

EFFERENT COPY AND VOLUNTARY EYECUP MOVEMENT IN 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

The movable eyecups of crabs are stabilized in position in the horizontal plane by their visual input, and optokinetic responses are a consequence of this. In the dark a crab's eyecups stabilize upon a single small light-source and follow its movement, but in complete darkness they drift aimlessly. In contrasting surroundings the eyecups follow the nett rotation of all objects within the visual field. When an eyecup is pushed to a new position it acts as though 'locked' in place by the new visual input because a movement away from this position causes contrasts in the visual field to move in the opposite direction across the eyecup.

In spite of this strong visual stabilization the eyecup makes voluntary movements. This paper asks the question: how are the effects of visual feedback overcome during voluntary movements? Experiments have been restricted to the voluntary extension movement of the eyecup after a withdrawal. By the eyecup, which holds the retina or eye, is meant the terminal, movable, segment of the eyestalk.

METHODS

The same technique of recording eyecup movements was used as in previous papers (Horridge, 1966). Movements of both eyecups were recorded simultaneously by photocells which operate over the whole range of the eyecup's motion. Many of the experiments measure the movement of a blinded left eyecup that is driven by a seeing right eye. Movements of the striped drum were recorded with another similar photocell.

RESULTS

Driving of one eyecup by visual input to the other eye

When one eye of a crab is blinded by coating the cornea with black paint, it nevertheless continues to respond almost normally. The central programme of impulses in about forty motoneurons to the two eyecups is generated by the brain irrespective of whether the visual input is from one eye or both. Small differences between the movements of a blinded and a seeing eye occur, however. The movements of the blinded eye tend to be more irregular, presumably because irregularities are not compensated by its own visual feedback. The response of a blinded eye soon fatigues during repetitive oscillations of the striped drum at frequencies greater than 1 Hz. Moreover, the blinded eye sometimes ceases to respond after a long series of experiments. It

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

therefore appears that the neural pathways to the contralateral eyecup muscles are more labile than those to the ipsilateral eyecup muscles. So long as these limitations are known, and guarded against by suitable experimental procedure, the movements of the blind eye are an indicator of the amount of movement that the seeing eye *infers*.

Vision during extension of the eyecup

It has been shown already that an eye which is tightly retracted into its socket nevertheless continues to see, as revealed by a driven optokinetic response of the other, blinded, eye (Burrows & Horridge, 1968). The stimulus is an oscillation of the striped drum through an excursion of a few degrees and at a frequency of 0.1–0.5 Hz.

The primary observation, which is the basis of this paper, is that when an eyecup voluntarily extends it sweeps across the contrasts in the visual field without conveying that movement stimulus to the other, blinded, eyecup.

