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INTERACTION OF THE MOVEMENTS OF THE TWO EYECUPS IN THE CRAB *CARCINUS*

BY W. J. P. BARNES* AND G. A. HORRIDGE†
Gatty Marine Laboratory, and Department of Natural History, University of St Andrews, St Andrews, Scotland

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INTRODUCTION

The compound eyes of decapod crustaceans are carried on the ends of stalks called eyecups. Although the eyecups are separately movable, their gross movements, except for protective retraction, appear closely linked. This linkage is well illustrated in optokinetic nystagmus, which is the response of the eyecups to movement of the visual field, usually elicited by rotation of a vertically striped drum around the animal. During the slow phase of the response both eyecups follow the movement of the stimulus with a constantly increasing lag, one eyecup moving towards the animal's midline, the other away from it. During the subsequent fast phase, the eyecups flick back in the opposite direction at about the same moment to start a new traverse. This similarity in the responses of the two eyecups led to a model in which a single central driving mechanism governed both eyecups in *Carcinus* (Horridge & Sandeman, 1964). This model of the eyecup-movement control system incorporated a visual negative feedback loop, since the movements of the eyecups in following the visual field reduces the apparent velocity of that field. This is the only feedback loop involved, however, for Horridge & Sandeman showed that any information from possible proprioceptors in the region of the eyecups is not used in the control of eyecup movements.

However, accurate records have not been made from both eyecups simultaneously and there is, in fact, no account of how the eyecups are linked in detail. Other types of eyecup movement, including optokinetic memory responses (Horridge & Shepheard, 1966), and the small movements of the eyecups, classified as tremor, saccades and drift (Horridge & Sandeman, 1964; Horridge, 1966*b*), have also been described from recordings of a single eyecup, but again there is no information about the relation between the eyecups in these movements.

METHODS

Large male specimens of the shore crab, *C. maenas* L., collected locally, were held for the experiments in a simple metal clamp at the crab's normal inclination to the vertical. All experiments were carried out with the crab in air, a perfectly natural situation for an intertidal species. Responses persisted for many hours, especially if the crab was moistened from time to time. Light flags, made of a Nylon bristle and a square of black paper, were attached to the crab's eyecups. They did not interfere with

* Present address: Department of Zoology, University of Glasgow.
† Present address: Research School of Biological Sciences, P.O. Box 475, Canberra City, A.C.T. 2601.

eyecup movements and were invisible to the crab. Two units, each consisting of a source of collimated infrared light and a pair of infrared sensitive photocells, whose outputs were fed into a DC pen recorder, were used to record eyecup movements. The photocells responded to the shadow cast by the flag, the experimental arrangement being similar to that used by Horridge (1966*a*). These devices enabled accurate measurement of eyecup movements down to 0·01°.

The optokinetic stimulus used in many of these experiments was a drum of equally spaced black and white stripes of repeat distance 30° illuminated through a diffusing screen by a 60 W. bulb. The smoothness of the drum movement was tested by an arrangement of flag and photocells similar to that used for the recording of eyecup movement. No irregularities could be detected in the movement and no vibration was transferred from the drum motor to either the drum or the crab. The actual movements of the drum were recorded by a potentiometer geared directly to the drum spindle. When different optokinetic stimuli were presented to the two eyes, the crab

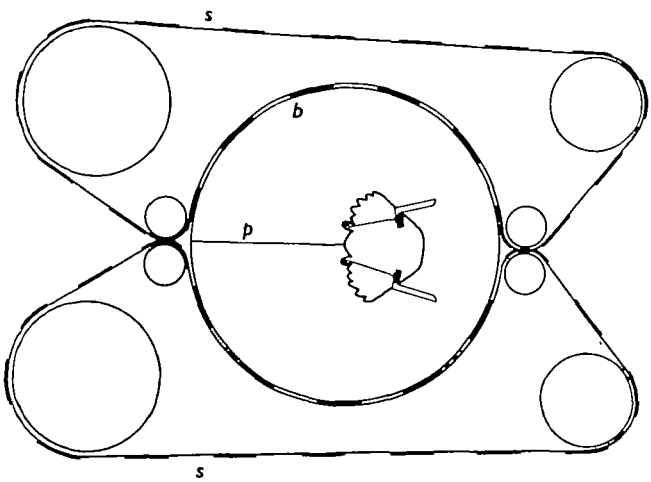

Fig. 1. Arrangement enabling the two eyes of a crab to be separately stimulated. The crab is clamped in the centre of a 35 cm. diameter glass bowl (*b*), around which two loops of stripes (*s*) can be moved in either direction at different controlled velocities. The partition (*p*) was present in only a few experiments; its absence did not affect the results in any way. The clamp holding the crab is omitted for simplicity.

was clamped in the centre of a large cylindrical glass bowl around which two loops of striped paper could be moved separately in either direction at a variety of different velocities (Fig. 1). The stripes were driven by reversible multispeed motors and their movements were recorded by potentiometers mounted on the shafts. In some experiments a partition was placed between the eyes of the crab so that neither eye could see the stripes on the opposite side of the drum. However, removing the partition did not change the responses in any way, so, for convenience, it was left out in most experiments.

In some experiments one of the eyes of the crab was reversibly blinded by painting it over with two coats of quick-drying black paint. The success of this procedure was checked by covering the other eye with a segment of a ping-pong ball and slowly rotating a striped drum about the crab; if the painted eye was blind no eyecup movement resulted.

RESULTS

Simultaneous recordings of the small movements of the eyecups

Tremor movements of the two eyecups were independent of each other in most crabs (Fig. 2A), though usually of a similar frequency, amplitude and general pattern. In two of the many crabs examined, however, the dominant tremor oscillations of the eyecups were closely linked. In one (Fig. 2B), both eyecups oscillated at 1·6–1·8 Hz and 0·01–0·02° peak-to-peak, 180° out of phase with each other. In the other (Fig. 2C), the eyecups were in phase, tremor being 1·7–1·8 Hz and 0·03–0·06° peak-to-peak. In both of these crabs the correlation in tremor movements was maintained for the 3–4 hr.

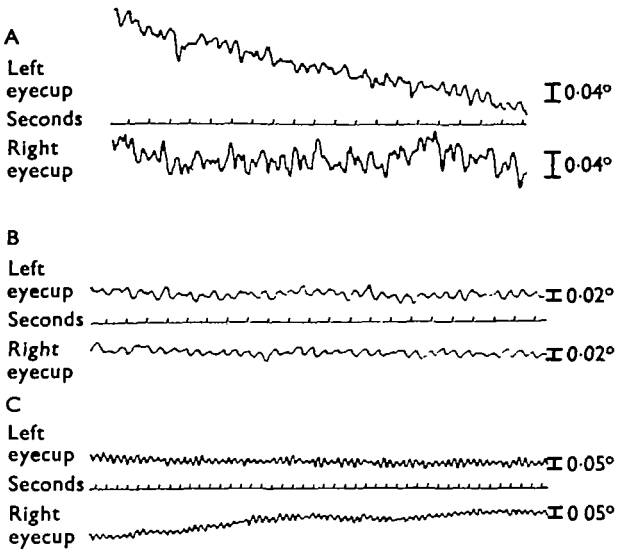

Fig. 2. Eyecup tremor from both eyecups of three different crabs. (A) Normal situation in which the tremors of the two eyecups are independent. Note independent drift of left eyecup. (B) Unusual situation where the tremors of the two eyecups are 180° out of phase with each other. (C) Unusual situation where the tremors of the two eyecups are exactly in phase but of independent amplitude. *Movement to the right is shown downwards.*

that the crabs were observed. Though such a close linkage is an unusual phenomenon for which we have no explanation, it shows that, in some crabs at least, tremor is under central control. Even in these crabs, however, the eyes were not absolutely linked, for many smaller oscillations of the eyecups were independent of each other.

