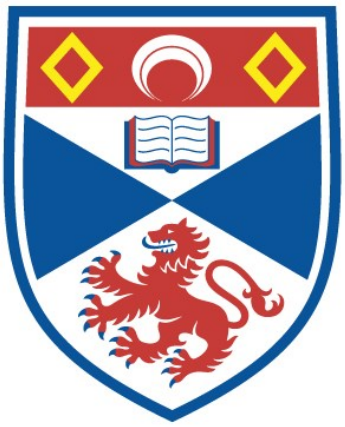
THE NERVOUS CONTROL OF THE EYE MOVEMENTS OF THE SHORE CRAB CARCINUS MAENAS

David C. Sandeman

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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The Nervous Control of the Eye Movements of the Shore Crab *Carcinus maenas*

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Thesis submitted for the degree of Doctor of Philosophy.

DECLARATION

I hereby declare that the work recorded in this Thesis has been carried out by myself, and that it is of my own composition. I further declare that it has not been submitted in any previous application for a higher degree.

RESEARCH CAREER.

I completed a B.Sc degree at the University of Natal, South Africa, in 1959, after which I carried out research on the flight mechanism of the migratory locust in fulfillment of the requirements for an M.Sc degree which was awarded at Natal in 1961. The results obtained from research on the eye movements of the shore crab are presented in this thesis for the degree of Ph.D.

SUPERVISORS CERTIFICATE

I certify that David Sandeman has fulfilled the conditions laid down in the regulations for a Degree of Doctor of Philosophy, under the Ordinance No. 16 of the University Court of the University of St.Andrews and that he has accordingly qualified to submit this Thesis for the degree of Doctor of Philosophy.

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PREAMBLE.

My topic is the nervous control of the eye movements made by Carcinus maenas when a vertically striped black and white drum is rotated horizontally around the animal. These eye movements are called optokinetic nystagmus and are characterised by a slow phase during which the eye moves in the same direction as the striped drum, followed by a rapid phase when the eye returns to its original position.

The anatomy of the eyestalk assembly and the innervation of the ten eye muscles and the five types of cuticular receptors on the eyecup and eyestalk, are described in so far as they are relevant.

The optokinetic responses of both normal and unilaterally blinded crabs are measured during relative environmental speeds of movement which range from)0.001°/sec to 10.0°/sec, and the effect of apparent environmental movement induced by forcing the eye in different horizontal directions is reported. The eyes are found to be remarkably sensitive to very slow movements.

The nervous control of the eye movements, and the interaction between the reflex retraction of the eye and the optokinetic responses, is investigated electrophysiologically by recording from the optic tract and oculomotor nerve with stainless steel micro-electrodes.

A new finding of general interest is that the eye movements are controlled without reference to proprioceptive feedback mechanisms.

INTRODUCTION.

Eye movements of Carcinus induced by optical stimuli have been used as a tool in this investigation, but the main interest is in the overall nervous control of eye movement. It is therefore necessary to review the literature over a wider field and to take into account eye movements induced by other means and also the visual perception of movement. The previous work is reviewed under the following headings:

1. Compensatory eye movements of the stalk-eyed Crustacea.
2. Investigations in which the optomotor response has been used to study the visual perception of movement and the properties of the photoreceptors.
3. Electrophysiological studies.
4. Anatomical accounts.
5. Optokinetic nystagmus.

Section I.

Compensatory eye movements of the stalk-eyed Crustacea.

Three different types of compensatory eye movements in Carcinus are described by Bethe (1897a). The first are the movements which can be induced by turning the animal about a transverse or longitudinal horizontal axis. The animals respond in these conditions by moving their eyes in the opposite direction to the forced movement, so tending to keep the eyes in a constant position relative to the environment.

This type of compensatory eye movement was first noticed by Kreidl (1893) in Palaemon, and by Clark (1896) in Gelasimus pugilator (the fiddler crab) and Platyonichus ocellatus (the lady crab).

The second type of compensatory eye movement described by Bethe occurs when Carcinus is placed on a turntable and rotated about a vertical axis. As in the first type of compensatory movement, the eyes move slowly in the opposite direction to the imposed rotation (the slow phase), tending to remain stationary with the environment. If the rotation of the turntable and animal continues the eyes flick quickly in the direction of the imposed movement (the fast phase), before beginning another slow traverse in the opposite direction. Lyon (1900) contra Clark (1896) found full compensatory movements for rotation about a vertical axis in Gelasimus and Platyonichus. The fast phase is referred to by Bethe and Lyon as "nystagmus" but since then this term has come to mean both the slow and fast phase of the response (von Buddenbrock and Friedrich 1933; Kunze 1963; Alpern 1962).

Bethe's third type of compensatory eye movement can be induced by mechanically stimulating a crab on its left side, so making it move. Before moving, say to the right, the animal looks quickly to its right and then moves in this direction, after which the eyes swing back and forth while it walks along. These eye movements do not have a slow and fast phase.

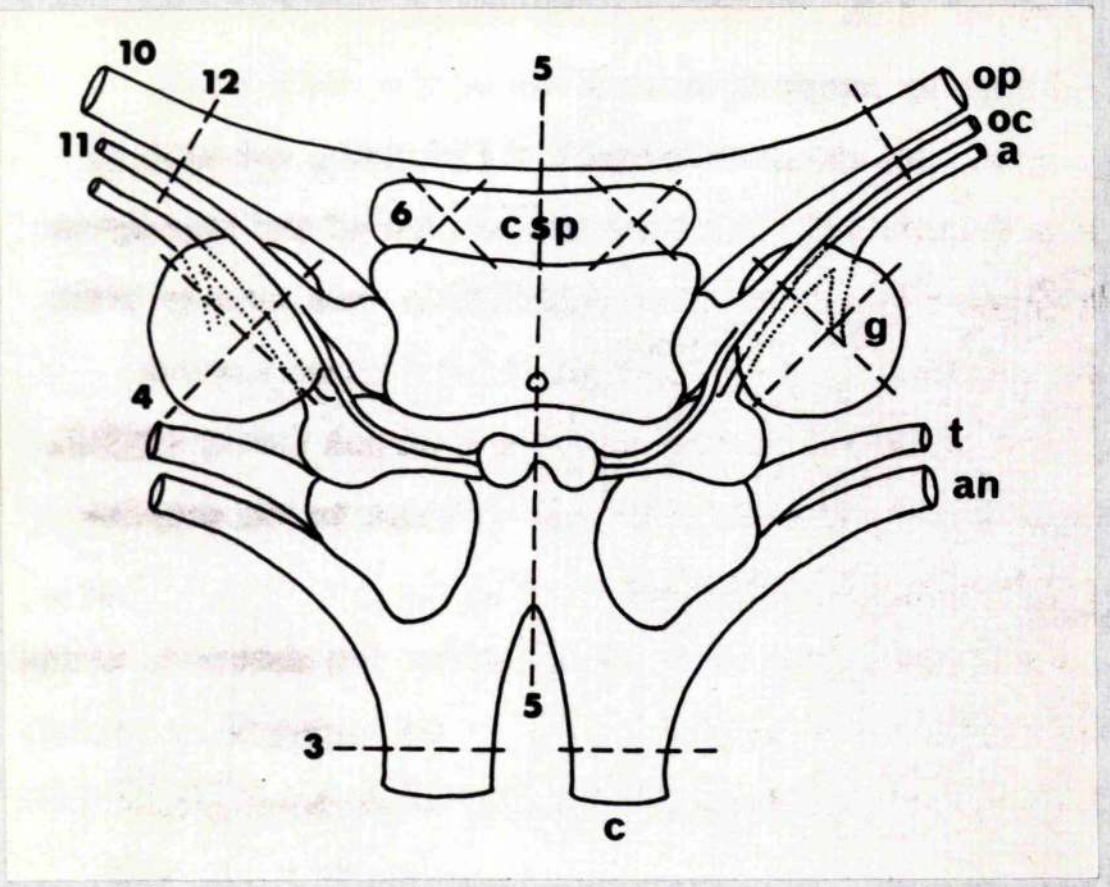


Figure 1. Dorsal view of the brain of Carcinus maenas (after Schöne, 1961) the broken lines indicate the lesions made by Bethe which are as follows: 3, cutting through neck connectives (c); 4, destruction of the globuli (g); 5, separate medial lesions of the brain from anterior to the centre and from posterior to the centre; 6, destruction of one or both sides of the cellulae superior mediales (csp), 10, section of the optic tract (op); 11, section of the oculomotor nerve (oc). The antennular nerve (a), tegumentary nerve (t), and antennary nerve (an) were not cut through by Bethe. The results of these experiments are shown in Table 1 under the same numerical references.

The three types of compensatory eye movements are hindered in different ways by surgical transection of the optic tract, oculomotor nerve, and circumoesophageal connectives, and also by brain lesions (figure 1), blinding, and removal of the statocysts (Bethe 1897 a and b). The surgical experiments were made by Bethe after he had gained a clear picture from his previous careful anatomical studies of the nervous pathways involved (Bethe 1895b). The results of his experiments which are relevant to the compensatory eye movements are summarised in Table 1.

The various operations which prevented the eye movements caused by passive rotation about both the vertical and horizontal axes led Bethe to conclude that the eyes, statocysts and visceral ganglia are important for the production of these movements. Of these three he regarded the statocysts as being the least important because removal of the globuli (figure 1), which he supposed from anatomical studies to be the integration centre for the statocysts did not impair the eye movements at all. At the time of Bethés investigation a controversy existed as to whether the statocysts, of the decapods, or otocysts as they were then called, were purely hearing organs (Hensen 1863), hearing and static organs (Delage 1887, and Bethe 1895a), or just static organs (Kreidl 1893, Clark 1896, and Prentiss 1901). Two types of sensory hairs had been found in the statocysts of Carcinus; long feather hairs and short hook hairs.

Hensen (1863) was of the opinion that the long feather hairs in the statocysts were undoubtedly for hearing and nothing else. A statolith was not found in Carcinus until 1956 (Dijkgraaf 1956a) and its apparent absence may have led some of the earlier workers to the conclusion that the organ was for auditory rather than static purposes.

TABLE 1.

	Static compensatory eye movements	Movements caused by passive rotation about a vertical axis	Eye movements during walking
1. **Eyes:**			
a. blacken both	weakened	weakened	no effect
2. **Statocysts:**			
a. remove one	weakened	weakened	no effect
b. remove both	greatly weakened	greatly weakened	no effect
3. **Neck Connectives:**			
a. cut one	asym. changed	sym. changed	sym. changed
b. cut both	changed	weakened	abolished
4. **Globuli:**			
a. remove one	no effect	no effect	no effect
b. remove both	no effect	no effect	no effect
5. **Brain:**			
a. slit ant. to mid.	abolished	abolished	no effect
b. slit post. to mid.	hardly changed	no effect	no effect
6. **Cellulae sup. med:**			
a. remove one	abolished	?	no effect
b. remove both	abolished	?	no effect
7. **Eyes and neck connectives:**			
a. blacken both and cut both	abolished	abolished	abolished
8. **Eyes and statocysts:**			
a. blacken both and remove both	abolished	abolished	no effect
9. **Neck connectives and statocysts:**			
a. cut both and remove both	abolished	abolished	abolished
10. **Optic tract:**			
a. cut through	weaken	no effect	no effect
11. **Oculomotor nerve:**			
a. cut through	abolished except for rot. about horiz. trans.axis	abolished	abolished
12. **Optic tract and Oculomotor nerve:**			
a. cut through both	abolished	abolished	abolished

The eye movements during walking are probably of ventral origin because they are less susceptible to the removal of the sensory input from the eyes and from the statocysts. The eye movements are also abolished when the oesophageal connectives are cut. Cutting through one oesophageal connective produces a symmetrical change in the eye movements and this suggests a certain amount of neural integration in the brain itself. However the brain lesion experiments have no effect (Table 1, No. 5a and b) showing that although neural integration takes place when one neck connective is cut, if both connectives are intact integration in the brain is not necessary for the production of symmetrical eye movements of this type. These eye movements are clearly to be linked in some way with locomotion.

Cutting through the oculomotor nerve was reported (Bethe 1897a) to abolish the fast retraction reflex but recent experiments have produced different results (Sandeman 1964a). Cutting the oculomotor nerves does, however, prevent all compensatory eye movements except the rotation of the eyes and eyestalks about a transverse horizontal axis which is produced by extraocular muscles, not innervated by the oculomotor nerve.

Cutting through the optic tract has little effect on the compensatory eye reflexes (Bethe 1897a) and this has been confirmed. However Bethe reports all eye reflexes to cease after cutting through both the optic tract and the oculomotor nerve. This does not agree with his finding that when the oculomotor is cut the eyes still respond

to displacement about a transverse horizontal axis and cutting through the optic tract alone does not prevent it.

The conclusions which Bethe drew from the surgical interference with the optic tract and the oculomotor nerve were that the optic tract contained both sensory and motor nerves and that the oculomotor nerve was purely motor. Electrophysiological recordings however, show the oculomotor nerve to contain both sensory and motor axons. Also surgical experiments alone can be misleading as it is impossible to judge whether the resultant behaviour of the denervated portion of the animal is due to the removal of excitatory and inhibitory commands or whether it is due to the removal of important afferent signals necessary for the accurate control of the appendage.