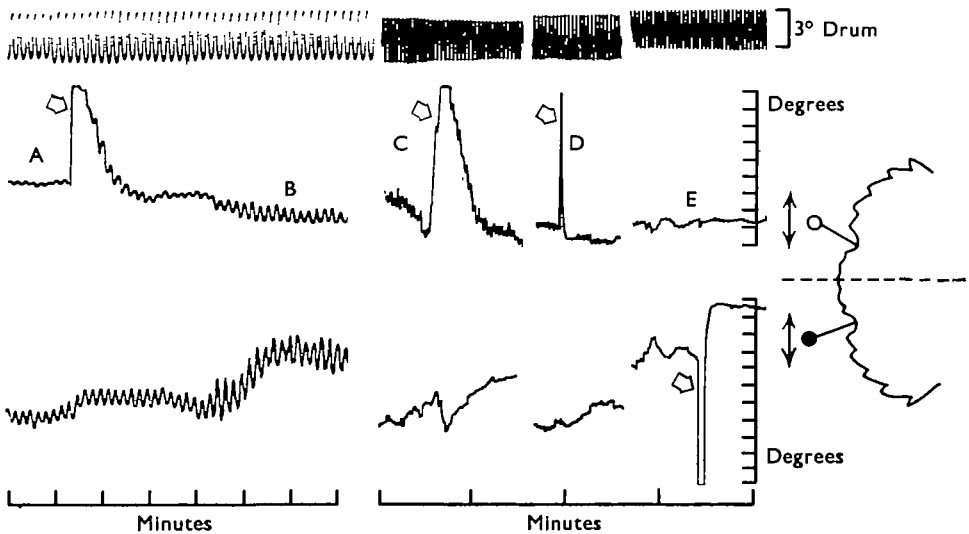


Fig. 1. Simultaneous records from the two eyecups, with a background oscillation of the drum. A, an extension of the seeing eyecup following a retraction (open arrow) is not reflected in a movement of the opposite blind eyecup. B, a spontaneous change in gain is seen for both eyecups. C, during a slow retraction (open arrow) the seeing eyecup responds to movements of the drum, as it also does during even slower extension to its former position. D, an extension of the seeing eyecup in the presence of a checkerboard also returns it to its former position without a movement of the blind left eyecup. E, an extension of the blind eyecup does not always return it to its previous position. Throughout all illustrations the seeing right eyecup is represented by an open circle, the blind left eyecup by a filled circle.

To discover whether vision fails during the process of extension the drum was moved with a background oscillation as the eyecup extended spontaneously after a withdrawal (Fig. 1 A). The blind left eyecup responds all the time to the oscillation seen by the seeing right eye, but the blind eyecup *does not* respond to the much greater relative movement caused by the sweep of the extending eye across the drum. The question is how the brain distinguishes between the two motions, that caused by movement of the drum and that caused by movement of the eyecup.

Extension of the eyecup is not entirely a horizontal movement and it rotates through about 10° as it emerges. The extension sweep may therefore cross few contrasting

edges at right angles so that little movement information is inferred. The experiment was therefore repeated with an oscillating black and white checkerboard in front of the eye, with the same result (Fig. 1 D). The voluntary withdrawal movement and the voluntary extension movement cause no movement of the blinded eyecup.

Eyecup retraction is usually so rapid that experiments cannot be carried out during its course, but occasionally, if a retraction is performed slowly, it is quite clear that the eyecup responds to oscillations while it is making a retraction movement (Fig. 1 C).

Changes in sensitivity with extension

When an eyecup extends in the presence of a continually oscillating drum its responses to the oscillation are greater during the extension and for up to 1 min. afterwards. This increase in the response is similar to that following stimulation of receptors around the eyecup (Burrows & Horridge, 1968). In a spontaneous extension this arousal effect, or temporary increase in optokinetic gain, could be caused by mechanoreceptors of the arthrodistal membrane at the joint between the eyecup and eyestalk. Sometimes the increase in gain is conveyed to the responses of a blinded driven eyecup on the other side.

Spontaneous changes in gain may sometimes affect one eyecup alone, sometimes both (Fig. 1 B). A temporary improvement in performance can also be obtained in most crabs by mechanically stimulating the legs or abdomen. So long as one is aware of these phenomena, they need not interfere in experiments where movement perception is tested by the response to a continually oscillating drum. In fact they show that vision is *better*, and certainly not suppressed, during extension.

Extension of the blind eye

If the blind eyecup makes a reflex withdrawal, caused by touching the carapace near to it, no movement occurs in the other, seeing, eye. As the blind eyecup extends again voluntarily there is again no movement of the other seeing eye. A blind eyecup, unlike a seeing one, extends to a position which is not necessarily similar to that which it occupied before. This is true even if the eyecup was withdrawn for only a few seconds (Fig. 1 E). Presumably this lack of control is because the eyecup does not see, and there is no opportunity for movement-perception systems of long time-constant to bridge the withdrawn period. Another explanation is that the positional cues all originate from the opposite, seeing eye, and there is drift in the mechanism transferring the excitation into the mirror-image set of muscles on the blind side.

Extension of the blind eyecup is often accompanied by a marked improvement in its response to oscillations of constant amplitude (Fig. 2).

Forced movements of the seeing eye

When the right seeing eye is pushed by a small probe attached to a micromanipulator, the visual field moves in the opposite direction across the eye. The left blind eyecup responds as if stimulated by this relative motion. This happens in either direction so that the eyecups converge or diverge (Fig. 3). The crab therefore interprets a forced movement of the seeing eye as if it were an equivalent movement relative to the crab of an object in the visual field. This is one of the many pieces of evidence that proprioceptors are not involved in the control of eyecup position.