Saccades are small flicks of the eyecup in any direction. Saccades of one eyecup alone are a frequent occurrence, although they can occur simultaneously in the two eyes. In unilaterally blinded crabs saccades of the seeing eye are often closely followed by movements of the blinded eye in the opposite direction. The movements occur either towards or away from the crab's midline and therefore cannot be partial retraction reflexes. As the seeing eye always flicks first, the movement of the blinded eye is presumably an optokinetic response to the displacement of the retinal image caused by the saccade. Therefore, for saccades, *Carcinus* acts as if unable to distinguish between

apparent movement induced by its own eyecup movement and real movement of the environment.

Besides drift, during which the eyecups move independently of each other, and the tremor and saccades described above, there is a further class of eyecup movements which has not been previously described. These movements, called eye waving, consist of oscillations of peak-to-peak amplitude 0·1–2·0° and frequency 2–3 Hz (Fig. 3).

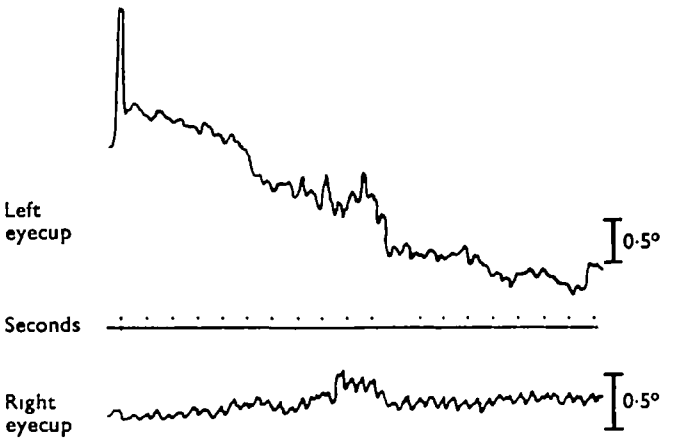

Fig. 3. Eye waving which is correlated with leg waving, as recorded simultaneously from both eyes. Note the independence of the eyes, the amplitude varying between 0·1 and 2°, and frequency between 2 and 3 Hz. Movement to the right is shown downwards.

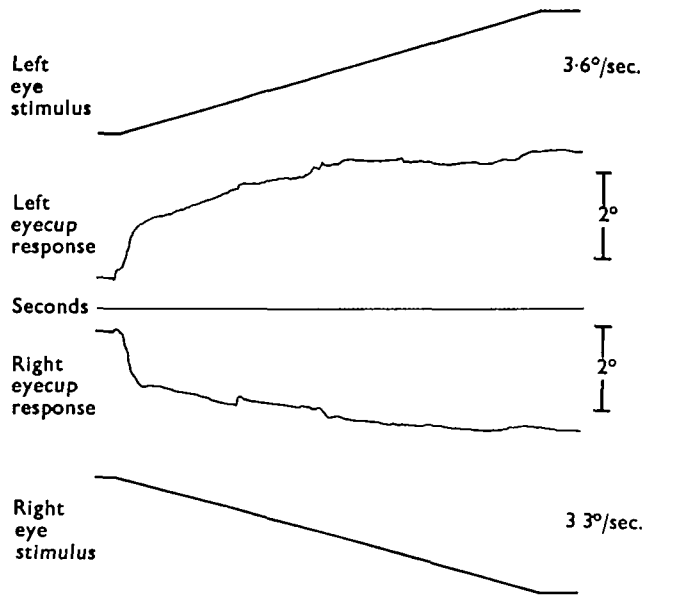

Fig. 4. The responses of the two eyecups when stimulated by different sets of stripes moving in opposite directions at approximately equal velocities. Each eyecup initially follows its own stimulus, but after a few seconds slows down. After about 40 sec. it is more or less stationary. Movement to the right is shown downwards.

Waving occurs predominantly in the horizontal plane and independently in the two eyecups. Since eye waving is always associated with periods of leg waving, it may be related to the movements of the eyecups during voluntary turning.

A different visual stimulus to each eye

Qualitative observations

In these experiments the crab was clamped at the centre of the apparatus shown in Fig. 1. When the two loops of stripes are moved in opposite directions at approximately equal velocities, *each eyecup initially follows the movement of its own stimulus* (Fig. 4). Therefore the optokinetic responses of the eyes are not inseparably linked and a com-

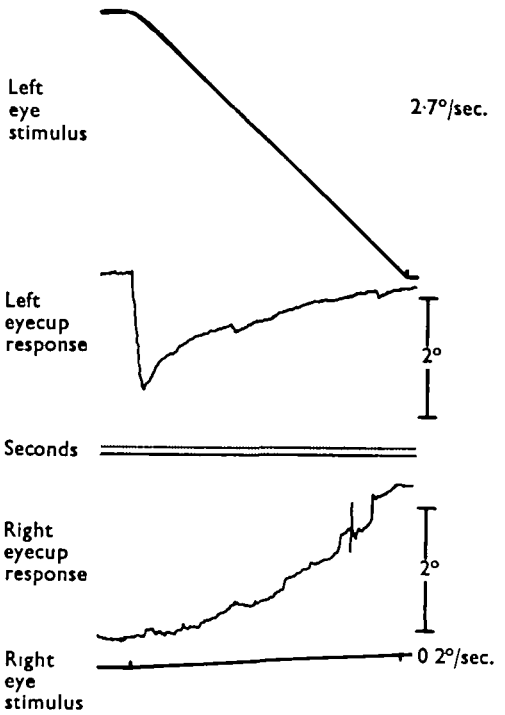

Fig. 5. The responses of the two eyecups when stimulated by different sets of stripes moving in opposite directions at very different velocities. Each eye initially follows its own stimulus. After a few seconds, however, the eye which observes the faster moving stripes reverses and then approximately follows the slower moving stripes. Movement to the right is shown downwards.

plete eye movement control system is present on each side. Yet, the eyecups do not continue indefinitely to move in opposite directions. There is a progressively increasing interaction between the two sides, with the consequence that both eyecups soon stop moving.

When the two sets of stripes are moved in the same direction at different speeds, the eye viewing the faster moving stripes initially moves much faster than its fellow. However, after about 30 sec. the eye viewing the faster moving stripes slows down so that the *final velocity of both eyes is the initial velocity of the eye that sees the slower moving stripes.*

When the two loops of stripes are moved at very different velocities and also in opposite directions, the eyes initially follow the movement of their own stimulus as before (Fig. 5). However, after a few seconds, the eye which sees the faster moving stripes reverses and makes the same response as the eye which sees the slower stimulus. Thus, as before, the slower moving of the two stimuli determines the direction and final velocity of both eyecups.

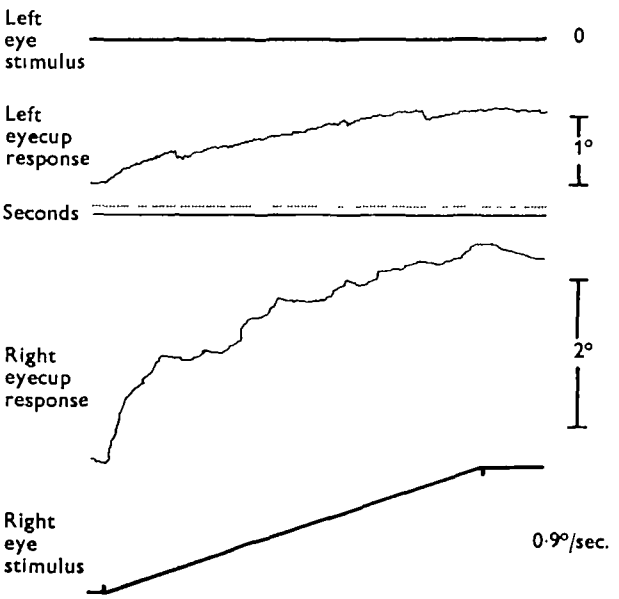

Fig. 6. The responses of the two eyecups when the left eye sees stationary stripes while the right eye sees moving stripes. Initially both eyecups respond to the moving stripes, the right eyecup at the greater velocity. However, after about 2 min. both eyecups slow down and become more or less stationary. Movement to the right is shown downwards.