Electrical stimulation of the optic tract and oculomotor nerve (Bethe 1897a) caused the eye to move up and down and back and forth respectively, and Bethe concluded correctly that there were motor-fibres in the optic nerve. One can however gain no more from this type of experiment because apart from the confused picture which will be obtained by simultaneously stimulating antagonistic muscles, the muscle blocks controlling the movements of the eyes are probably each innervated by fast, slow, and inhibitor axons. Coincident stimulation of all these is of little value in determining the neuromuscular mechanisms involved.

The eyes and antennules of Carcinus rapidly retract if certain clearly defined areas of the carapace are mechanically stimulated and this was also described by Bethe in his extensive work. These areas of the carapace are innervated by the tegumentary nerve and are bounded posteriorly by ~~by~~ the cervical groove. Stimulation of the one side of the anterior portion of the carapace with a brush produces the retraction of the eye of that side and both antennules. Stronger mechnical stimulation causes the reflex to spread to the contralateral eye and to the ipsilateral antenna but never involves the contralateral antenna. Mechanical stimulation of the eyes themselves produces retraction of the eye and the ipsilateral antennule but not of the antennae or contralateral antennule. These findings of Bethe have been confirmed in this investigation.

Flashing a bright light into the eye can elicit a retraction of the eyes and both antennules. If the light is moved to one side, only the eye and antennule of that side retract. A dark object introduced into the visual field does not produce such a remarkable effect and a small dark object has to be moved vigourously in order to have any effect at all. The antennules are themselves not sensitive to photic stimulation.

The withdrawal of the eyestalks in some crabs results in a disorientation of the ommatidia with relation to the environment and this has led Wiersma and Bush (1963) to postulate a need for a central adjustment of the visual input during retraction. No further information is available on this topic.

Bethe observed a number of other reflex activities of Carcinus but none of these involve eye movements.

The production of optomotor movements by rotating a vertically striped black and white drum horizontally around a stationary animal was first used by Radl (vonBuddenbrock 1952) on insects. The animals were found to turn either with or against the movement of the drum. Demoll (1909) used this method in his survey of the orientation abilities of Squilla mantis and reported the slow and fast phases of optokinetic nystagmus.

Squilla shows compensatory eye movements when displaced about the horizontal axis but the control of these eye movements has not been investigated. The main interest has been centred on the ability of the animals to orientate themselves with respect to gravity, for Squilla, unlike the decapods, do not appear to have static sense organs. It has been suggested that vesicular structures on the carapace could serve this purpose (Schiff 1963) but this statement is not borne out by experimental or anatomical evidence. Demoll showed that the animals take on an unusual stance if the eyes are blinded or removed and although he could find no trace of a static sense organ he was of the impression that one existed. No definite and satisfactory answer has been supplied as to what extent the eyes are involved in the orientation of this animal.

It has been suggested ~~that~~ (von Buddenbrock 1914) that they orientate by way of a general awareness of their position relative to gravity through contact of the limbs with the ground and also by the relative position of the long and pendulous abdomen.

The eyes of Squilla are thought to provide the animal with stereoscopic vision (Schaller 1953) which aids the animal in the capture of its food. When prey is sighted the eyes both assume a distinctive attentive posture and fixate on the prey until the capturing strike is made with the pair of raptorial thoracic appendages. The nervous control of these eye movements has not been investigated but it has been suggested by the author (Sandeman 1964b) that the importance of the eyes in the accurate control of the capture strike has been over-emphasized. It is said that Squilla is able to strike less accurately if unilaterally blinded (Schaller 1953) but the strike is never made before the long antennules have been extended towards, and gently touched the prey. This tactile link with the prey before striking may be of twofold importance to the animal. First to establish the acceptability of the prey and secondly to gauge more accurately the relation of Squilla to its prey, which can only be done through the proprioceptor mechanisms of the antennules because of the apparent absence of such mechanisms in the eyes (Sandeman 1964b).

Further evidence of the non-importance of eye proprioceptors in crustacean eyes has been suggested by an experiment of Schöne (1952).

Increased illumination on one side of a shrimp causes the stalked eyes to compensate by tilting towards the light so that the normally dorsal-facing ommatidia are nearest the greatest light source. Similarly the blinded eye of a unilaterally blinded shrimp will change its position relative to the carapace if the seeing eye is supplied with the appropriate photic stimulus, even if the seeing eye is fixed in an abnormal position relative to the carapace. Schöne's experiments were concerned with the orientation of the animal and not the control of the eye movements, but his results show that proprioceptive mechanisms, which monitor the position of the eye relative to the body, are unheeded in this animal.

The pointing or "signal reflex" of hermit crabs and shrimps also shows the same independence of forced eye displacement. In these animals one or both eyes can be tied up into unnatural positions so that the normal ventral-facing ommatidia face forwards. When an object is now presented, the antennae on the contorted side, which normally point directly at objects brought into the visual field, now point downwards, to the region from which the ommatidia nearest the object would normally receive visual stimulation, and ignore possible proprioceptive information from the changed position of the eyes.

A new interest in the optomotor movements of insects and eye movements of the decapods was inspired by the work of von Holst and Mittelstaedt (1950), and their formulation of the "re-afference principle".

This was an attempt to provide an explanation for the ability of of animals to distinguish between apparent environment movement induced by the movement of themselves, and actual movement of the environment. An example of this ability is provided by the following experiment: A fly is placed in the centre of a striped drum and passively rotated within the stationary drum or alternatively the drum is rotated around it; the insect responds to the relative movement of the stripes by turning itself in the same direction, so tending to reduce the relative movement of the stripes. If this is all, one may ask how the fly ever turns normally, for any movement which it makes will immediately tend to produce an apparent environmental movement in the opposite direction. The only previous interpretation suggested that the optomotor response was inhibited in actively turning animals. However Mittelstaedt (1949) showed that a fly with its head turned through 180 degrees and fixed in this position will continue to turn in one direction or another once started, and there is no evidence of the inhibition of the optomotor response induced by the animals own movements. Visual inversion experiments with fish (Sperry 1956) have produced the same results.

The re-afference principle supposes the existence of a central mechanism which anticipates the visual change ensuing when the animal initiates its own movement. The hypothesis supposes that this "anticipated" visual change or "efferent copy", neutralizes the resultant "re-afference" visual information induced by the turning and the animal perceives a stationary environment.

If the re-afference is not exactly neutralized, an additional correcting efferent order is emitted. The re-afferent principle has been applied in most cases to the optomotor reaction but is particularly relevant to eye movements. There is so far no electrophysiological or anatomical evidence of a neural mechanism of the kind proposed by the re-afference principle.

The validity of the re-afference principle was questioned by von Buddenbrock and Moller-Racke (1953) in the light of their own experiments with beetles, and also earlier experiments on Carcinus by Wolter (1936) who had induced the crab to run, facing outwards, around the inside of a round glass dish surrounded by a stationary striped drum. The resulting eye movements were the same as those which were induced by rotating the drum around a stationary animal. Also cinematography (von Buddenbrock et al 1954) showed that when Carcinus actively turns about a vertical axis in normal contrasting surroundings the eyes perform compensatory movements in which slow and fast phases appear. These eye movements were irregular in blinded animals or animals which turned in surroundings with no visual contrast, and the eye movements were therefore assumed to be optomotor reactions. This suggested that Carcinus induced optomotor eye reactions by its own movements.

In answer to these criticisms Dijkgraaf (1953) suggested that in Wolter's experiment the eye movements were caused by the "passive rotatory" movement imposed upon the animal when it was made to run around the inside of the round glass dish. Dijkgraaf (1955 and 1956b) also applied cinematographic techniques to actively turning decapods

and showed that although the eye movements of actively turning Carcinus are impeded by blinding the animals, they are not changed as von Buddenbrock and his co-workers suggest. In Palinurus, blinding the animals makes no difference to the eye movements. He suggests that these movements are not optomotoric reactions and explains the anomalous results of von Buddenbrock to be due to the experimental animals being either damaged or upset. Similarly he dismisses all other cases where optomotor effects are apparently produced by the animals' own movements as being artefacts and products of the abnormal experimental conditions.

The compensatory eye movements were then subjected to a thorough investigation by Dijkgraaf (1956b) who compared his conclusions with those of Bethe. Eye movements induced when he turned the animal about horizontal axes agree with those reported by Bethe, but he reaches a different conclusion on the importance of the statocysts in the production of the eye movements which occur during the passive rotation about the vertical axis. Passive rotation of the blind animals produces eye movements (Dijkgraaf 1956b) but not after the statocysts have been removed. The statocysts are therefore regarded by him to be the most important factor in the production of the compensatory eye movements. In other experiments (Dijkgraaf 1956a) he showed that the long "feather" hairs in the statocyst are sensitive to angular acceleration and are responsible for the sensory input which elicits the eye movements.

According to Dijkgraaf, Bethe's erroneous statement that the statocysts "... were not important in the production of the eye movement" could only have been made by his not investigating the reflexes of blinded crabs which were still in possession of their statocysts. This is untrue as Bethe clearly states that animals which are only blinded but still possess statocysts behave normally on the turntable. Bethe's incorrect conclusion stems from his relying on the experiment in which he removed the globuli and found no change in the compensatory ability of the eyes.

The eye movements of the crabs during walking, reported by Bethe, appear at first sight to be the same as those occurring in actively turning crabs described by von Buddenbrock and Moller Racke (1953). However Bethe describes the movements as a "swinging" of the eyes and states that there is no slow and fast phases. Also he did not observe these movements to occur only during the active rotation of the animal about a vertical axis. Dijkgraaf reports (1956b) that he has observed both types of movement; the slow and fast phasic eye movement during active turning, and the swinging movements of the eyes during walking. He remarks that both are centrally initiated and do not depend on external sensory input for their production as do the other compensatory movements, even though they are slightly impaired by blinding. The functional significance of these eye movements remains obscure and will be considered further in the discussion.

Section II

Investigations in which the optomotor response has been used as a tool to study the visual perception of movement and the properties of the photoreceptors

Optokinetic nystagmus of Carcinus was used to test their visual perception of colour (Schlieper 1927) but he found that they did not react to a rotating pattern of alternating grey and coloured stripes. This work was repeated by von Buddenbrock and Friedrich (1933) who used coloured stripes of equal relative brightness and found that Carcinus could distinguish between yellow and blue. In the same way Schlegtendal (1934) found Crangon crangon and Palaemon squilla to be specifically colour sensitive.

The visual acuity of a number of animals was tested by using the optomotor method (Hecht and Wolf 1929; Hecht and Wald 1934; Clark 1935) and the resolving power of the compound eyes of the bee and beetle Chlorophanus was found to correspond with the smallest interommatidial angle (Hassenstein 1951 and Varju 1959). It was concluded from this (Reichardt 1962) that the effective fields of vision of the ommatidia do not overlap, but other reasons could lead to the same result. However it has been shown that the light from a point source is absorbed by many rhabdomes in the compound eye of the bee (de Vries unpublished). Reichardt (1962) regards these finding to be in conflict and suggests that the solution may lie in lateral neural inhibition of the same type which is found in the eye of Limulus (Hartline, Wagner and Ratliffe 1956).

Lateral nervous connections in the compound eyes of Musca have been described (Meyer 1951) but this work is inconclusive and no pathway for lateral inhibition has been found in the eyes of insects, although there are many paths available in the optic lobes. These conclusions are relevant to the consideration of movement perception.

The analysis of movement perception by the compound eye was studied by Hassenstein (1951) who used an ingenious Y-maze globe to test the optomotor reactions of the beetle Chlorophanus. The beetle was suspended by its thorax and allowed to hold the Y-maze globe in its feet. In response to suitable stimulation the insect "walked" around the Y-maze globe so presenting itself every few paces with a choice of "turning" either to the left or right. Single adjacent ommatidia were stimulated by using an optomotor arrangement of three concentric drums, and the optomotor response was measured by noting which way the suspended beetle turned the Y-maze globe.

The most elementary stimulus needed to produce an optomotor response is the successive stimulation of two adjacent, or subadjacent ommatidia. Successive stimulation of ommatidia further apart than this produces no optomotor response. The optomotor reaction is therefore produced by the physiological interaction of the after-effect of one ommatidium with the effect on the other. Alternating stimuli gave an opposite or negative optomotor effect. From these results Reichardt (1962) was able to produce a mathematical model of the nervous integration mechanisms of the beetle eye. This model successfully predicted the results of a number of different optomotor stimuli which were applied to the insect.

The perception of movement by flying bees was investigated by measuring the torque exerted by the suspended flying insect around the vertical axis, while optomotor stimuli of different intensities were applied (Kunze 1961). Fermi and Reichardt (1963) used the same technique to study the properties of the photoreceptor mechanisms with reference to the absorption of light quanta by the eyes of Musca.