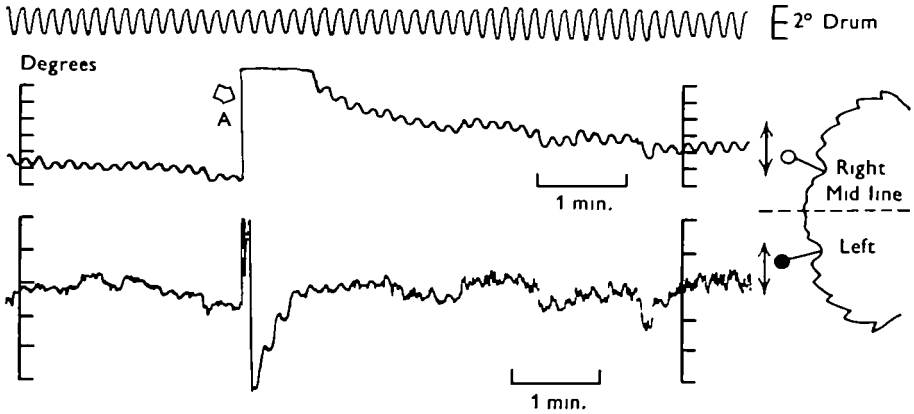


Fig. 2. Movements of a left blind eyecup (lower trace) as driven by the right seeing eye (upper trace). The drum oscillates the whole time at a frequency of approximately 0.1 Hz. and amplitude 2° peak to peak. A, the seeing eyecup retracts spontaneously (open arrow) and then slowly recovers its former position. The blind eyecup flicks spontaneously and then retracts but recovers more quickly. The record shows: (a) the seeing eye still drives the blind eyecup when it is retracted, (b) the blind eyecup responds better during its own extension, (c) the blind eyecup does not respond as the seeing eyecup extends and sweeps across the drum to its former position.

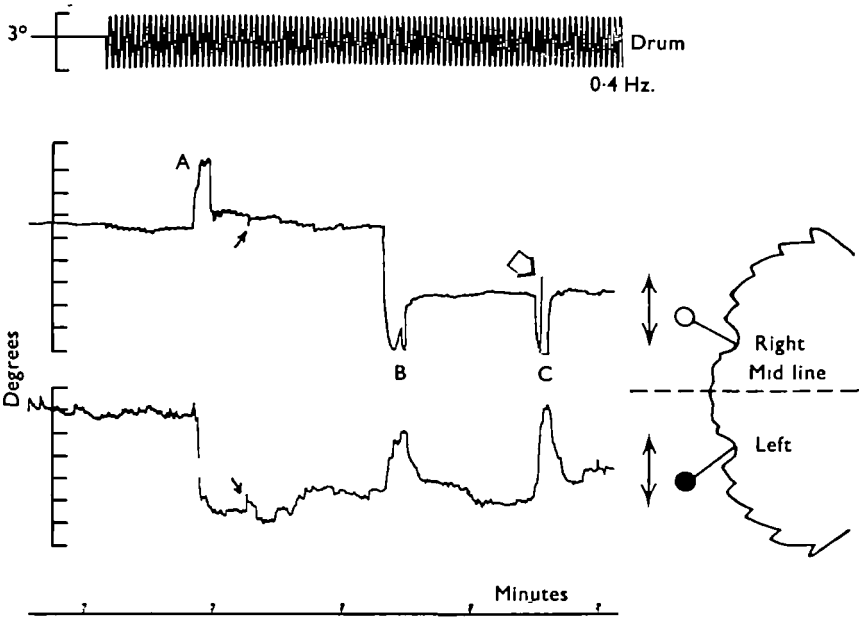


Fig. 3. Movements of the right seeing (upper) and the left blind (lower) eyecups in response to forced movements, with a background oscillation of the striped drum. A, a forced movement of the seeing eye away from the mid line causes a similar movement of the blind eyecup, so that the two eyecups diverge, while a forced movement of the seeing one toward the mid line (B, C) causes the two eyecups to converge. However, a partial retraction (open arrow) during the forced movement at C is not reflected in a movement of the blind eyecup. Note the larger tremor of the blind eyecup, the simultaneous occurrence of flicks in both eyecups (small arrows) and the increased response of the seeing eye after the forced movements.

If oscillatory movements of the drum are going on at the same time as a forced movement, the two eyecups respond to these by both moving in the same direction as the stimulus. However, with reference to the forced movement component, the two eyecups move in opposite directions relative to the midline of the crab. They will, of course, only retain this position so long as the force is applied to the seeing eyecup, and during this time only the blind eyecup is free to oscillate.