When the stripes before one eye remain stationary while those before the other start to move, both eyecups initially follow the motion seen by one (Fig. 6). The eye which actually sees the movement at first moves faster but both progressively slow down. After about 2 min., when the eye seeing the moving stripes has moved through about 3°, the other eye rather less, both eyes have slowed almost to a standstill. This result, though a little different from that obtained by Horridge & Sandeman (1964) with less sensitive equipment, is in accord with the above results. The eyecups initially show a partial independence and the final velocity of both is the velocity of the slower of the two stimuli, in this case zero. A difference between this and the previous results is that the eye seeing stationary stripes initially follows the stimulus to the other eye, albeit slowly, whereas in the previous experiments both eyes initially respond to the stripes which they themselves view. Thus stationary stripes initially have less influence in the determination of an eyecup response than do moving stripes.

In none of these experiments do both eyecups follow the faster of the two stimuli when both are moving. Such a response can be induced only if the faster movement of the stripes seen by one eye begins several seconds after a slower movement seen by

the other. In Fig. 7, the right eye, which views the slower moving stripes, is temporarily induced to change the direction of its response when the stripes facing the other eye begin to move. Thus for a time both eyecups follow the faster of the two sets of stripes. However, as would be predicted from previous experiments, the normal state of affairs, with the slower stimulus dominating, is soon restored. This apparently contradictory result shows that, when newly presented, the faster stimulus is for a time more effective than the slower one.

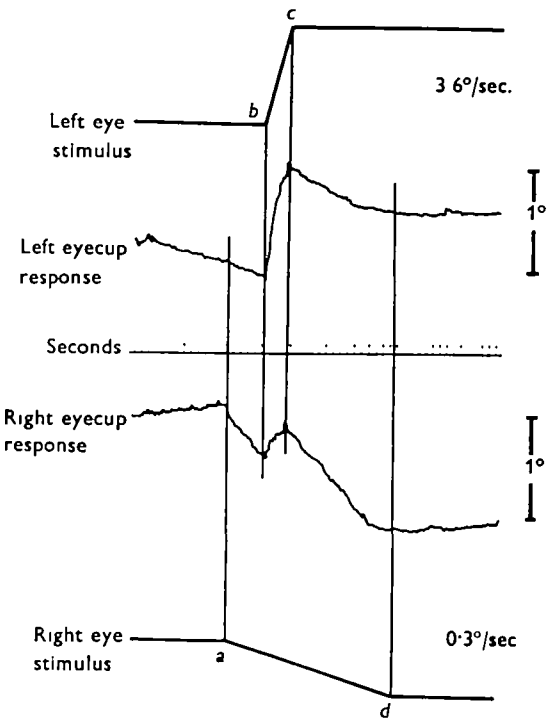

Fig. 7. The responses of the two eyecups when the stripes they see start to move at different times as follows: (*a*) Right stimulus moves to the right at 0·3°/sec. (*b*) After 5 sec., left stimulus moves to the left at 3·6°/sec. (*c*) 3 sec. later, left stimulus stops. (*d*) After a further 15 sec., the right stimulus stops. Movement to the right is shown downwards.

The general finding is that the eyecups move more or less independently at first when they see different stimuli, but after a few degrees of movement, they come to a standstill or move together at more or less the same velocity. Stationary or slow moving stripes seen by one eye take precedence over fast moving stripes seen by the other in that the final velocity and direction of the movement of both eyecups is determined by the slower (or stationary) of the two visual inputs. This agrees with the observation that the gain of the response is higher at slower stimulus speeds. There are only two situations in which an eye follows, even for only a few seconds, a faster stimulus than it itself sees. These are (*a*) when the eye is facing a stationary set of stripes and (*b*) when the stimulus to the other eye is a novel one.

Quantitative results

As a quantitative measure of interaction the velocity of the two eyecups was plotted against the velocity of the stimulus to one of the eyes. The stimulus to the other eye was kept constant. As illustrated in Figs. 4–6, the eyecups do not move at constant velocity and therefore two arbitrary measures of the velocity of an eyecup's response have been selected: (*a*) the initial velocity, and (*b*) the final velocity. Interaction between the eyes, at the start and in the steady state of a response, can be conveniently assessed from these graphs. Responses in different directions are separated in different graphs, but in fact no differences are observed between responses towards and away from the crab's midline. To avoid effects of novel stimuli, the loops of stripes always start to move at the same time.

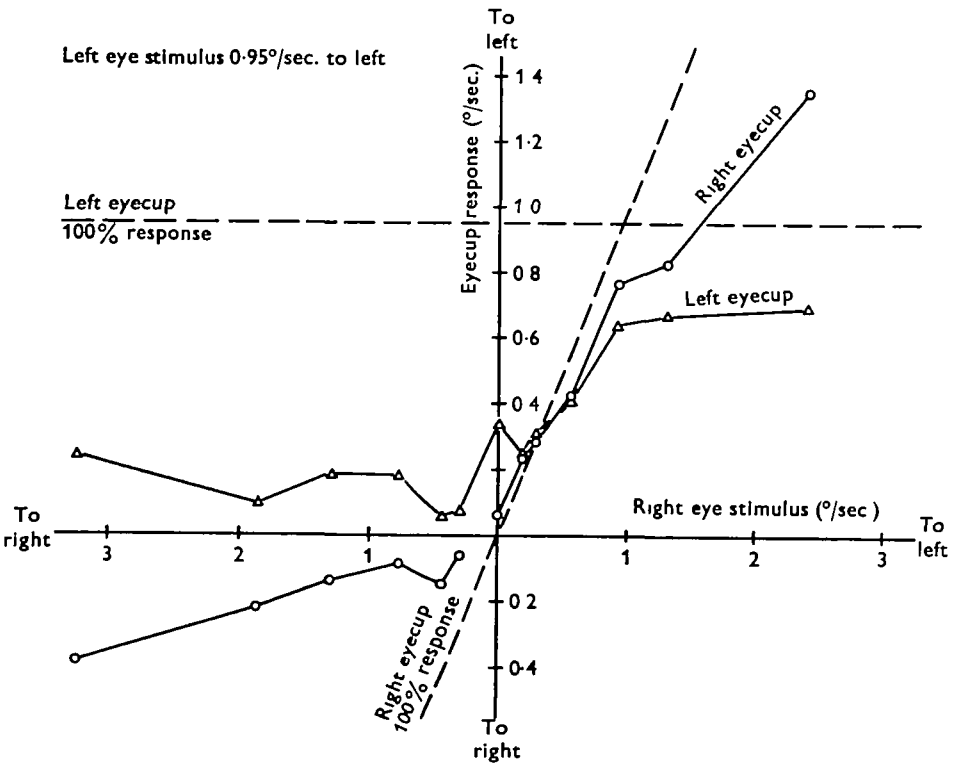

Fig. 8. The *initial* velocities of the two eyecups when each eye sees a different set of stripes. The eyecup velocities are plotted against the velocity of the right stimulus, with the left stimulus constant at 0·95°/sec. to the left. Note that the responses of both the left eyecup (triangles) and the right eyecup (circles), though governed largely by the movement of the stripes they view, are far from independent of the stimulus to the other eye. Each point is the mean of several responses from the same crab. The theoretical dashed lines represent 100% responses of each eyecup.