In all the above cases the insect's head and eyes were artificially fixed in relation to the body during the experiments so that the optomotor response was not complicated by optokinetic nystagmus.

Section III

Electrophysiological studies

Electrical responses in the central nervous system of the arthropods, corresponding to photic stimulation of the compound eyes, have been known since the work of Hartline and Graham (1932), but electrical responses related to the visual perception of movements were not noticed until Burtt and Catton (1954) recorded these from the ventral cord of the locust. Later the same type of response was recorded from single nerve units by means of microelectrodes placed in the locust optic lobes (Burtt and Catton 1956). Electrophysiological methods show the eyes of insects to be sensitive to smaller movements of the visual field than had been previously reported by investigators using behavioural techniques. It has been suggested (Burtt and Catton 1959) that the threshholds of visual acuity obtained by the previous workers were the thresholds for the whole behavioural response and not necessarily for the visual apparatus.

Also the compound eye of the locust is more sensitive to a moving point source of light than to a pattern of stripes.

Recordings of single nerve units in the "optic nerve" of Podophthalmus vigil showed the presence of a number of visual and non-visual responses (Wiersma, Waterman and Bush 1961). The visual units respond to a variety of moving and still optic stimuli and are classified by their response to (i) wide or small visual fields (ii) types of visual stimulus eliciting maximal response, and (iii) the amount of contrast necessary for maximal stimulation.

Nerve fibres carrying information to the eye can respond also to visual stimulation of the other eye and to stimulation of hairs and joints of the body. From this information Wiersma and co-workers make the point that not only are the optic lobes an important portion of the central nervous system, but, because the animal still reacts normally to non-visual stimuli without the eyes and optic lobes, parallel integration takes place in different parts of the central nervous system.

A further investigation of the visual and non-visual responses from the optic peduncle of various decapods (Waterman and Wiersma 1963) showed visual responses from (i) movement sensitive fibres which respond to a moving object but not to flashes of light, (ii) units which respond only to "on" or "off" photic stimuli, and (iii) "sustaining" units which fire continuously during a maintained photic stimulus. Evidence is provided for the ability of some of the sustaining units to respond to stationary objects in their visual field;

for example, if a white card was placed in front of the eye which had been looking at a black environment, the sustaining unit fired continuously until the card was removed. The possibility that the unit was responding to a greater amount of light reflected by the white card seems to have been overlooked. No figures of the sensitivity of the movement neurones are available from these studies.

The responses from three non-visual types of neurone were recorded from the optic peduncle and found to be efferent in nature (Waterman and Wiersma 1963). Two types respond to the movement of the eye during optokinetic nystagmus. Type 1 correspondingly increases its frequency of discharge with the progression of the slow phase of nystagmus and is completely inhibited during the fast phase. Type 2 fires only during the fast phase. Type 3 termed "efferent mechanoreceptor", responds to movements of the legs and may be involved in the control of afferent mechanisms in the eye.

Five types of interneurones in the oesphageal connectives, sensitive to mechanical stimulation of the eye, had previously been described in the cray-fish Procambarus clarkii. (Wiersma 1958). Four of these respond to tactile stimulation of the eye and one to flexion of the eyestalk joint. The tactile types are sensitive to mechanical stimulation of ~~the~~ (i) the homolateral corneal surface, (ii) the hairs on and around the eyestalk, (iii) the eyestalk hairs and the hairs on the flagellum of the homolateral antennule and antenna, and (iv) the hairs around the eyes, more particularly ~~to~~ the region between the rostrum and anterior carapace.

The fifth type responded phasically to the backward flexion of the eye joint, which is of particular interest in any consideration of the eyestalk movement because it immediately suggests the possibility of proprioceptive control of the eyestalk. However in these experiments the eye was not blinded and the investigations on Carcinus show that displacement of the eye can cause an apparent movement of the visual field and subsequent activity of visual movement neurones. A proprioceptor which gives a maintained discharge to a maintained displacement of the eye has not been found.

Section IV

Anatomical accounts.

The anatomy of the nervous system of the Crustacea has been well investigated. Undoubtedly Bethe(1895b and 1897a and b) has contributed most to the knowledge of the central nervous system of Carcinus by revealing with methylene blue vital staining techniques a number of different types of motor-, sensory-, and inter-neurones in the brain and ventral ganglia. Of the twenty different types of neurone which he found in the optic ~~nerve~~ tract, three had their cell bodies in the brain, and the remainder were presumed to have their cell bodies situated in the optic ganglion. One motor and one sensory neurone crossing from one optic ganglion to another are described. These fibres could account for the responses observed by Wiersma, Waterman and Bush (1961) but no doubt there are many others.

The oculomotor nerve has two types of motor neurones with cell bodies in the cellulae superiores laterales and in the cellulae inferiores mediales respectively. After lesions in these areas the eye movements did not appear.

The anatomy of the central nervous system of the Crustacea has been extensively studied by Hanstrom (1931, 1933, 1934a, 1934b, 1936, and 1948) and he also reviewed the previous work in this field.

The investigation of the peripheral innervation of the crustacea has been relatively neglected and where studies have been made these are of insufficient detail (Heath 1941). No detailed account of the head nerves of Carcinus has been produced and the nervous supply to the eye muscles has been described only for the shrimp Penaeus (Young 1956).

The musculature of the American blue crab Callinectes, was described by Cochran in 1935 and is found to be similar to that of Carcinus.

The numbers of axons contained in the optic tracts of crayfish have been found to be considerable by the application of the techniques of electron microscopy (Nunnemacher, Camougis, and MacAlear 1962), and details of the sheath structure of single crab axons have been shown in electron microscope studies (Horridge and Chapman 1964)

Section V

Optokinetic nystagmus.

A clear distinction between the optomotor response and optokinetic nystagmus can be drawn. In the former, elicited by the rotation of a striped drum about the animal, the animal turns its whole body either in, or opposite to, the direction of the moving drum; the movement is slow and continuous in the one direction for a maintained stimulus.

Optokinetic nystagmus, although elicited by the same stimulus, is a response which involves the eyes only, in animals with stalked eyes, or the eyes and the head only, in animals with the eyes fused to the head. It is always characterised by a slow movement of the eyes or head in the direction of the moving drum followed by a quick flick of the eyes or head back to the original starting position. There has been no previous work on the central nervous control of optokinetic nystagmus in any invertebrate.

Partial reduction of the visual field prevents optokinetic nystagmus in Carcinus due to the various eye areas being differentially sensitive to movement (von Buddenbrock and Friedrich 1933). Optokinetic nystagmus is similarly prevented in Uca but because of the visual astigmatism of the compound eye of Uca, horizontal reduction of the field of view is more effective than vertical reduction (Kunze 1963). Differentiation in the sensitivity to movement of the different eye areas has also been observed in water beetles (Ludtke 1938,) Anax (Wolf 1942) and Goniopsis (Waterman and Barber 1955, unpublished.)

Little else has been reported on the optokinetic nystagmus of arthropods although this behaviour is being investigated in the Locust (Thorsen unpublished).

In mammals the control of optokinetic nystagmus has been more extensively investigated. Motor nerve impulses corresponding with fast and slow phases of the compensatory eye movements of cats, recorded by MacIntyre(1939), showed the onset of the fast phase to be independent of peripheral proprioceptive control mechanisms.

The presence of proprioceptors in the eyes of mammals was at first denied on behavioural evidence. They have since been demonstrated by histological techniques, although there is no satisfactory explanation of their function.

Optokinetic nystagmus in Carcinus is probably never elicited during its normal life but fast and slow eye movements do occur naturally when the animal turns itself about a vertical axis. The fast and slow phases of optokinetic nystagmus mimic this natural response and can be more easily studied because they are elicited by controllable visual stimuli. The stalked eyes of the crab provide a unique preparation for the study of optokinetic responses as the receptors are borne on the effector organ, the nervous pathways are accessible, and additional feedback mechanisms concerned with the proprioceptive control of the locomotory appendages, and involved in the optomotor responses of insects, are excluded.

MATERIAL AND METHODS

Carcinus maenas, the common shore crab, has been used in all the experiments. This animal is ideal for the study of optokinetic nystagmus because (i) the animal in its natural state spends long periods of time out of the water, (ii) the widely separated eyes have long optic tracts and oculomotor nerves extending from the brain, (iii) the shape of the animal and its hard carapace make it easier to mount within a drum, and (iv) the preparation requires no especial care as to saline, oxygenation or cooling and with the techniques described below the activity of single nerve units can be observed for several days.

Most of the experiments work as well with the animal out of water as in it. Animals of between 6 and 8 cms. across the widest portion of the carapace are used in the experiments but a number of animals had to be rejected because normal eye movements were prevented by the presence of small ecto-commensal bivalve molluscs within the eye sockets.

Histological sections of the cuticular receptors of the eyecup have been prepared from crabs which have just moulted and in which the exoskeleton has not yet hardened. These specimens are preserved in a mixture of sea water and Bouin's fixative and after appropriate dehydration, embedding, and sectioning are stained with Heidenhain's Iron Haematoxlin.

The musculature of the eyecup and eyestalk can be best observed in specimens which have been fixed in sea water-Bouin's and then transferred to 70% alcohol. To facilitate dissection of the small hard eyecup it is embedded in a wax dish and the outer exoskeleton carefully removed with a dental drill without damaging the endothelial tissue. The dissection of the muscles after removal of the exoskeleton is carried out with fine forceps.

To stain the axons in the eyestalk and in the eyecup regions, about 1cc of 1% solution of methylene blue diluted with 1% sucrose solution (1:1), is injected into the eye. The sucrose prevents the methylene blue from crystallising out in the blood stream. One to three hours after the injection the animal is dissected and the appropriate regions exposed to allow oxidation of the leuco dye. Alternatively, well dissected specimens are soaked in a very dilute solution of methylene blue (10 drops of 0.1% methylene blue in

in 100ccs of sea water). The only fixative which can be used with methylene blue is ammonium molybdate, and as this is unsatisfactory for thick whole mounts, diagrams of the nervous system have been made from the freshly stained and unfixed preparations. The complete innervation of the eye muscles can not be worked out from any single preparation and a complete picture has to be built up from a large number of dissections. Permanent preparations of small portions of tissue are made by pinning the specimen out in a wax dish and fixing it for 12 hours in ammonium molybdate, dehydrating, and then clearing and mounting in xylene Dammar.

Thin sections ($\frac{1}{2}$ mu) of the optic tract and the oculomotor nerve are cut with a glass knife on an ultra-microtome after fixing portions of the freshly dissected nerve bundles in osmic acid and then embedding them in araldite. These sections are stained with Toluidine blue.

In experiments on the retraction reflex or the optokinetic responses, the crabs are held firmly in a screw clamp which grips them on either side of the carapace, dorsad to the bases of the legs so that their movements are not impeded but at the same time the carapace, brain, and nerves of the head are stationary. Optokinetic nystagmus is elicited by rotating a drum, with black and white vertical stripes on the inside around a glass tank filled with sea water in which the animal is suspended. Stripes 3.5 cms wide and at a distance of approximately 15 cms from the crab's eyes provide an adequate stimulus and are used throughout. A kymograph provides an adjustable smooth drive. The stimulus is monitored by small metal contacts placed on the drum in