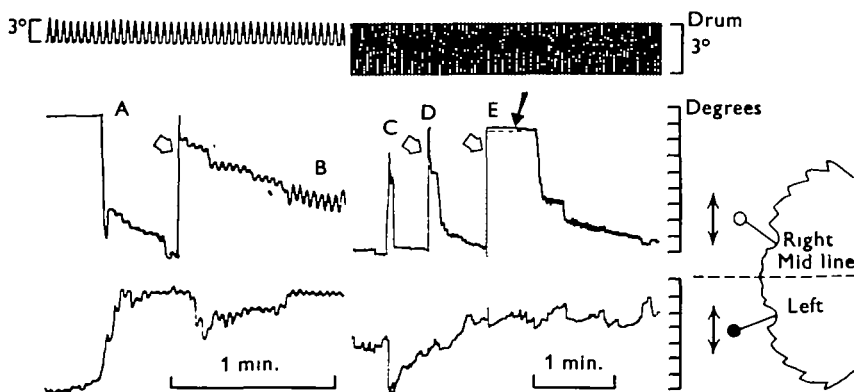


Fig. 4. Movements of the right seeing eyecup (upper trace) and simultaneously of the blind left eyecup (lower trace). For details see text.

The contrast between forced and spontaneous eyecup movements can be seen in one preparation if the crab happens to perform spontaneously at the appropriate moment. Consider first the extensions of each type. A forced extension of the seeing eyecup causes a squint as the blind eyecup also moves toward the mid line (Fig. 4A). The seeing eyecup then retracts spontaneously and subsequently extends more slowly. Although slower movements are in general seen better than faster ones, the slow spontaneous extension of the seeing eyecup causes no response of the blind one (Fig. 4B). The same is true for the two types of retraction. A forced retraction of the seeing eyecup causes a divergent movement of the blinded one, but immediately afterwards a spontaneous retraction of the seeing eyecup causes no movement of the blind eyecup (Fig. 4C,D).

In these experiments there is a considerable latency, sometimes as long as 1 sec., between the forced movement of the right seeing eyecup and the response of the left blind eyecup in the opposite direction (Fig. 5). This latency indicates that the causal connexion between the two sides is more complex than previous experiments have shown.

Mechanical prevention of extension

As the eyecup extends voluntarily it might be supposed that a compensatory signal equal and opposite to that caused by the relative movement is conveyed to the motor centre for the blinded eye (or for both eyes). To test this, the voluntary extension was prevented with a stop that was placed in position after a voluntary withdrawal. The eyecup was allowed to move $\frac{1}{2}^\circ$ from its withdrawn position before hitting the stop, so that an indication of an attempted extension was available on the record. As the seeing eyecup tries to extend it comes up against the stop. The significant point is that the blind eyecup makes no response in either direction (Fig. 4E). Therefore there is no

evidence that an equal but opposite compensating signal to the blind eyecup is responsible for the failure of the latter to respond during a voluntary extension.

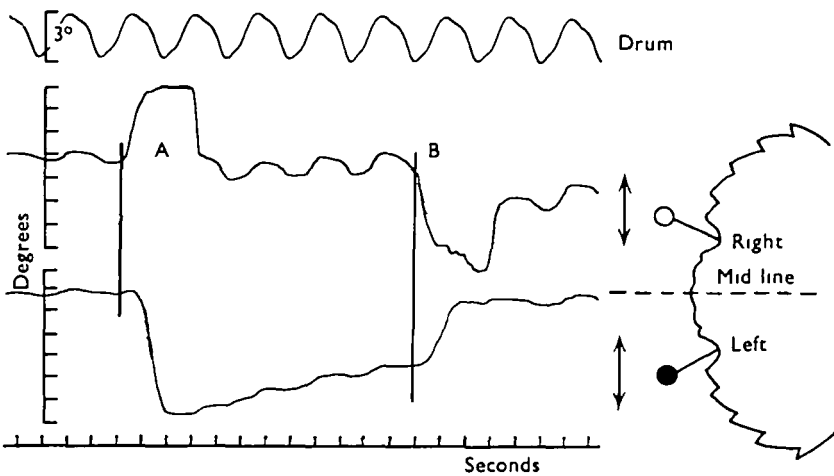


Fig. 5. Latency to forced movements. A forced movement of the right seeing eyecup away from the mid line (A) is followed in 1 sec. by a divergent movement of the left blind eyecup. A similar latency exists for a forced movement toward the mid line (B). Note the increased response of the seeing eyecup to the oscillation after the forced movements.