The initial velocity of each eyecup is plotted against the stimulus to the right eye, with the stimulus to the left eye moving at a constant velocity of 0·95°/sec. to the left in Fig. 8. Although the eyes respond initially in the direction of movement of the stripes they view, they show some interaction, even during their initial responses. If

the eyes had acted independently, the initial velocity of the left eyecup response would have been constant at some value between 0·4 and 0·8°/sec., irrespective of the stimulus to the right eye. However, the left eyecup only moves faster than 0·4°/sec. when the other eye sees a movement of the stripes in the same direction at a velocity above 0·6°/sec. If the stripes viewed by the right eye move slower than this, are stationary, or move in the opposite direction, the initial response of the left eyecup is reduced. The reduction is greatest when the stripes viewed by the other eye move in the opposite direction at a velocity between 0·2 and 0·6°/sec. Under these conditions the initial velocity of the left eyecup falls below 0·1°/sec. Conversely, the initial response of the right eye is greater than the velocity of the stripes it views when the right stimulus

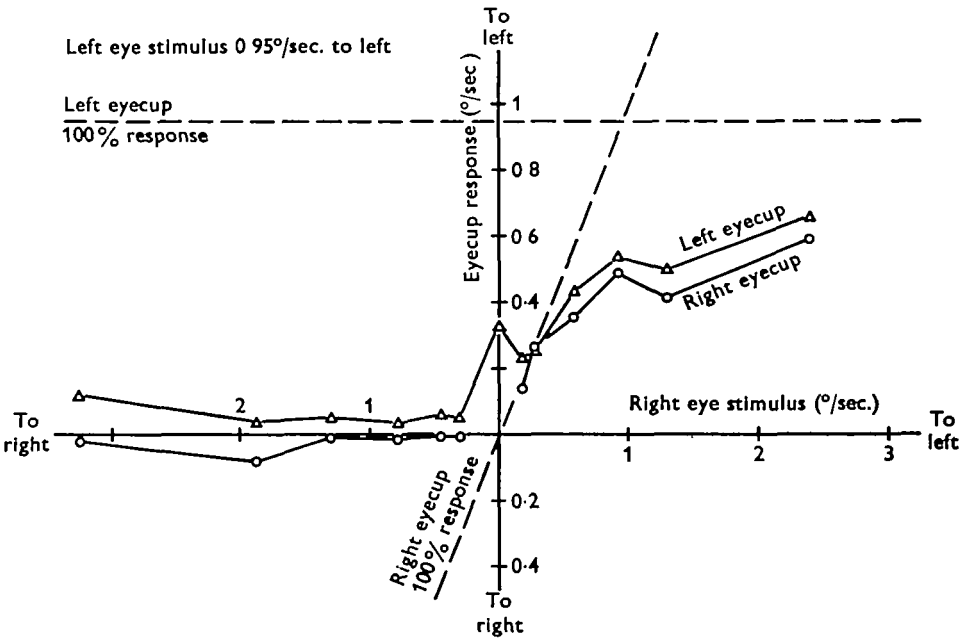

Fig. 9. The *initial* velocities of each eyecup plotted against the velocity of the right stimulus, as in Fig. 8, but for a different crab. Unlike those shown in Fig. 8, the responses here show a close interaction between the eyecups. With stimuli in opposite directions the velocities of the responses are reduced more than in Fig. 8. With stimuli in the same direction at different velocities, both eyecups nevertheless set off at approximately the same velocity.

velocity is less than one-third of the left stimulus velocity, with both sets of stripes moving in the same direction; i.e. one eye can be dragged along faster than its stimulus by the stimulus to the other eye.

In some crabs the interaction between the eyes during the initial part of a response is even greater than that shown in Fig. 8. In one crab (Fig. 9), the stimulus to the left eye is again a movement of the stripes to the left at 0·95°/sec. The responses differ in two respects from the more typical ones shown in Fig. 8. With the stimuli to the two eyes moving in opposite directions the velocities of the responses are reduced far more than in Fig. 8 and few responses exceed 0·1°/sec. Secondly, when the two sets of stripes move in the same direction at different velocities, both eyecups move at approximately the same velocity.

This degree of linkage between the eyes at the start of a response, though unusual, was exceeded in one particular crab. With the stripes viewed by the left eye moving at a constant velocity of 2·74°/sec. to the right, and those viewed by the right eye moving at velocities between 0·3 and 0·9°/sec. to the left, both eyecups moved to the left. In no other crab was the interaction so great as to eliminate altogether the initial response of the eyecup seeing the faster stimulus.

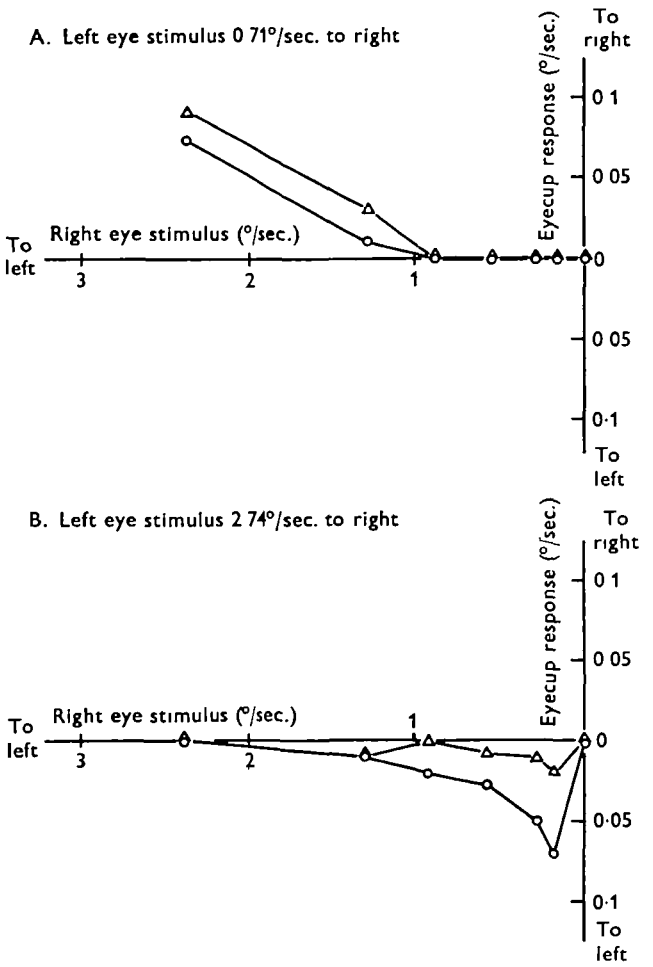

Fig. 10. The *final* velocities of the two eyecups when each sees a different set of stripes. The velocities of the left eyecup (triangles) and right eyecup (circles) are plotted against the velocity of the right stimulus. In (A), the left stimulus is constant at 0·71°/sec. to the right; in (B), it is constant at 2 74°/sec. to the right. Each point on the graphs is the mean of several responses, the two graphs being the responses of different crabs.