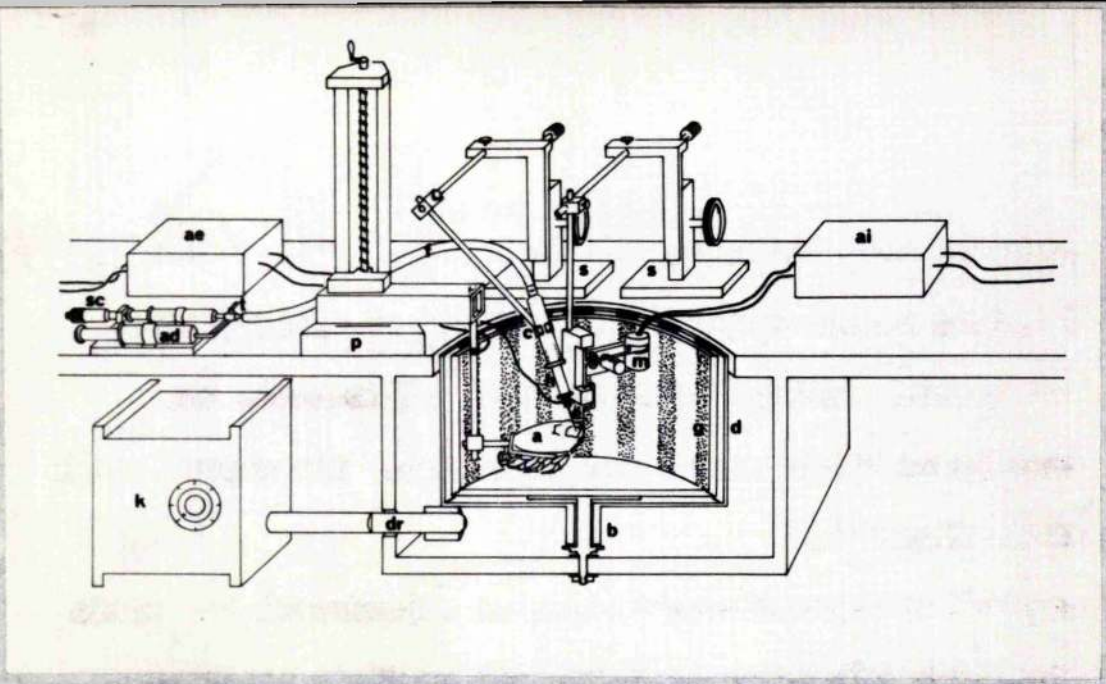
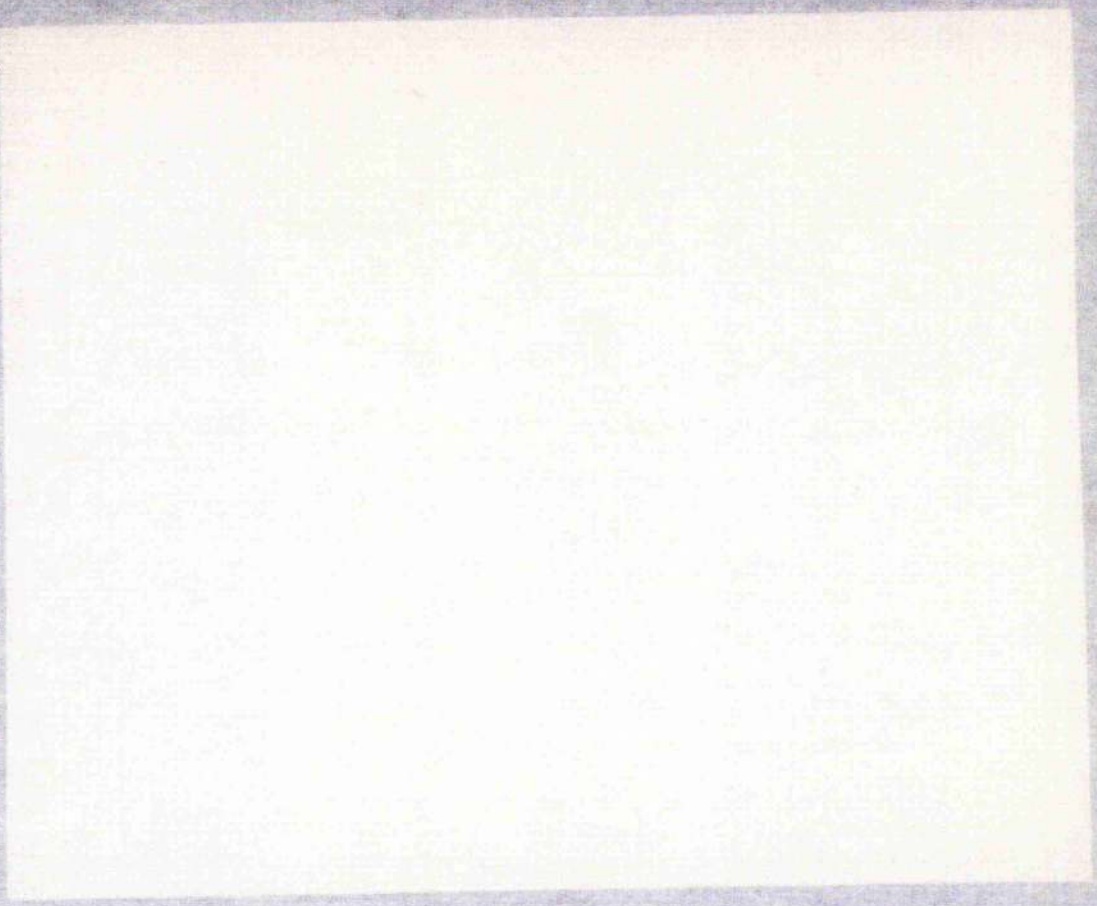


Figure 2. The experimental set-up for the investigation of optokinetic nystagmus. The crab (a) is firmly clamped to the adjustable stand (p) and lowered into a glass dish (g) around which a striped drum (d) is rotated. The dish and the drum are both supported on a bearing (b) which allows the drum to be driven round by the shaft (dr) of the kymograph (k) without disturbing the dish. The slave unit of the hydraulic electrode advance (h) with its electrode (e) is attached by a spring clip (c) to a micromanipulator (s), and a second micro-manipulator supports the eye movement monitoring apparatus (m). The outputs from the amplifier units for these (ae, ai) are fed into an oscilloscope. The control unit for the hydraulic advance (ad) with its micrometer screw (sc) and three-way tap (t) are connected to the slave unit by means of the flexible polythene pipe (f). Prior to electrical recording experiments, enough sea water is run into the dish to cover the animal.

in positions coinciding with the stripes. Movement of these contacts over two small spring strips completes an electrical circuit which records the drum speed. Diffuse overhead light illuminates the stripes and there is no vibration of the apparatus. The experimental set-up is shown in figure 2.

In the surgical and preliminary recording experiments the optic and tract and the oculomotor nerve are exposed by first removing a portion of the dorsal carapace above the brain and then dissecting in the body cavity taking care not to damage either the gut or the main blood supply to the brain and eyes. However, this procedure is adequate only for short term or preliminary experiments because preparations made in this way soon deteriorate if not carefully perfused. Even so, using this method, the initial recording experiments require an electrode which will record the two way flow of impulses in short uncut nerves in situ beneath the surface of the sea water around the animal. To achieve this a silver wire of 50 mu diameter is fused at the tip forming a small ball approximately 0.25 mm in diameter. The wire is threaded through thin polythene tubing which is predrawn to 0.3 mm inside diameter, leaving the ball just within the end of the tube. In operation the ball and its polythene sheath are lowered onto the nerve and liquid paraffin is forced down the tube with a syringe. The paraffin flows around the ball and on the surface of the nerve forming an insulating curtain about the recording electrode (figure 3). The surrounding sea water is earthed giving



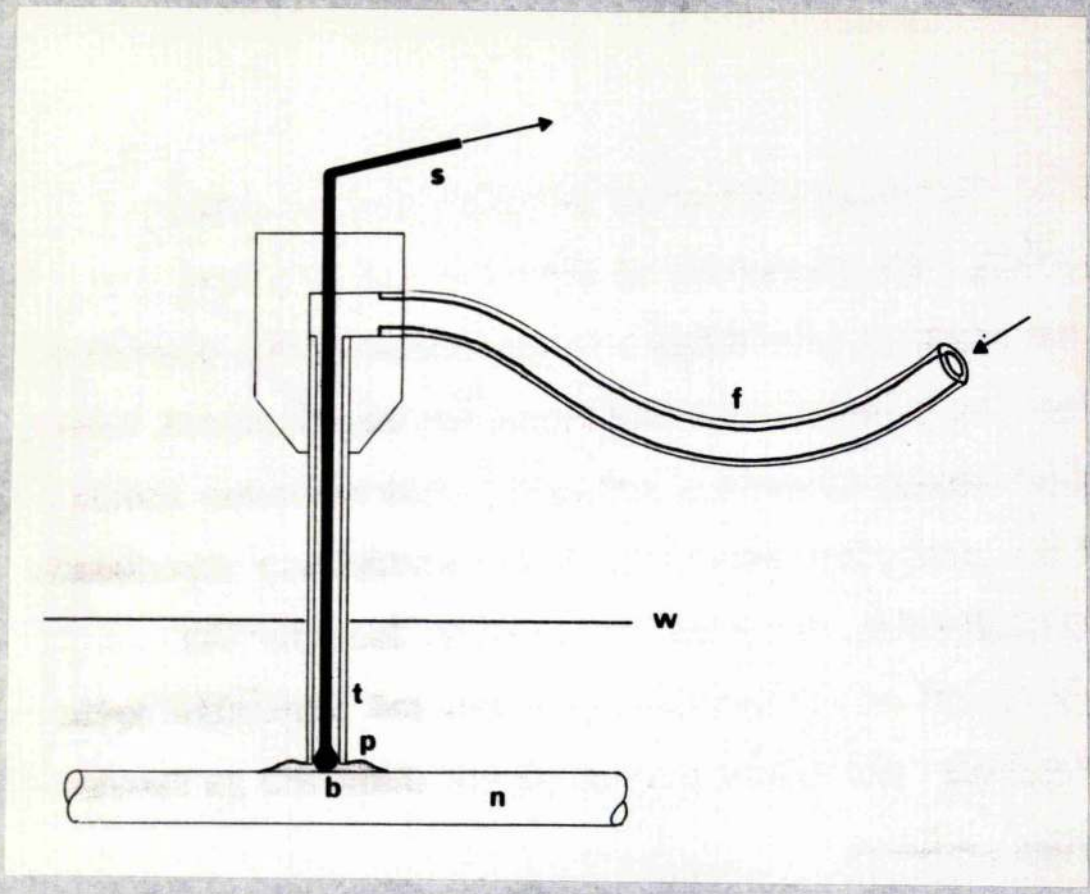


Figure 5. The silver wire electrode. A silver wire (s) contained within a polythene sheath (t) and with its end fused to form a ball (b) is lowered onto the nerve (n) which is below the level of the surrounding liquid (w). Paraffin is pumped down the flexible pipe (f) and flows out on the surface of the nerve (p), so insulating the electrode tip from the earthed surrounding medium.

relatively stable electrical conditions in which movement artefacts are short circuited. Two electrodes of this type can be placed along the length of the nerve so permitting a determination of the direction in which the impulses travel. Hook electrodes can not be placed under the nerves without severe dissection and optokinetic nystagmus invariably fails if the nerves are stretched. After preliminary experiments with the silver electrodes, which are essential to discover the characteristic response of the intact but exposed and identified optic and oculomotor nerves, the silver electrodes are abandoned in favour of stainless steel needles.

Stainless steel electrodes are made by electrolytically sharpening O size insect pins, and then insulating them to the tip with I.C.I. air drying insulating varnish (No. F168/585). The head ends of the pins are crimped and then forced into Luer Lok hypodermic needle bases from which the fine bore needle has been removed. Once mounted in this base the electrodes are easily handled during the sharpening and coating processes. The bases also provide a quick and convenient coupling mechanism between the electrodes and the micro-manipulator.

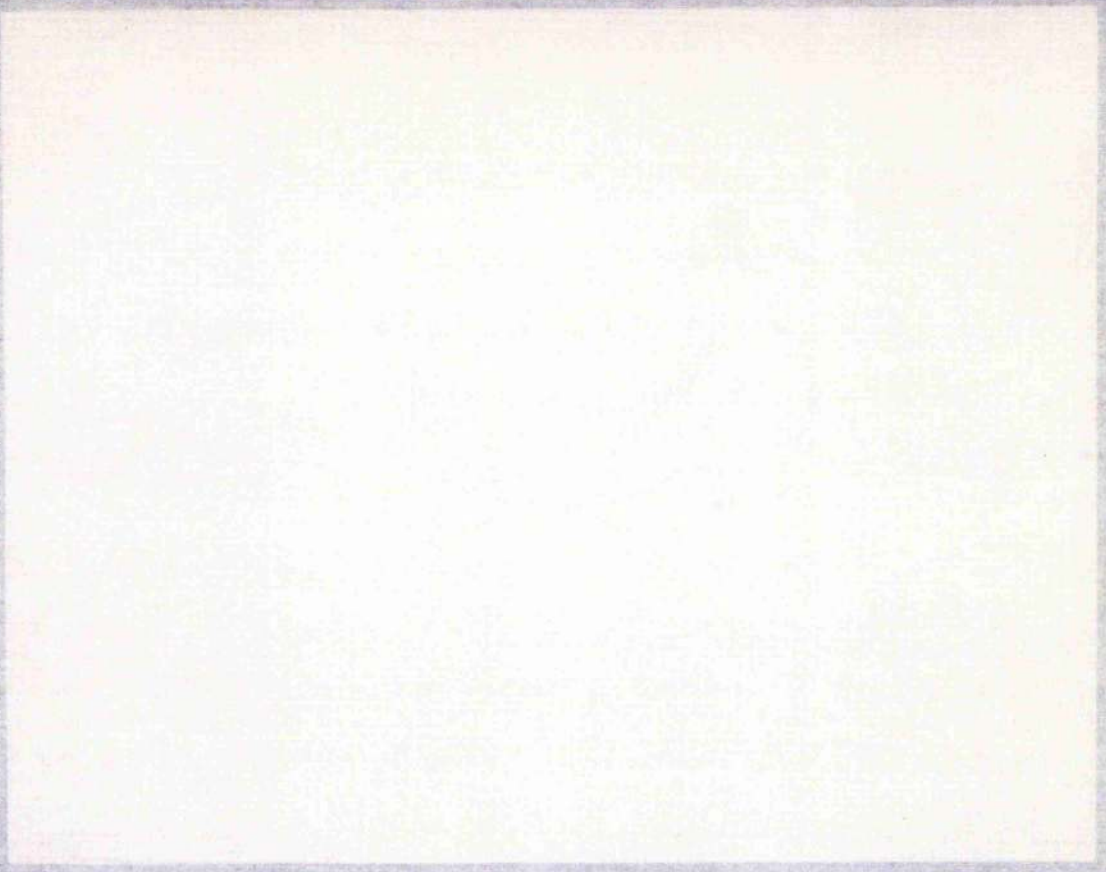
The electrolytic sharpening is achieved by immersing a $\frac{1}{4}$ inch diameter brass electrode and the stainless steel insect pin in a bath of concentrated hydrochloric acid and applying to them an alternating current of five volts. In this way the stainless steel pin is rapidly and evenly eroded. The shape of the electrode tip is controlled by withdrawing the needle from the acid at different speeds;

a slow withdrawal producing a finely tapering tip and fast withdrawal a more rapidly tapering one. The corrosive fumes caused by the rapid erosion of the stainless steel are controlled to some extent by covering the surface of the acid with a layer of xylene. Direct current does not erode stainless steel evenly.