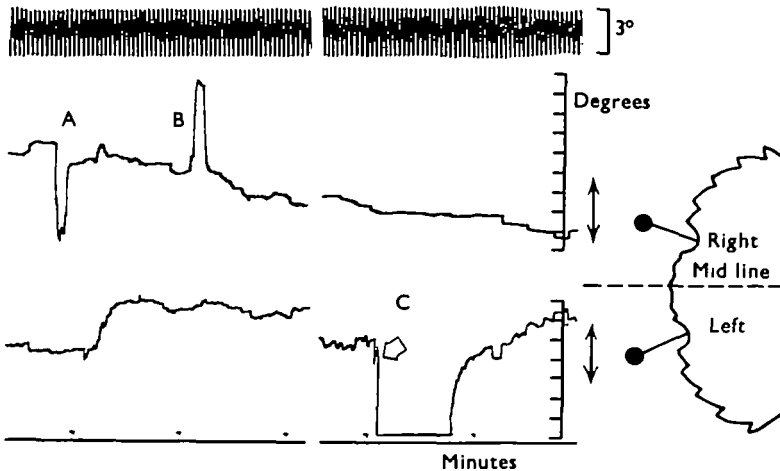


Fig. 6. Eyecup movements when both eyes are blind. A forced movement of the right blind eyecup towards (A) or away from (B) the mid line (upper trace) causes no movement of the left blind eyecup (lower trace). C, a spontaneous extension of the left eyecup after a retraction (arrow) is not reflected in a movement of the right eyecup. The drum is moving sinusoidally at 3° peak to peak at 0.4 Hz. throughout, as a check that the eyes are really not able to see.

Both eyes blind

The reason for working with both eyes blind is to test for effects of proprioceptors which may be overridden by the visual control of eyecup movement. When both eyes are properly blinded with black paint, they drift about a midpoint which is near the

normal posture. This is because the principal muscles are in balance with each other. In the horizontal plane, muscles 20a and 21 both have low frequencies of slow junction potentials when the eyecup is near its rest position (Horridge & Burrows, 1968).

Forced movement of one blind eyecup in either direction is not followed by any response of the other eyecup (Fig. 6A, B). A spontaneous withdrawal and subsequent voluntary extension is not followed by any response in the other eyecup (Fig. 6C).

When one blind eyecup is prevented from voluntarily extending, by a stop that is inserted when it withdraws, there is similarly no movement of the other, blind, eyecup. A normal crab in complete darkness retracts and then extends one eyecup without accompanying movement of the other eyecup.

DISCUSSION

A blind eyecup responds to movements of the drum across the seeing eyecup and to relative movement caused by forced movement of the seeing eyecup, but the crab acts as if it does not see the relative movement caused by its own voluntary eyecup movement. The question is how it does this.

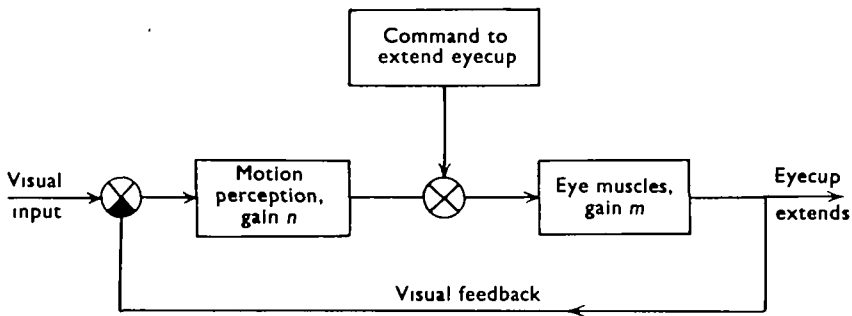


Fig. 7. The relation between the optokinetic mechanism and the central command to extend the eyecup by which a single movable eyecup (or head with fixed eyes) can move voluntarily while vision is in no way hindered. The visual feedback loop reduced the effect of the command but cannot prevent it. This system would respond to an oscillation during the course of a voluntary eyecup movement, but is not adequate for two movable eyecups.