Whatever the initial interaction between them, the eyecups become less independent over a period of up to several minutes. They gradually come to a standstill, or move at similar velocities in the same direction. Steady-state measurements are shown in Fig. 10, for two crabs. When the two stimuli move in opposite directions at approximately equal speeds, the final response is zero. With a stimulus of 0·71°/sec. to the left

eye this occurs when the right eye stimulus is below 1°/sec. (Fig. 10A); with a stimulus of 2·74°/sec. to the left eye there is no response when the stripes seen by the right eye move at a velocity above 2°/sec. (Fig. 10B). The angle through which the eyecups move and the time they take to come to a halt varies considerably, but depends to some extent on the stimulus velocity. When the conflicting stimuli to the two eyes move at velocities between 0·2 and 1°/sec., the eyecups come to a standstill in a mean of 70 sec. after moving through a mean angle of 2·5°. These values were decreased to 55 sec. and 2° respectively with stimulus velocities between 2·4 and 3·4°/sec. When the two loops of stripes move in opposite directions, the only occasions when the final velocities of the eyecup responses are not zero are when the velocity of the stimulus

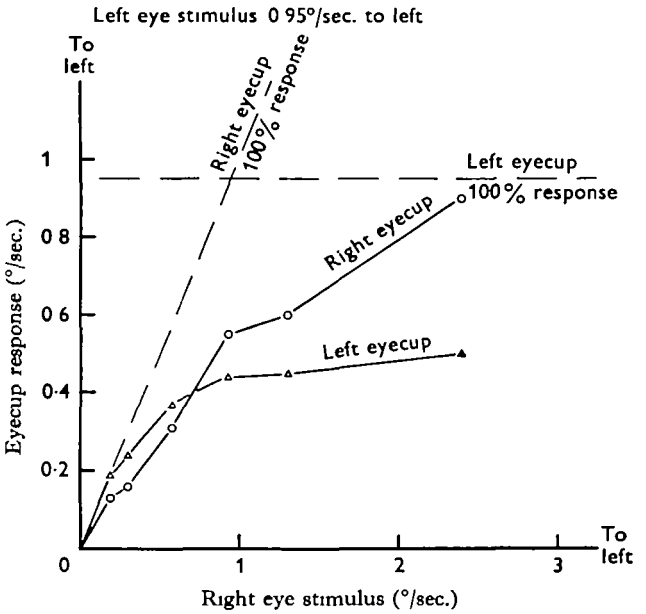

Fig. 11. The *final* velocities of the two eyecups when each eye sees a different set of stripes. The velocity of the left eyecup (triangles) and right eyecup (circles) are plotted against the velocity of the right stimulus, with the left stimulus constant at 0·95°/sec. to the left. Each point on the graph is the mean of several responses from the same crab. The theoretical dashed lines represent 100% responses of each eyecup.

to one eye is at least twice as great as that to the other eye. Under these circumstances the eyecups finally respond in the direction of movement of the slower stripes, and the response velocity seldom exceeds 0·1°/sec. With conflicting directions presented to them, the two eyes move independently through about 2° and then, about 20 sec. after the start of the response, the eye viewing the faster moving stripes slows to a standstill and then begins to move in the opposite direction, though often at a lower velocity than the other eye (Figs. 10A, B).

When the two loops of stripes move in the same direction, it is difficult to observe to what extent the eyes maintain their initial partial independence because of the changes in gain that occur just before and after a fast phase. However, when the mean velocity of the eyecups during the middle part of all traverses except the first is plotted

against the stimulus to one of the eyes, as in Fig. 11, the eyes are seen to have much less independence than at the start of a response, although they seldom move at exactly the same velocity. The steady-state velocities of both eyes are, as expected, governed mainly by the slower of the two visual stimuli, but they are not entirely independent of the faster stimulus. In some crabs, however, the steady-state velocity of the eyecup moving away from the midline is consistently lower than that of the other eyecup, irrespective of the velocities of the two stimuli. This reduction in gain appears to be fatigue, perhaps of muscle 20a, since it occurs progressively and was observed to a small extent in all crabs tested in this way.

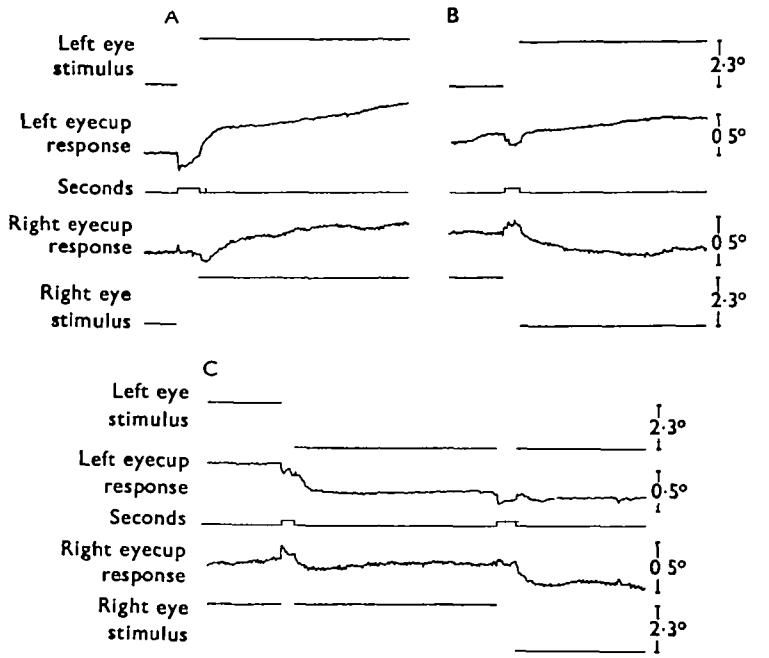

Fig. 12. Memory responses of the two eyecups when stimulated by different sets of stripes. The two sets of stripes are moved independently during short periods of darkness. (A) Both sets of stripes move in the same direction through 2·3°. (B) The two sets of stripes move in opposite directions through 2·3°. (C) One set of stripes moves through 2·3°; the other remains stationary. The time trace is interrupted during the periods of darkness. Movement to the right is shown downwards. Note the independence of the eyecups.

Memory and oscillation

The interaction between the eyes has also been examined during optokinetic memory responses and during the responses to independent sinusoidal oscillation of the stimuli seen by the two eyes.

In the optokinetic memory experiments the two loops of stripes move independently during a short period of darkness. Typical eyecup responses occur upon re-illumination (Fig. 12). At first, both loops of stripes are moved in the same direction through the same angle, and both eyecups respond in the direction of inferred movement of the stripes, the left eyecup response being 28% of the stimulus, the right 16% in the example figured. Following this, the loops of stripes are moved in opposite

directions through the same angle. Both eyes now respond *in the direction of movement of the stripes they view* showing that, in the memory situation, the eyes have a considerable degree of independence (Fig. 12B). The responses are, however, reduced in amplitude, the left now being 12% of the stimulus, the right 14%. Finally, when one loop of stripes is moved while the other remains stationary, both eyecups respond in the direction of the inferred movement, the response of the eye facing the shifted stripes being 10–12% of the stimulus, the other eye much less (Fig. 12C). The interaction between the eyes in the memory situation is thus very similar to that observed at the onset of movement which is actually seen by the crab.

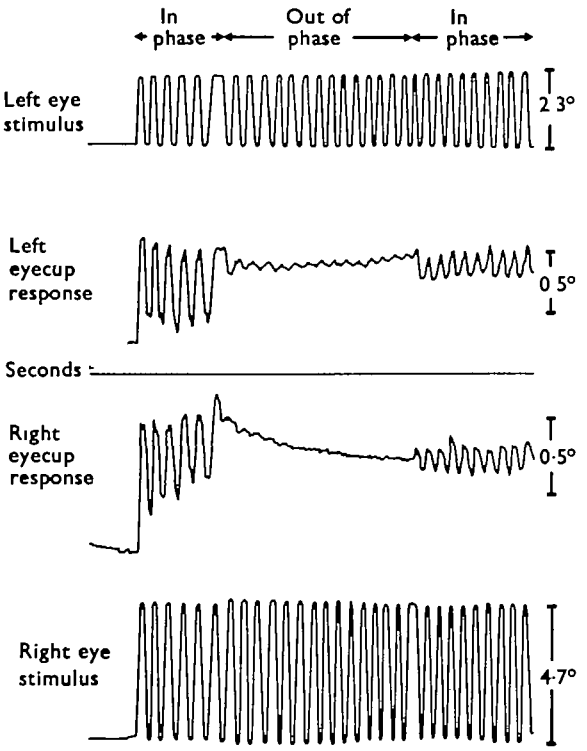

Fig. 13. Oscillatory responses of the two eyecups when each sees a different set of stripes. The two loops of stripes oscillate approximately sinusoidally at 0·4 Hz, first in phase and then 180° out of phase. Note that the out-of-phase responses of each eye, though small and showing some adaptation, are in phase with the movement seen by that eye. When the stripes are again oscillated in phase, the responses are smaller than before and for a while they continue to grow in amplitude. Movement to the right is shown downwards.