The electrodes are coated with insulating varnish after cleaning them in distilled water, alcohol, and then varnish thinner. Lowering them tip first into the insulating varnish, and slowly withdrawing them from the unthinned laquer ensures an even coating. The electrodes are then placed with their tips uppermost in an oven at 50°C for ten minutes before applying a second coat of varnish. After the second coating and subsequent baking they are ready for use. In most cases the varnish dries away from the tip of the electrode, but if this does not happen it is possible to expose the bare metal by carefully pushing the tip against a rubber bung, controlling the movement with a micro-manipulator and observing the process through a microscope. If the needles become bent the varnish can be dissolved away with thinner and the needle resharpened and recoated. An electrode cannot be used more than once without re-sharpening and revarnishing. The best type of electrode for recording from the optic tract and oculomotor nerve has a fairly rapid taper and a final tip diameter of approximately 3 to 5 mu.

The stainless steel electrodes have a resistance greater than one megohm so that it is necessary to employ a cathode follower input, but the advantage in using steel needles is that apart from the initial removal of portion of the dorsal carapace, as described below, no dissection of the crab is necessary and loss of blood by the animal is prevented.

Preparation of the crab for electrical recording experiments is achieved in the following way: A small dorsal portion of the carapace is removed by first carefully cutting through the exoskeleton with a dental drill and then prizing up the piece of exoskeleton without damaging the underlying tissue. Blood pressure in the haemocoel of the crab often forces the endothelium upwards after the carapace has been removed, and before probing with an electrode a small plastic plate is placed within the posterior half of the cavity to depress the bulging tissue. The brain and the eye nerves are now protected only by muscle and connective tissue but the crab survives as well as an intact animal. The stainless steel electrodes are driven through the soft dorsal tissues and impale the optic tract or oculomotor nerve. In practice the optic tract or oculomotor nerve is first located by using an electrode with a large tip diameter which will not be ruined if it is accidentally driven into the carapace beneath the nerves. Once the position and relative depth of the nerve has been ascertained the large electrode is replaced by a finer tipped needle which will record from a more restricted area. Previous experience with the silver electrodes makes it possible to identify, by its characteristic response, which of the unseen nerves is impaled in each instance.



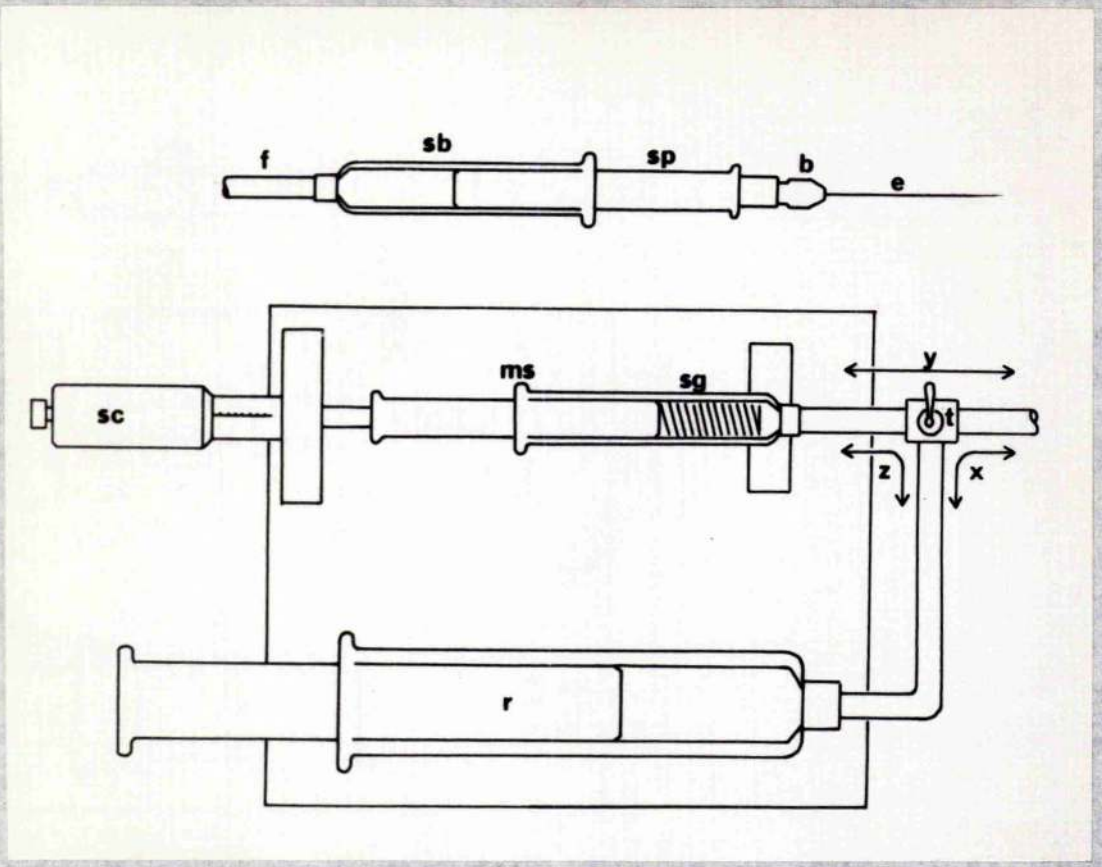
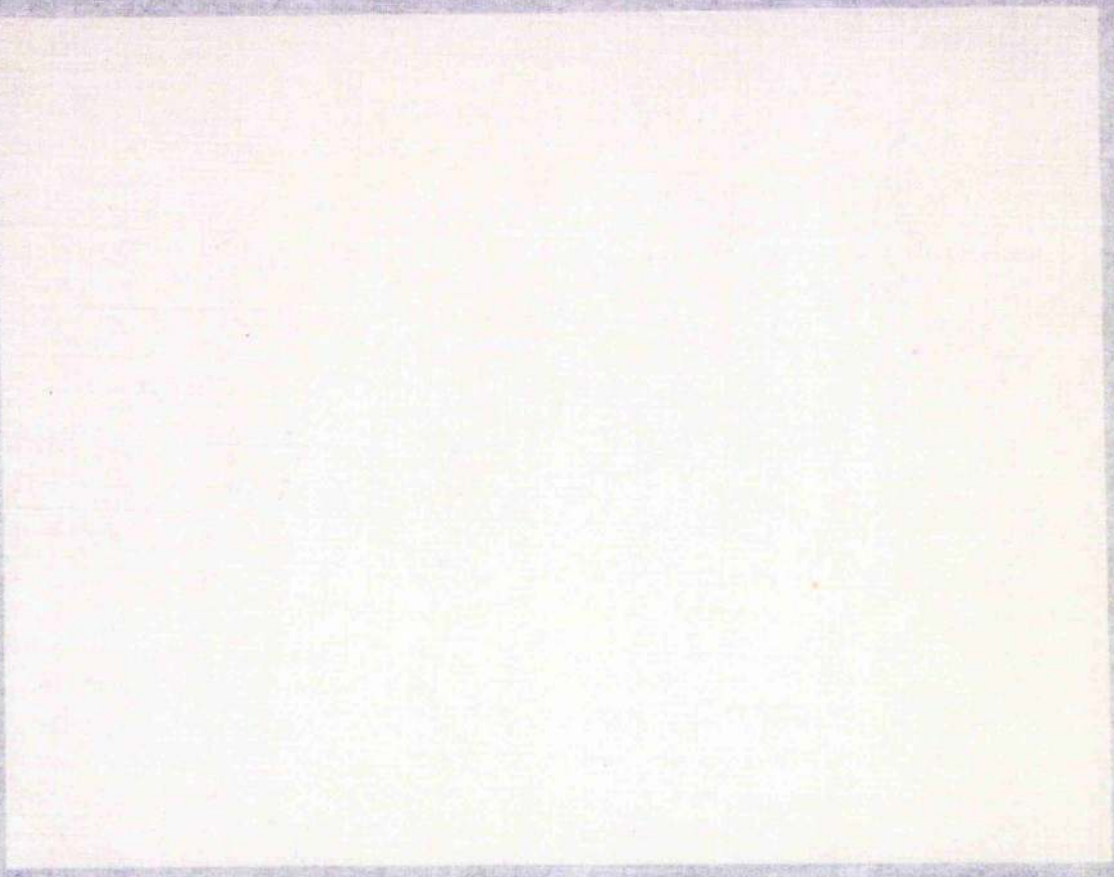


Figure 4. The hydraulic electrode advance. A stainless steel electrode (e) with its "Luer Lok" base (b) is attached to the plunger (sp) of the slave unit syringe. A flexible pipe (f) connects the barrel of the slave unit syringe (sb) to the master unit and the whole system is filled with liquid paraffin. Coarse movements of the electrode are made by connecting (x) the slave unit to the large reservoir syringe (r) through the three-way tap (t) and then depressing or withdrawing the plunger of the reservoir syringe. Fine movements of the electrode are made by connecting (y) the slave unit to the master syringe (ms) through the tap and then turning the screw of the micrometer (sc) which acts on the plunger of the master syringe. Should the micrometer and the master syringe reach the end of their traverse, and further advance of the electrode is required, the master syringe can be refilled (z) from the reservoir without moving the electrode. The internal spring (sg) holds the plunger of the master syringe against the micrometer screw. It is essential to keep the system completely free from air bubbles and so ensure the direct and accurate transfer of movement from the master syringe to the slave unit and electrode.