The first point to emphasize is that the perception system of the seeing eye is not in some way suppressed. This is shown by the fact that the blind eye continues to respond to drum oscillations while the voluntary movements are in progress. This result also shows that the voluntary movements do not cause relative movements that are too rapid for the crab to see. So it must be concluded that the visual system is sensitive to the relative movement of the drum caused by the voluntary movement of the eyecup. For this reason the visual feedback loop cannot be eliminated in the argument which follows.

For many years there was a controversy as to how an animal with a strong optomotor response could turn voluntarily. Then Mittelstaedt (1960) showed that the problem is resolved for an insect (with eyes fixed on the head) which turns voluntarily if the command to turn is injected at the appropriate point into a feedback loop (Fig. 7). If the voluntary command is added at the point shown to the motor system which maintains the visual stabilization then while the command operates it causes a continual

turning which cannot be completely compensated for by the feedback loop although all parts of the system are in action. Meanwhile movement of the environment is compensated for with an accuracy that depends on the over-all forward gain, $n \times m$.

If a comparable diagram is made for the situation in the crab, with both eyes movable and one (say the left) eye blind, it is difficult to avoid the conclusion that the blind left eyecup is an indicator of *all* the net motion perceived by the right eye (Fig. 8). Therefore, the parts of Fig. 8 drawn in continuous line are incomplete because, in fact, the left eyecup does not respond to the relative motion caused by the *voluntary* movements of the right eye. The command does not suppress the motion-perception system, as shown by the observation that the responses to oscillations continue unchanged, and are even improved, during extension. The voluntary command must

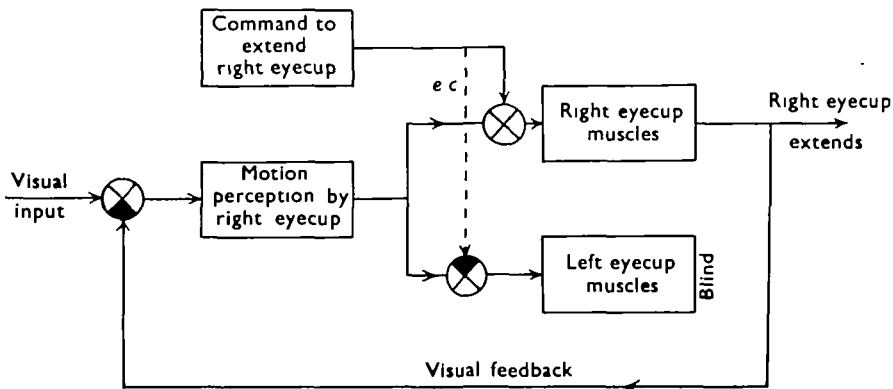


Fig. 8. The system with two movable eyecups, one of which (the right) sees and drives both. In this scheme a command to extend the right (seeing) eyecup invokes a relative motion which is inevitably conveyed to the blind eyecup unless prevented by the efferent copy (dashed line *e.c.*), which is a parallel channel of the command carrying a signal to move by a certain amount in the opposite direction. This system does not agree with experiment.

therefore be accompanied by a second action that prevents the response of the blind left eyecup. The technical term for the simplest form of this second action is 'efferent copy', which implies a second (and central) effect of the motor activity, or of the premotor driving activity, which controls the voluntary movement. The efferent copy is the missing element which is required to cancel the visual stimulus that the movement causes. The question is whether the efferent copy is the simplest hypothesis, or even an adequate hypothesis, to explain the control of the eyecups in this situation.

On inserting the efferent copy (*e.c.* in Fig. 8) into the diagram for the crab with two free eyecups, of which the left is blind, it is evident that there could be an equal and opposite signal that would just cancel the response invoked by the voluntary movement but not impair vision, and so leave the response to the oscillation unchanged. But this compensatory signal is still inadequate when tested, because the equal and opposite efferent copy should be seen as a movement of the blind eyecup in the opposite direction under three conditions: (a) when the voluntary extension is prevented by a stop, (b) when both eyes are blind, and (c) in the normal intact crab in the dark.