To an oscillation of the striped patterns the eyecups again interact in the same way. In this experiment the two loops of stripes are oscillated sinusoidally at 0·4 Hz, either in phase or 180° out of phase with each other. The responses illustrated (Fig. 13) are from the same crab as produced the memory responses described above. When both loops of stripes are oscillated in phase with each other, the left eyecup responds at an amplitude of 25–36% of the stimulus, the right at an amplitude of 9–18%. When the two loops of stripes oscillate 180° out of phase, the responses are reduced to under

2% of the stimulus (Fig. 13). The responses of the two eyes are still, however, *in phase with the oscillation of the stripes they each view.* Resumption of in-phase oscillation results in an increase in amplitude of the responses, but only to about a third of the initial value. Thus the previous conflict of input has a persistent effect.

Model describing the linkage between the eyes

The above experiments describe the interaction between the two eyecups but give no indication as to the point of interaction in a model of the optokinetic control system. The following experiment takes advantage of the fact that when one eye of a crab is blinded, the seeing eye, if stimulated optokinetically, will drive the blinded eye. A constant-velocity movement of amplitude 2° is presented to the seeing eye, and a graph is plotted of responses of the blind eyecup against those of the seeing one.

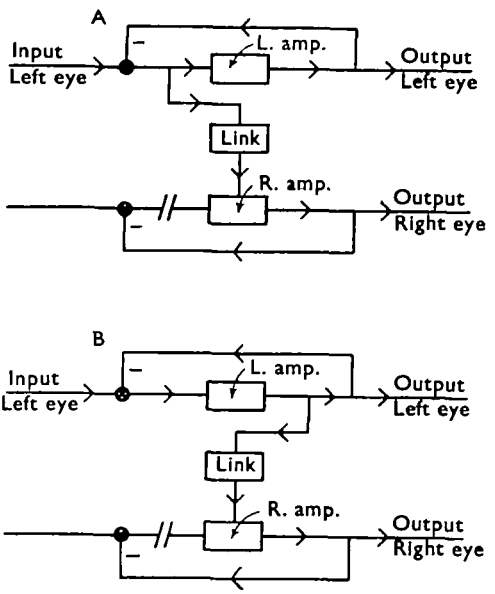

Fig. 14. Two possible models for the linkage between the eyes when the blind right eye is driven by the left seeing eye. In (A), the stimulus to the blind eye comes from the *input* to the seeing-eye amplifier, while in (B) the stimulus to the blind eye comes from the *output* from the seeing-eye amplifier. If model (A) holds, then the spontaneous changes in the responses of the two eyes will be inversely related to each other when one eye is blind; if (B) holds, the relationship will be a direct one.

In crabs with one eye blinded two different models describe possible linkages between the eyecups (Fig. 14). In both models the blind right eyecup is driven by the left seeing one and each eyecup has its own control system as described above. In model A the stimulus to the blind eyecup comes from the *input* to the seeing-eye amplifier, while in model B the stimulus to the blind eye comes from the *output* from the seeing-eye amplifier.

If model A holds, a spontaneous increase in the gain of the left amplifier (and variations in gain are common enough) causes an increase in the left eye output. This output, fed back and subtracted from the input, would cause the slip speed to be less,

and, assuming the rest of the system to be constant, would cause a decrease in the response of the right eye. With a constant stimulus therefore, model A predicts an inverse relationship between spontaneous variations in the responses of the blind and seeing eyes.

If model B holds, a spontaneous increase in gain of the left amplifier would cause not only an increase in the left eye output, but also an increase in the input to the link amplifier and hence of the right eye. Thus model B predicts a direct relationship between the spontaneous variations in the responses of the two eyes.

These predictions can only be expected to be statistical, because simultaneous but uncorrelated variations must occur in the gains of the other components of the whole system.

Scatter diagrams of seeing-eye responses against corresponding blind-eye responses were made for five different crabs with a standard stimulus, and lines of best fit were calculated by the method of least squares. Similar measurements were also made on the same five crabs when both eyes were free to see and move, to determine whether there was any correlation between the spontaneous variations of the two normal eyes which might mask an opposite correlation when one eye was blinded. Product-moment correlation coefficients were calculated from all the data so that the best statistical relationship between pairs of eyes could be established.

When both eyecups are free to see and move the points on the scatter diagrams show considerable dispersion. In four out of these five cases no correlation could be established between the responses of the two eyes, and therefore spontaneous fluctuations in the gains of the left and right amplifiers are independent.

In the fifth graph calculation of the correlation coefficient demonstrated, at a 1% level of significance, a positive correlation between the spontaneous variations of the responses of the two eyes. Further analysis of the data from this crab, however, showed this direct relationship to be a consequence of a progressive failure of both eyes with time. Such a decrease is not unusual in crabs which have been responding for 3–4 hr., but seldom occurs at the beginning of an experiment. Therefore the responses of this crab were not further studied.

In all four of the remaining crabs the slope of the line of best fit shows an inverse relationship between the fluctuations in response of the two eyes when one is blinded. In two of these graphs, calculation of the product-moment correlation coefficient demonstrates this at the 1% level of significance. One of these graphs is shown in Fig. 15. In the third crab an inverse relationship was significant at the 2% level. In the fourth the relationship was inverse but not significantly so. An inverse relationship is a significant positive result in the sense that several undesirable factors, especially progressive fatigue, tend to give the opposite result.

The gain of the link amplifier in Fig. 14A cannot be measured directly, as it cannot be isolated. However, by comparing the response of a seeing eye with the response of the same eye when blinded and driven, the gain of the link which drives it from the other side may be determined approximately, for the link amplifier is involved in only the latter of the two situations. In the four crabs whose responses are considered above, calculations of the gain of the left-to-right link gives values of 0·2, 0·3, 1·3 and 1·8. Although these values should be viewed with caution, since the calculation does not account for possible differences between the two movement detection systems, it

is clear that the link amplifiers are not necessarily of unity gain. Nor is the gain independent of stimulus velocity, for the seeing eyes, but not the blinded eyes, of unilaterally blinded crabs respond to drum velocities below 0·004°/sec. Also, at drum velocities above 1°/sec, the blinded eye often responds much more slowly than the seeing eye. Thus in terms of the block diagram (Fig. 14A) the frequency range of the link amplifiers is smaller at both extremes than that of the rest of the optomotor system.

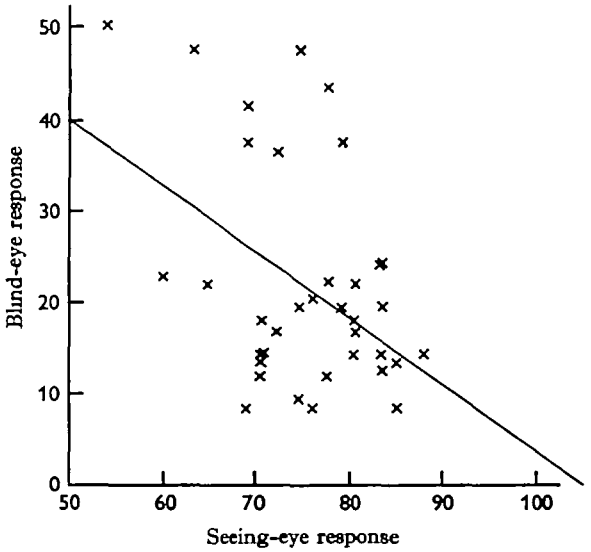

Fig. 15. Seeing-eye responses to a constant stimulus plotted against blind-eye responses. Responses are expressed as a percentage of the stimulus, which is a constant velocity shift through 2°. The line of best fit is calculated by the method of least squares and demonstrates an inverse relationship between the spontaneous changes in the responses of the two eyes when one is blind.