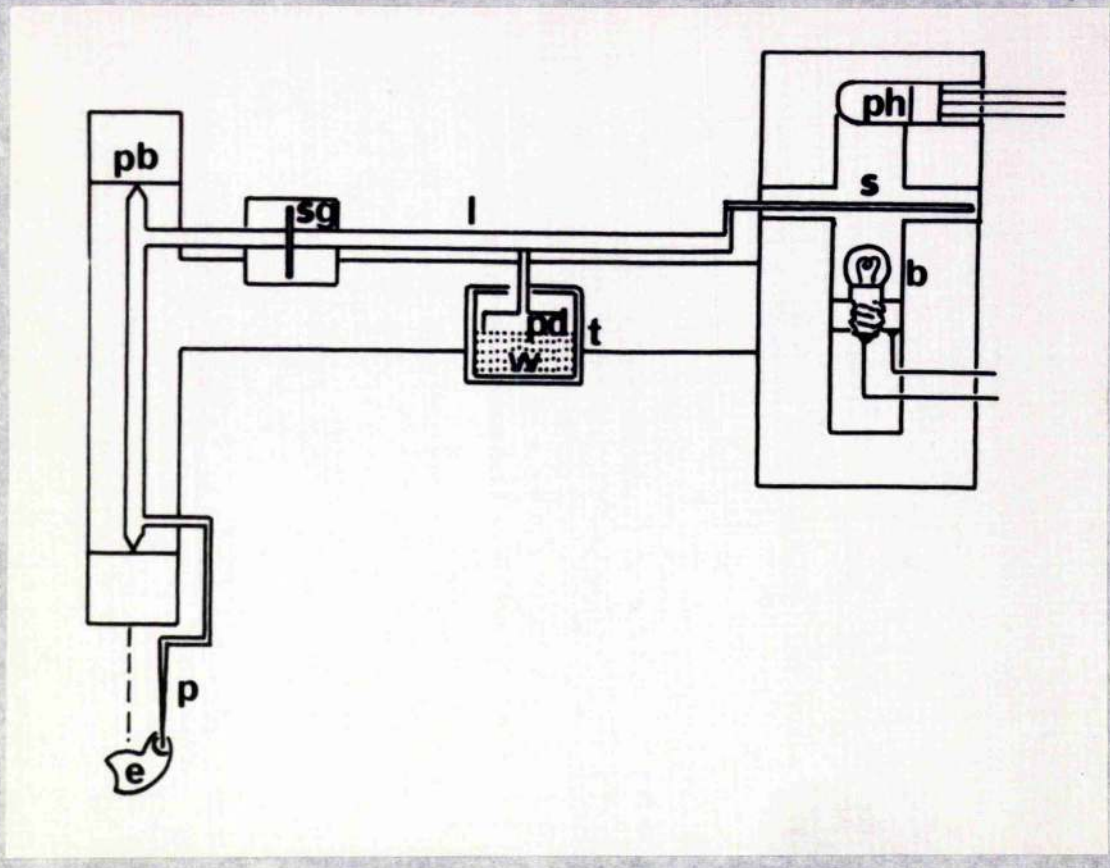
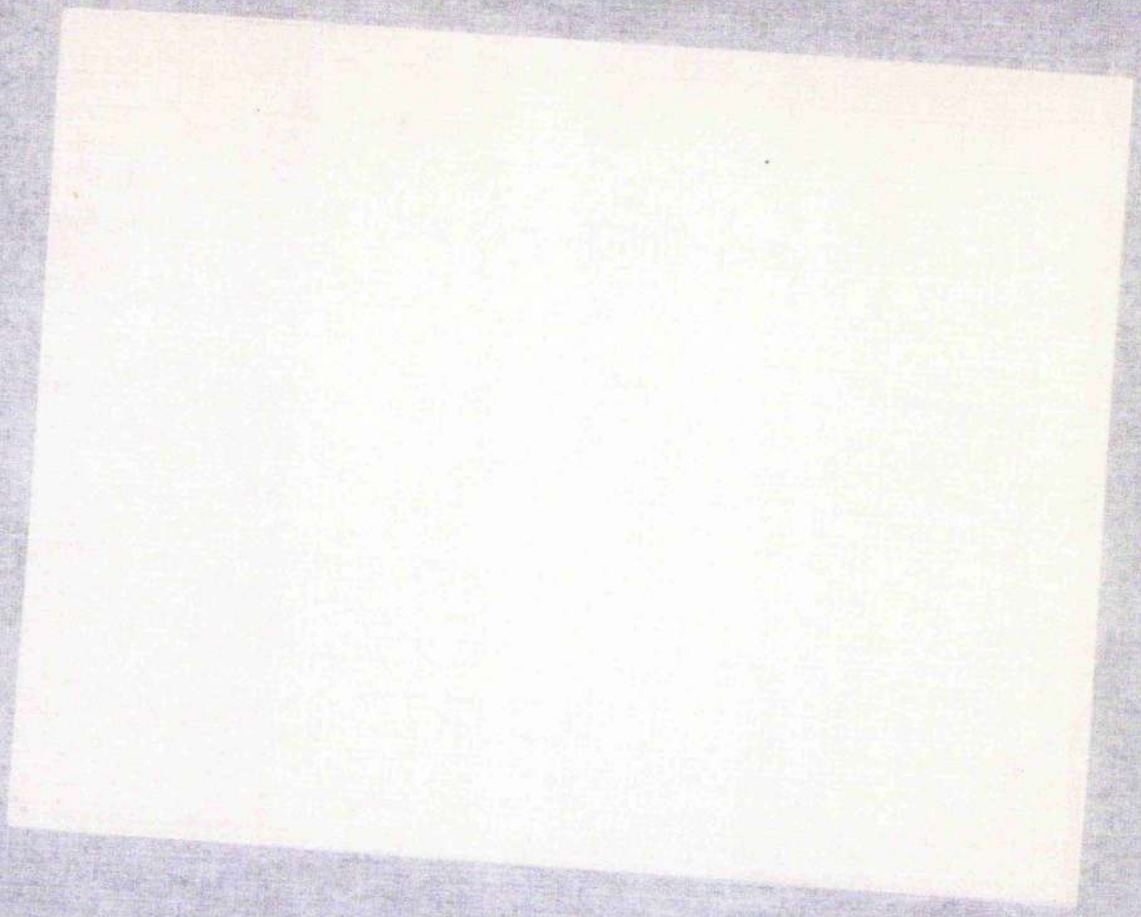


Figure 5. The mechanism for monitoring gross angular deflections of the eye. Movement of the eye (e) against a peg (p) moves a lever, (l) pivoted on point bearings (pb), which causes a shutter (s) to alter the amount of light (b) reaching a phototransistor (ph). The movement of the lever is adjusted and restricted by a hairspring (sg) and oscillations are damped by a paddle (pd) moving in a trough (t) of liquid (w). The fulcrum of the lever system is coincident with that of the eye.



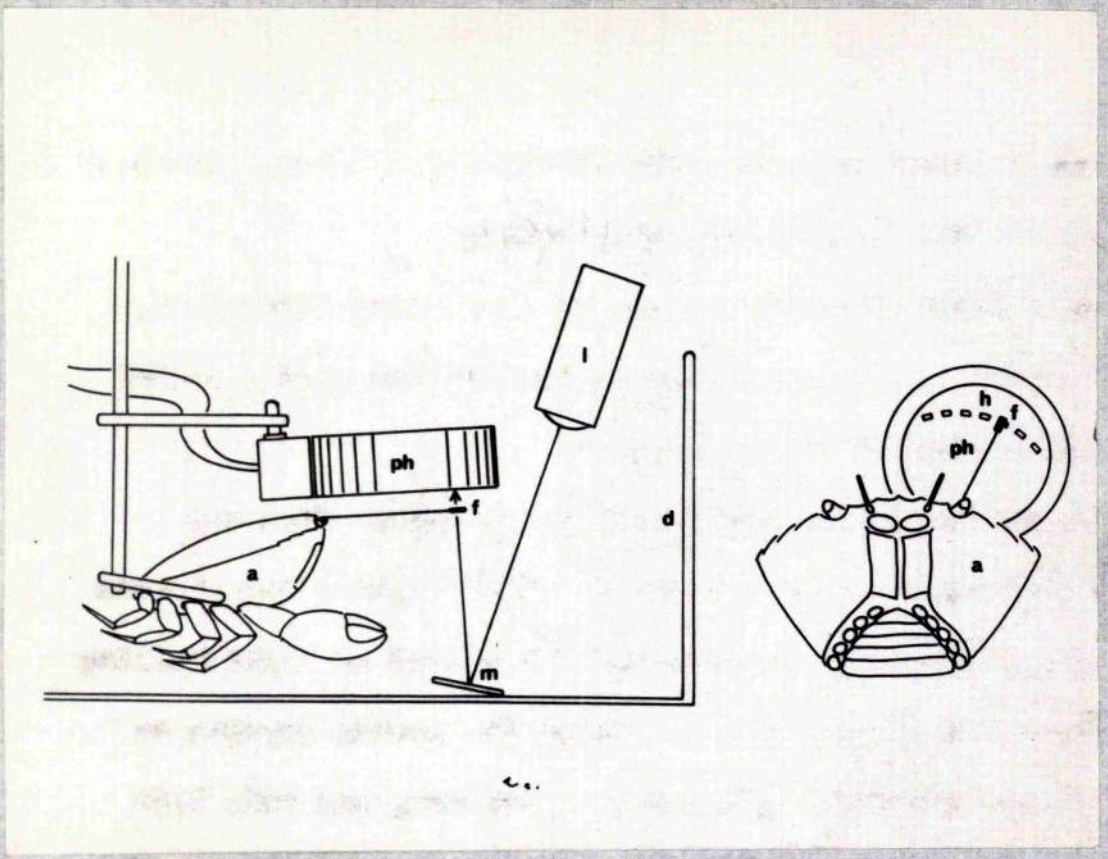


Figure 6. Lateral and ventral views of the system used to measure the angular deflection of an unrestricted eye. A focussed beam of light from a light source (l) is reflected by a mirror (m) onto the surface of a selenium cell (ph) which has a hole plate (h) covering its surface. The animal (a) is clamped within the striped drum (d) and arranged so that the flag (f) attached to its eye intercepts the focussed beam of light and casts a shadow on the surface of the photocell. The flag is the same size as the holes and the spaces between them.

The neurones of interest are also well known from previous experiments with silver electrodes as afferent or efferent.

A hydraulic system mounted (figure 4) on a micro-manipulator allows the electrode to be accurately controlled and slowly driven into the dorsal surface of the animal.

Movements of the eye are monitored in two ways. For some experiments a mechanism is used in which a very light lever pivoted on point bearings varies by its movement the amount of light falling on a photo-transistor (figure 5). Although the system imposes an initial load of approximately 0.03 grms. on the eye, and this load increases with the eye movement, optokinetic nystagmus appears to be unaffected and the animal shows no irritation. This method of recording cannot be used in experiments where the angle through which the unrestricted eye moves must be accurately estimated from a known zero which does not drift. Measurements of this kind are made by mounting a thin glass fibre on the eye and allowing the shadow of a small flag attached to the distal end of the glass fibre to fall across the surface of a selenium cell which is covered with a screen pierced by a pattern of fixed holes. The glass fibre with its small flag weighs approximately 0.003 grms., and once it is in position the animal appears to be unaware of its presence (figure 6). As the flag moves over the holes, so fluctuations in the potential from the photocell are registered by a pen-recorder. From these records the angular deflection of the unrestricted eye is readily calculated and because the sweep of the eye movement is divided into as many segments as there are holes in the screen, the method combines

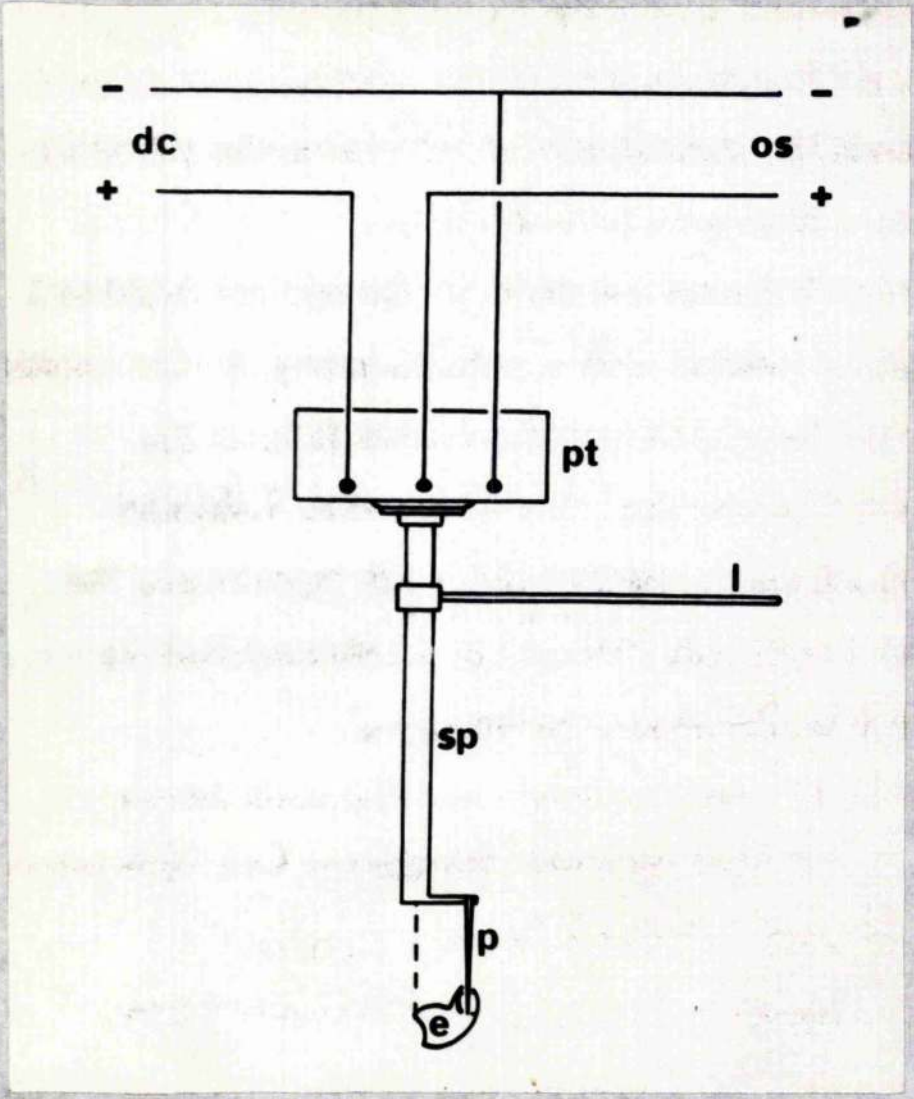


Figure 7. The apparatus used to forcibly deflect the eye to its left or right. Movement of the lever (l) rotates the spindle (sp) of a potentiometer (pt) and causes the offset peg (p) to force the eye (e) to one side. Slow and evenly applied pressure to the eye by way of the fine forcing peg does not trigger the fast retraction reflex. A direct current (dc) is applied to the potentiometer and the variations of this caused by the rotation of the potentiometer spindle are recorded by the oscilloscope (os).

high local sensitivity with a wide range of measurement.

