governing eyecup suppresses the onset of the fast phase; similar stimulation of a governed eyecup has no effect on fast phases.

4. After shocks applied near the governing eye the onset of the fast phase occurs earlier in the slow phase. Mechanical stimulation has the same effect.

5. If the eyecup receives a shock whenever it moves too near the mid line in a slow forward phase, it soon changes the position of onset of the fast phase so that the shocks are avoided. The tonic motor frequency to muscle 21 at which the fast phase normally occurs is reduced. The effect is lasting.

6. This plastic change is adaptive but is not learning; the earlier onset occurs irrespective of how or when the shocks are applied. The reinforcement need not supply any possibility of association.

7. In a behaviour pattern which depends on a centrally determined programme of motor impulses for each stimulus situation the element of plasticity is one further component of the central pattern, so arranged that it is adaptive.

REFERENCES

BARNES, W. J. P. (1968). Ph.D. Thesis. St Andrews University.

BURROWS, M. (1967). Reflex withdrawal of the eyecup in the crab *Carcinus*. *Nature, Lond.* **215**, 56–7.

BURROWS, M. & HORRIDGE, G. A. (1968*a*). The action of the eyecup muscles of the crab, *Carcinus*, during optokinetic movements. *J. exp. Biol.* **49**, 223–50.

BURROWS, M. & HORRIDGE, G. A. (1968*b*). Motoneurone discharges to the eyecup muscles of the crab, *Carcinus*. *J. exp. Biol.* **49**, 251–67.

BURROWS, M. & HORRIDGE, G. A. (1968*c*). Eyecup withdrawal in the crab, *Carcinus*, and its interaction with the optokinetic response. *J. exp. Biol.* **49**, 285–97.

HORRIDGE, G. A. (1962). Learning of leg position by the ventral nerve cord in headless insects. *Proc. R. Soc.* B **157**, 33–52.

HORRIDGE, G. A. (1966). Optokinetic memory in crab, *Carcinus*. *J. exp. Biol.* **44**, 233–45.

HORRIDGE, G. A. (1967). Position of onset of fast phase in optokinetic nystagmus. *Nature, Lond.* **216**, 1004–5.

HORRIDGE, G. A. & SANDEMAN, D. C. (1964). Nervous control of optokinetic responses in the crab *Carcinus*. *Proc. R. Soc.* B **161**, 216–46.

SANDEMAN, D. C. (1967). Excitation and inhibition of the reflex eye withdrawal of the crab *Carcinus* *J. exp. Biol.* **46**, 475–85.