When both eyes are seeing, each amplifier has two inputs, one from each eye. These inputs are not simply additive, because a crab with both eyes seeing does not move its eyecups twice as far or fast as one with one blinded eye. Vision in both eyes improves the response amplitude to a ramp function by at most 15%. Since an improvement from 60 to 75% represents an increase in the forward gain from 60/100–60 to 75/100–75 or twofold, it could be that the additive feature is some function of the amplifier gain. However, no simple formula has been found for the summation of gain between the two sides.

Bilateral recording of fast phase

The fast phase of optokinetic nystagmus is a rapid return of the eyecup to its starting position after it has followed the rotation of the environment. The response, which occupies 200–500 msec., is usually a smooth movement, though small, jerky fast phases are sometimes observed in fatigued crabs. It always involves both eyecups; neither eyecup ever performs a fast phase alone. When they make a fast phase, the two sets of eyecup muscles are active in quite different combinations because the

eyecups move in opposite directions relative to the midline (Burrows & Horridge, 1968*a*).

Bilateral recording reveals that, for drum movement to the left, the fast phase of the right eyecup leads that of the left eyecup by 30–80 msec. (Fig. 16). With the drum moving to the right, the fast phase of the left eyecup leads by a similar amount. This suggests that each eye-control system initiates fast phases towards it own side. If so, this will be revealed in unilaterally blinded crabs.

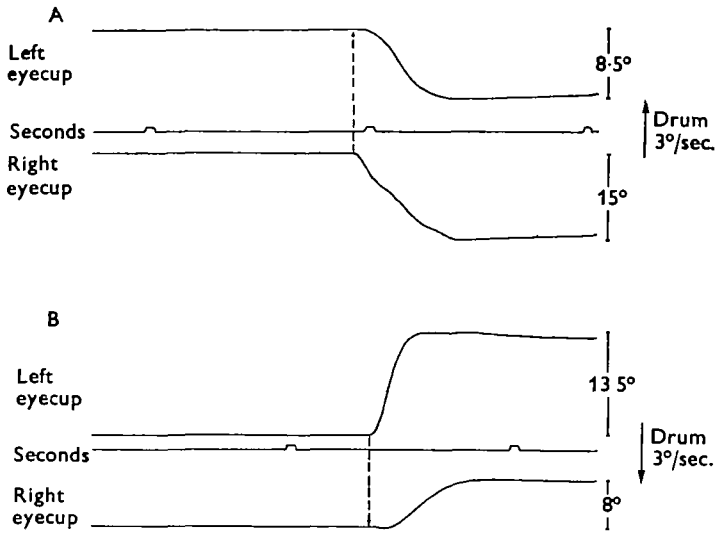

Fig. 16. Fast phases of optokinetic nystagmus recorded from both eyecups simultaneously. (A) Drum moves to left; note that the right eyecup leads the left eyecup, and moves through a larger angle. (B) Drum moves to right; left eyecup leads and moves farther. Movement to the right is shown downwards.

To test this, fast phases were counted during the time that the drum rotated at a velocity of approximately 5°/sec. through 360°. During drum movement to the right, there were 18 fast phases to the left when both eyes could see the drum. Blinding the right eye with black paint reduced this number to 15. This reduction was mainly due to a slowing of the slow phase, as discussed earlier. When the left eye was temporarily covered, i.e. when the left eye-control system had no input, there were no fast phases to the left. When both eyes could again see, 24 fast phases occurred during one turn of the drum. Similarly, during drum movement to the left, which produced fast phases to the right, there were no fast phases when the right eye was temporarily covered.

This experiment has been repeated on more than twenty-five crabs. In most, as in Fig. 17, some fast phases occur when the seeing eye is presented with movement away from the midline. The frequency of such fast phases is, however, less than one-third of those occurring in the more effective direction. The eye which initiates the fast phase and which, by its action as a pacemaker determines the frequency of fast phases for both eyes, is henceforth termed the governing eye, while the other is termed the governed eye. The crab is qualitatively similar to the rabbit in this respect (ter Braak, 1936; Fukuda & Tokita, 1957). These experiments give little indication of the

mechanism involved in the initiation of the fast phase of optokinetic nystagmus, but they do show that a directional mechanism must exist on each side.

The experimental situation in which the two eyes are separately stimulated by different sets of stripes makes it possible to vary the response of an eyecup while the visual stimulus to it remains constant. The onset of fast phases can therefore be studied when the response has been partially dissociated from the stimulus. When this is done, fast phases still occur at approximately a constant point in the eyecup's traverse. When both eyecups are made to move more slowly by decreasing the velocity of the striped pattern seen by either eye, the frequency of fast phases is decreased, but this is mainly because the critical point where fast phases occur is now reached later (but see below).

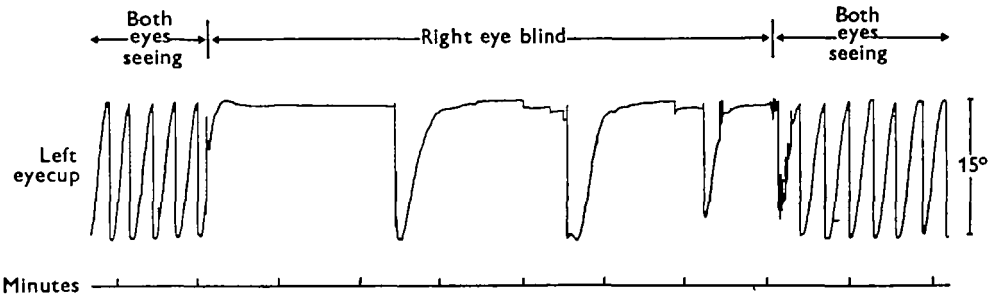

Fig. 17. Slow and fast phases of the optokinetic response of the left eyecup in response to continuous movement of a striped pattern around the crab at 1·2°/sec. to the left. When the right eye is blind few fast phases occur, although the left eyecup reaches the normal position at which fast phases are initiated. Movement to the right is shown downwards.

The motoneurone impulse patterns which cause fast phases are generated irrespective of whether the eyecup actually moves, and numerous experiments designed to show that the onset of the fast phase is controlled by proprioceptors have failed to do so (Horridge & Sandeman, 1964). The only physiological sign which can be recorded and which could inform the crab of the position of its eyecup is the frequency of impulses in the motoneurones to the eyecup muscles (Horridge & Burrows, 1968). This is not the whole story, however, for Horridge & Burrows have found that both mechanical and electrical stimulation of the region of the governing eye cause an earlier onset of subsequent fast phases. The impulse frequencies in the motoneurones to all the muscles reach their peak a little before the fast phase occurs (Burrows & Horridge, 1968*a*) so a different but equivalent signal may be involved instead. Eyes frequently 'stick' at the end of a slow phase and will not make a fast phase, especially when the stimulus to a single eye is not a simple movement of all contrasts towards the animal's midline. For instance, memory and step stimuli, which cause large slow-phase responses, often fail to initiate a fast phase. The frequency of fast phases is also considerably reduced when the governing eye does not see the stripes (Fig. 17). Yet blinding the governing eye alone hardly changes the frequency of impulses in the motoneurones to the eyecup muscles of either eye. Therefore, while it is true that fast phases are centrally controlled by some aspect closely tied to the efferent optomotor impulse frequency in muscle 21, which pulls the eyecup towards the midline, the mechanism is not entirely independent of the visual input to the governing eye.