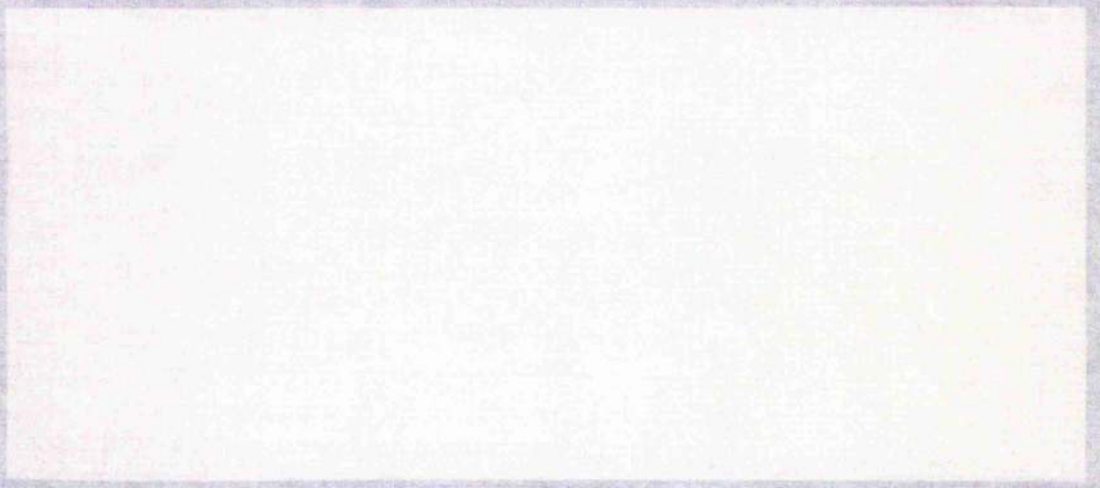
The change in light intensity detected by the photocell is small and in order to increase the sensitivity of the system the photocell was battery coupled to a high gain D.C. amplifier.

The manually produced forced movements of the eye are monitored by varying a fixed D.C. potential with a potentiometer, to the spindle of which the forcing peg is eccentrically attached (figure 7).

Blinding is effected by painting the cornea with a rapidly drying black laquer which can be removed after the experiment. The animals are tested for functional blinding by subjecting them to optomotor stimuli and directly observing the eyes.

Electrical stimuli are supplied by a neon triggered Tekronix square pulse generator, isolated from the preparation by a transformer. Fine platinum wires are used as stimulating electrodes.

Nerve impulses are recorded with A.C. coupled preamplifiers with cathode follower inputs and displayed on a Cossor Mark 4 oscilloscope. The records are photographed on Ilford blue-sensitive recording paper with a Cossor oscilloscope camera.



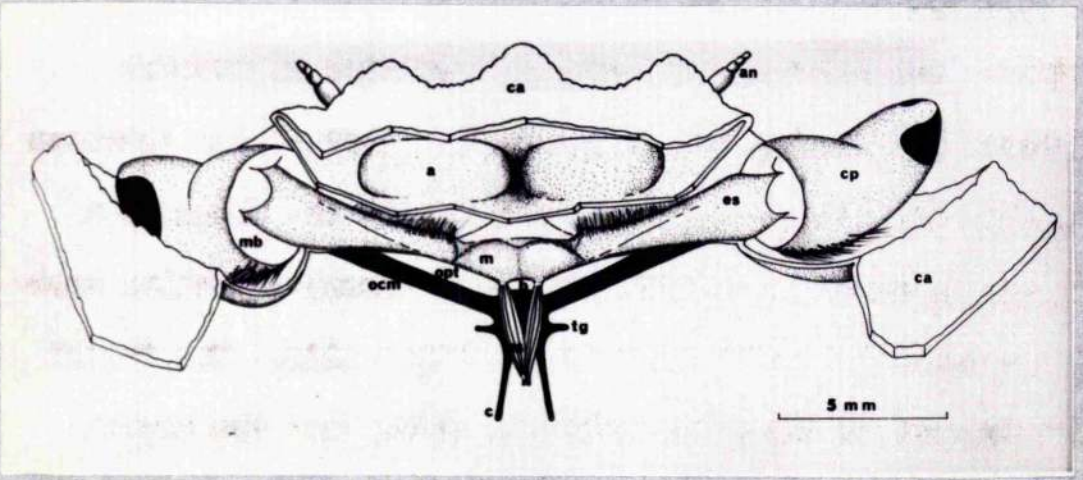


Figure 8. The eyestalk assembly of Careinus. A portion of the carapace (ca) dorsal to the eyestalks (es) has been dissected away to expose the five skeletal parts. The median plate (m) lies just above the brain (b) and attached to its posterior edge are two muscle blocks (muscle 15 of Cochran) which among others rotate the eyecups (cp) and eyestalks about a transverse horizontal axis so causing upward gazing. The muscles which produce a rotation of the eyestalks in the opposite direction are shown in figure 14. The eyecups are flexibly linked to the eyestalks only by the arthrodial membrane (mb) and internal musculature. The eyestalks are attached by their posterior edges to the body and have their anterior surfaces covered with fine hairs. They are protected by the anterior fold of the carapace or rostrum. The antennules are also enclosed in the same protective rostral pocket (a). The antennae (an) project from beneath the rostrum but cannot be retracted. The eyecups have many cuticular sense organs distributed over their surface apart from the cornea, of which the most noticeable are a group of thick ventral bristles. The left eyecup in the diagram is retracted and the right partly extended. Of the nerves of the brain only the tegumentary nerves (tg), oesophageal connectives (c), oculomotor nerves (ocm) and optic tracts (opt) are shown. Scale = 5.0 millimetres.

RESULTS Section I

Anatomy.

1. The Eye Assembly

The complete eye assembly of Carcinus consistes of several skeletal portions (figure 8), and is similar to that of the American blue crab Callinectes (Cochran 1935). Anterior to the brain is a small median plate, articulated with two long extensions called eyestalks, which project laterally from it on either side. The distal ends of these extensions carry the eyecups, which have the corneal surfaces on the rounded ends. The eyestalks are attached to the body along their posterior edges and are completely enclosed in a fold of the carapace which also protects the antennules. The eyecups are the only portion of the whole eye assembly visible in the intact animal.

2. The Cuticular Receptors.

Several kinds of cuticular receptors are distributed over the surface of the eyecup and eyestalk.

(a) Hair peg organs: The hair peg organs (Laverack 1961) consist of a hollow central spigot surrounded by fine bristles (figure 9A). Their distribution over the eye assembly is limited to the dorsal and anterior surfaces of the eyecup, but they are also found on the carapace, abdomen and pereipods of Carcinus (Bethe 1897, Luther 1930).

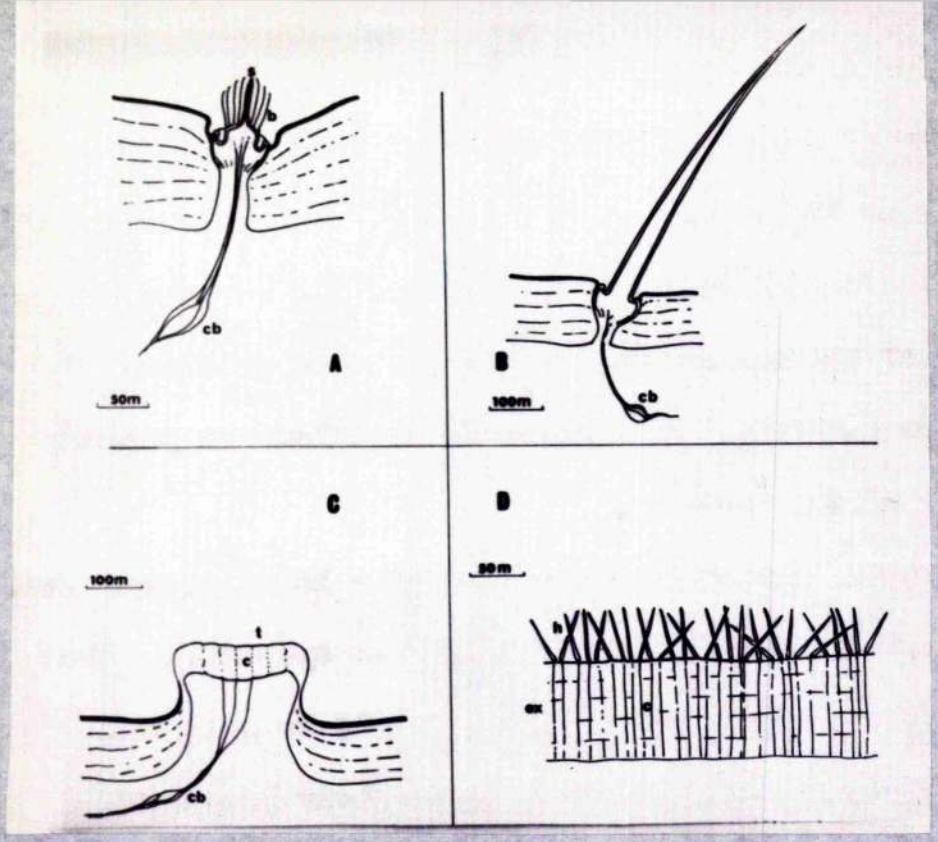


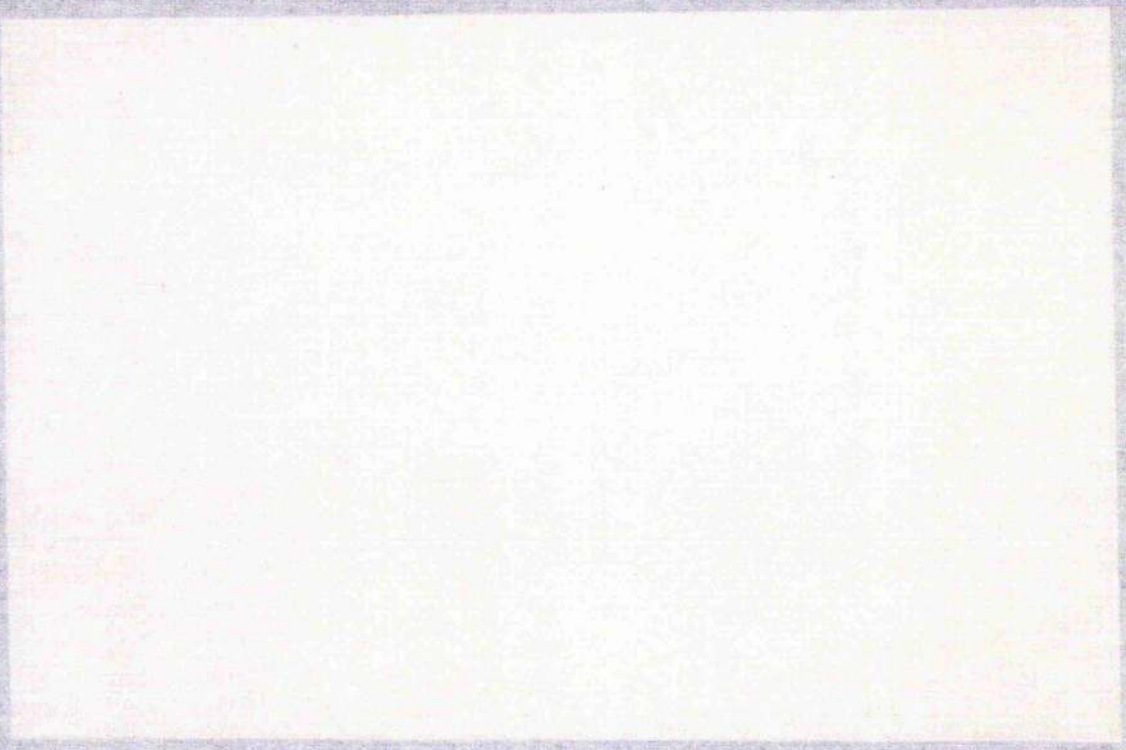
Figure 9. Cuticular structures on the surfaces of the eyestalks and eyecups. Scales in microns.
A, hairpeg organs consisting of a central hollow spigot (s) surrounded by fine bristles (b) and innervated by sub-skeletal nerve cell bodies (cb).
B, stiff hollow bristles, present on the ventral surface of the eyecup and on the distal end of the eyestalk. The long shank has no side branches and the base is innervated by sub-skeletal nerve cell bodies (cb). The bristles on the eyestalks are generally smaller than those on the eyecup. The dendrites of the nerve cell bodies in A and B could be traced only as far as the bases of the sensilla.
C, raised tubercles (t) with fine canals (c) perforating their apices. These structures are thought to be chemosensory but electrophysiological evidence for this is not available and it is not known if the canals are open to the exterior. The fine dendritic endings of the nerve cells (cb) cannot be traced with any certainty.
D, fine hairs (h) which are distributed over the surface of the eyecup. Nerve cells have not been found in association with these hairs but the presence of canals (c) extending through the exoskeleton (ex) to the base of each one suggests that they are innervated.

b) Bristles: A number of large stiff bristles (figure 9B) are situated on the ventral surface of the eyecup and have their long axes directed towards its apex (figure 8). They are well arranged for keeping foreign particles out of the eye socket, but there is no evidence that this is their sole function. Similar small bristles are present on the distal surfaces of the eyestalk.

c) Feather Hairs: A thick mat of fine feathery-like hairs extends over the surface of the proximal protected portions of the eyestalks. The function of these structures is obscure but they would be maximally stimulated by the rotations of the eyestalks about their long axes. The innervation of these hairs is not known.