When the voluntary extension is prevented by a stop no visual feedback results from

the extension command and there is no further movement of either eyecup. When both eyes are blind there is voluntary movement of one eyecup but not of the other, and again there is no visual feedback. Therefore, when there is no visual feedback as a result of the command to extend the seeing eyecup, it makes no difference whether the seeing eyecup moves or not. This leads to the conclusion that proprioceptors are not acting as a gate which would allow the efferent copy to be subtracted only when the extending eye actually moves. Therefore the scheme shown in Fig. 9, in which the proprioceptive gate is indicated by the experiment of preventing the extension by a stop, is ruled out by the results with both eyes blind and with the intact crab in the dark.

A single simple model based upon a central efferent copy as in Figs. 7-9 therefore

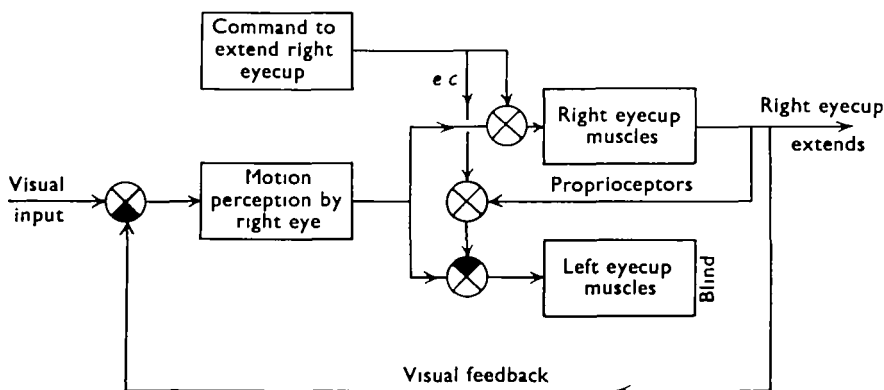


Fig. 9. The diagram as in Fig. 8 with the addition of an interaction whereby eyecup proprioceptors could allow the efferent copy to act only when the seeing eyecup actually moved. This is still not adequate because it fails to explain the result with both eyes blind or with the crab in the dark.

cannot be made to agree with the experimental results unless one introduces a special set of relations for each experimental arrangement and that would amount to no more than a re-statement of each experimental result.

Spontaneous retractions of either eyecup occur at a rate of several per hour, which implies many thousands per year. The crab has therefore considerable experience of the visual consequences of voluntary retraction and extension of the eyecup, both in the light and in darkness. The experiments reported here indicate that an efferent copy is not an adequate explanation, and that perhaps the visual system of *the eye itself* has innate or learnt cues which enable it to distinguish between relative movement of the environment that is and is not caused by voluntary movement of the eyecup. Such cues are quite possible, for example they could come from the rotation of the eyecup as it extends, or from the apparent motion of stationary parts of the crab. Such ideas would have to be tested by experiments of quite a different kind from those reported here.

SUMMARY

1. Use is made of the fact that a freely moving blind eyecup is driven by movement perceived by the opposite seeing eye when the crab is in an optomotor drum.
2. Forced extension of the seeing eyecup causes movement of the other blinded eyecup in the opposite direction, because it is driven by the perceived relative motion.

3. Voluntary extension of the seeing eyecup causes no movement of the other blinded eyecup, although simultaneous oscillation of a striped drum round the crab is seen perfectly.

4. Preventing voluntary extension of the seeing eyecup with a mechanical stop causes no movement of the other, blinded, eyecup.

5. With both eyes blinded, or with the crab in the dark, voluntary or forced movement of one eyecup causes no movement of the other.

6. This behaviour is that expected of an animal which can retract and extend either eyecup in the light or in the dark without disturbing the other, but no simple model is compatible with all the experiments.

REFERENCES

- BURROWS, M. & HORRIDGE, G. A. (1968). Eyecup withdrawal in the crab, *Carcinus*, and its interaction with the optokinetic response. *J. exp. Biol.* **49**, 285-97.
- HORRIDGE, G. A. (1966). Optokinetic memory in the crab, *Carcinus*. *J. exp. Biol.* **44**, 233-45.
- HORRIDGE, G. A. & BURROWS, M. (1968). Tonic and phasic systems in parallel in the eyecup responses of the crab, *Carcinus*. *J. exp. Biol.* **49**, 269-84.
- MITTELSTAEDT, H. (1960). The analysis of behaviour in terms of control systems. In *Trans. 5th Conference on Group Processes*, 1958. New York: Josiah Macy Jr. Foundation.