Careful scrutiny of the records shows that the stimulus combination can influence the point on the eyecup's traverse at which fast phases are initiated, although a very accurate measure of the position of fast phase initiation is not possible if at the same time the whole eyecup traverse is recorded. When the stimulus to the governed eye is constant, the faster the stimulus to the governing eye the farther it travels before the fast phase. When the stimulus to the governing eye is constant, the slower the stimulus to the governed eye the farther the governing eye travels before the fast phase. The differences are small, being 1–2° for a stimulus velocity change of 0·2–3°/sec., and take place against a background of considerable variation in the actual position of the fast phase, but when the point of initiation of the fast phase was plotted against stimulus velocity, the slope of the regression line was significantly different from zero in about half of the crabs whose fast phases were examined.

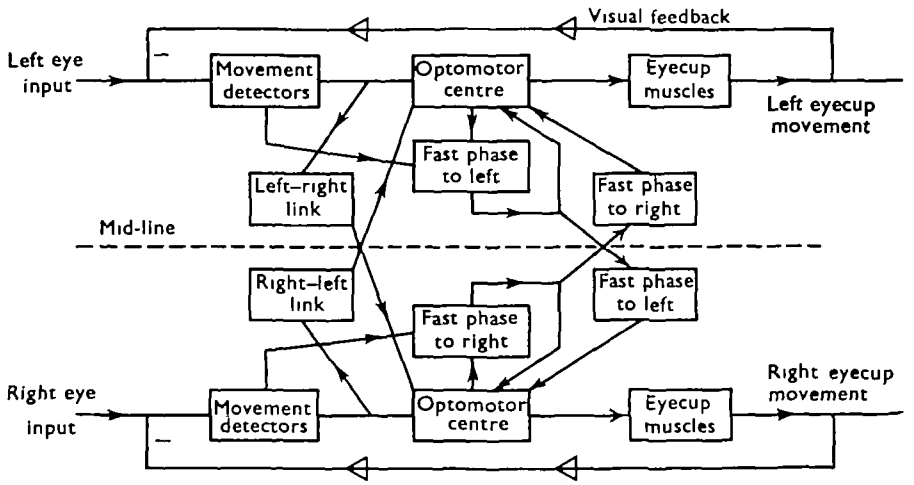

Fig. 18. The control system for both slow and fast phases of optokinetic nystagmus showing the pattern of interactions which can be inferred from the behavioural observations.

DISCUSSION

These experiments, the first in which the optokinetic responses of the two eyecups have been recorded simultaneously, have demonstrated that the eyecups can move independently. Although the degree of interaction varies considerably in different specimens, at the start of a response both converging and diverging movements of the eyecups are possible. Therefore each eye has its own control system. Within the control system on each side three different parts can be distinguished: a *movement detector* on the sensory side of the brain, probably in the optic medulla; a centre called the *optomotor centre* of unknown location which converts interneurone impulses signalling movement into motor impulses to the eyecup muscles; and thirdly, the *eyecup muscles*. The model of the complete system (Fig. 14A) may thus be expanded as in Fig. 18.

This model also incorporates our findings concerning the mode of initiation of the fast phase of nystagmus, for each control system initiates fast phases towards its own side. The fast-phase initiators receive their main input from the optomotor centre of the governing eye, for fast phases are centrally initiated by some aspect closely tied to

the frequency of impulses in the motoneurones to the eyecup muscles. However, since the mechanism is not independent of the visual input to the governing eye, the fast-phase initiators also receive a subsidiary input from the ipsilateral movement detector. Since the fast phases of one eyecup always lead the other by 30–80 msec., paired centres are proposed rather than single ones. It is suggested that one of each pair always fires off the other, and that this causes the delay.

Our experiments indicate that the two control systems are linked on the movement-perception side of the optomotor centres (Fig. 18), and Wiersma, Bush & Waterman (1964) have recorded abundant efferent activity of contralateral visual movement receptors in the optic nerve of the crab, *Podophthalmus*. Therefore the linkage between the eyes probably occurs in each optic ganglion. The links in the model do not carry signals for very fast or very slow movements as effectively as do the other components of the system. This has an obvious functional significance, in that visual signals resulting from the slow independent drift of the eyecups on the one hand and high-frequency eyecup tremor on the other are not conveyed from one control system to the other.

During the first few seconds of a response in which the eyes have conflicting visual inputs, each optomotor centre is governed largely by the movement detector on its own side, whereas the input from the contralateral eye influences but slightly the velocity of the response. After a few degrees of movement, however, both optomotor centres become dominated by the slower of the two visual inputs. The reason for this is as follows. The forward gain of the optomotor system is higher at low stimulus velocities (Horridge & Sandeman, 1964), and so the slip speed is small for the eye seeing the slow stimulus. Thus if the slower eyecup speeds up even a little, it greatly reduces its own input signal and may even generate a signal in the opposite direction by going faster than its stimulus. The eye seeing the faster stimulus, on the other hand, is more easily held back because the gain is lower, and holding it back merely generates a slightly stronger forward signal for both eyes. This conclusion is in agreement with the finding that when one eye sees a stationary contrasting pattern while the other eye sees a moving pattern, both eyecups make a small movement at first, but then they both slow to a halt under the influence of the stationary pattern.

In these experiments, the eyecups often have steady-state speeds that differ. There is therefore no fixed link on the efferent side such as could be formed by T-shaped motor axons. Motoneurone impulses to muscles that move one eyecup do not bear a one-to-one relation with those that move the other eyecup in the same direction (Burrows & Horridge, 1968*b*).

The only other crustacean in which converging and diverging eyecup movements have been observed is the mantis shrimp, *Squilla*, in which each eye fixates separately upon prey (Demoll, 1909). However, Sandeman (1964) failed to find proprioceptors in the eyestalks or eyecups of *Squilla*, although with the same methods he found proprioceptors in the bases of the antennules. Also, *Squilla* touches its prey with an antennule before striking (Schaller, 1953). The convergence of the eyecups may thus be an incidental consequence of independent following by the two eyes.

Although convergence of the eyes is essential for binocular measurement of distance in man, there is no reason to suppose that *Carcinus* estimates distances by this means. There is no fovea or equivalent area of acute vision upon which the two corresponding

images of an object could be aligned. There is no evidence for any proprioceptive mechanism that could evaluate the convergence of the eyecups; nor is there any evidence that converging movements ever occur in response to objects at different distances from the eyes. Theoretically, a crab could determine the relative positions of objects in the visual field by moving one eyecup and observing the parallactic displacements of such objects relative to one another, but there is no evidence of this ability. In fact, the exact significance of these partially independent eyecup movements awaits further detailed studies of the part played by eyecup movements in normal behaviour.

SUMMARY

1. The movements of the two eyecups of the crab, *Carcinus*, have been recorded simultaneously during optokinetic responses.

2. Experiments in which the eyes view different visual stimuli reveal that, at the start of a response, the eyecups have a considerable degree of independence and can even move in opposite directions. As the response progresses, interaction between the eyes increases, until the eyecups move at similar velocities in the direction of the slower of the two visual inputs, or are stationary.

3. Similar interactions between the eyes were observed during memory responses and during the responses to sinusoidal oscillation of the two sets of stripes.

4. Each eye has its own system for converting perceived motion into eyecup movement. These two systems are linked on the afferent rather than the efferent side of the brain.

5. The fast phase of optokinetic nystagmus is governed by the eye whose fast-phase movement occurs away from the midline, and the fast phases of this eyecup lead the other by 30–80 msec. Also, fast phases only occur at their normal frequency when the governing eye can see the stripes.

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