d) Tubercles: Raised tubercles (9C) perforated by fine canals are found on the ventral surface of the eyecup and on the distal portion of the eyestalk. It is not possible to determine the exact structure of these organs from light microscope preparations but it is thought that they respond to chemical rather than mechanical stimulation. They are also found on the carapace of Carcinus (Bethe 1897)

e) Fine Hairs: Very fine hairs are distributed over the entire surface of the eyecup except for the cornea (figure 9D). The innervation of these hairs is not visible but a fine canal extends through the exo-skeleton to each one. Any movements of the eye would probably excite these structures but there is no evidence that the behaviour ~~of the~~



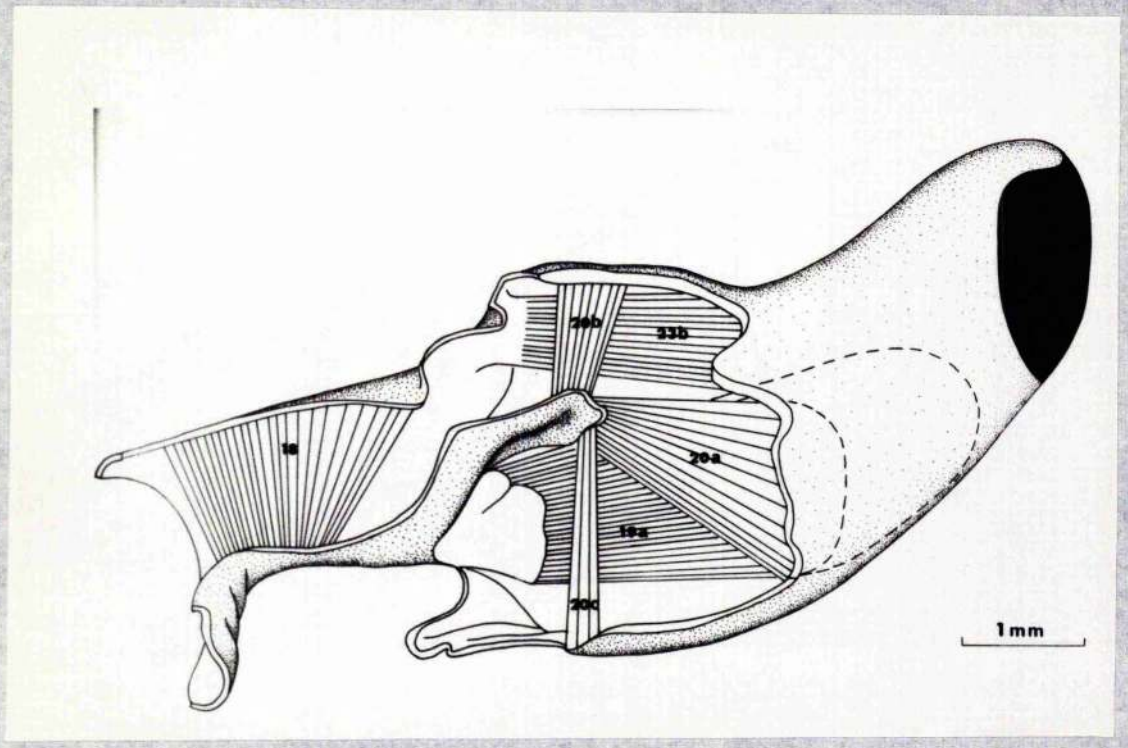
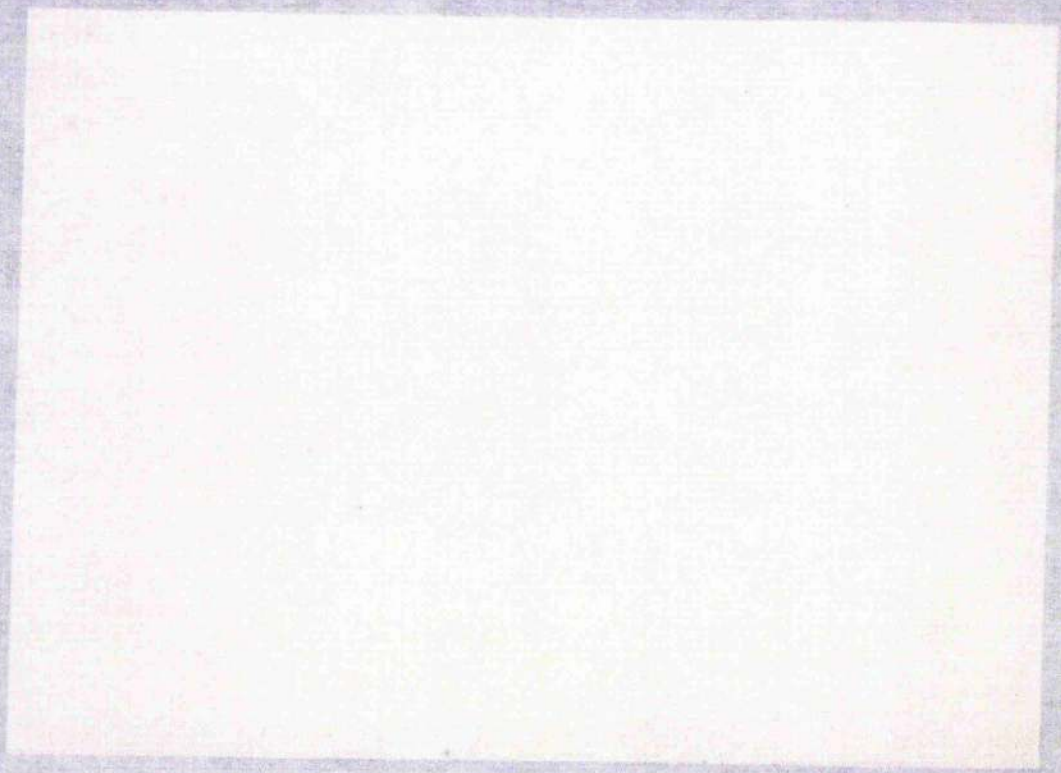


Figure 10. Posterior view of the right eyecup and eyestalk, opened to show the eye muscles. The posterior exoskeleton of the eyecup has been removed but no muscles have been dissected away. All the eye muscles except number 18 are attached proximally to the eyestalk and distally to the interior of the eyecup. Muscle 18 is attahhed between the eyestalk and the main body skeleton. The broken lines show the insertion of the eye muscles 19a and 20a on the nearside of the eyecup. The muscles are numbered according to Cochran and the deeper lying eye muscles are not shown. Scale = 1.0 millimetres.



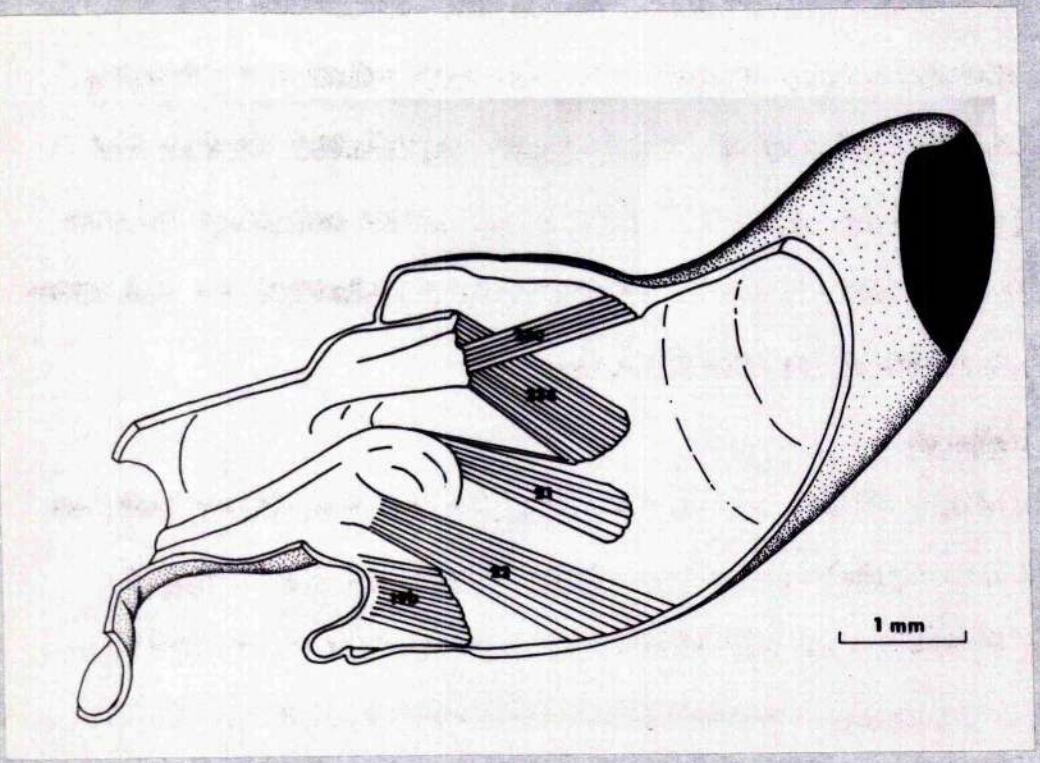


Figure 11. Posterior view of the right eyecup and eyestalk opened to show the eye muscles. The main retractor muscles and the muscles inserting on the nearside of the eyecup (shown in figure 10) have been removed. All the muscles are attached proximally to the eyestalk and distally to the eyecup. The muscles are numbered according to Cochran except number 23c which is not figured by Cochran for Callinectes. Scale = 1.0 millimetres.

of the animal is altered by the nervous information relayed from these hairs. They were reported in Carcinus by Bethe (1897).

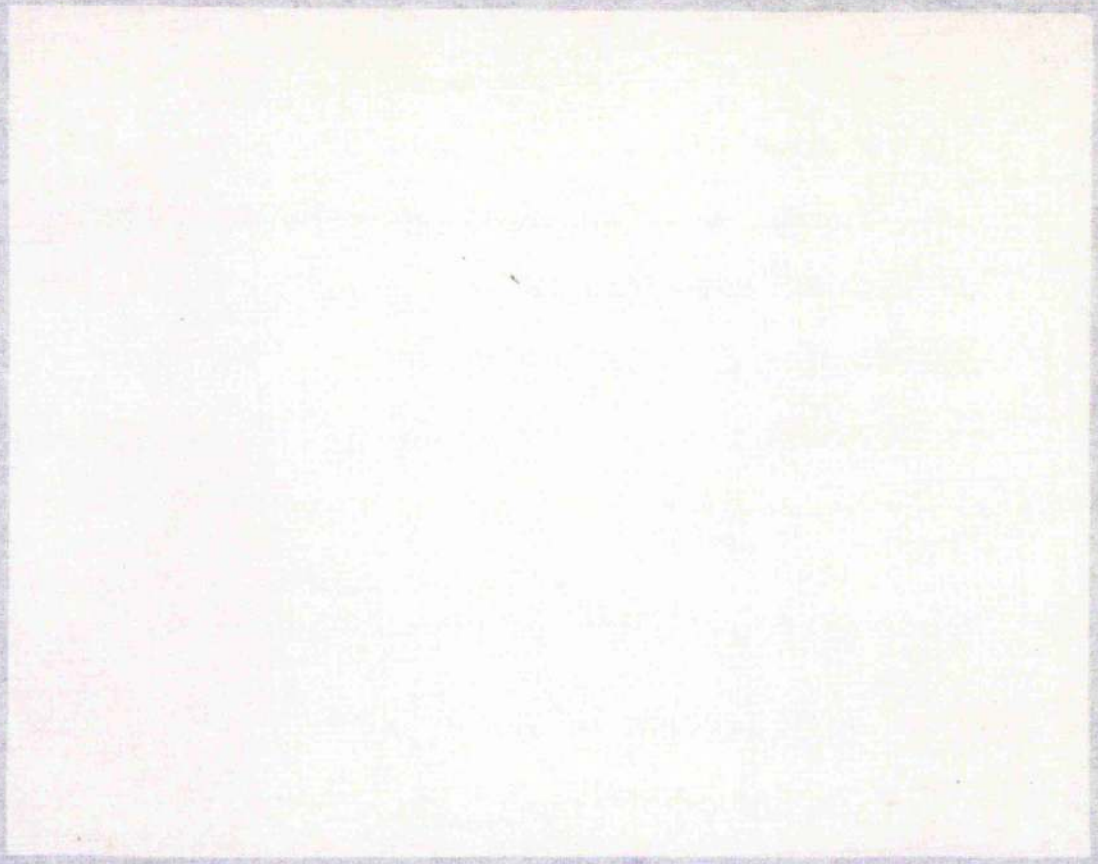
The bases of the hair peg organs, bristles, and tubercles are innervated by the dendrites of nerve cells but it is not known how far the dendritic processes extend into the cuticular structures. The various mechanoreceptors of the eye are stimulated during the movements of the eye and the significance of their activity in relation to monitoring the movement of the eyecup relative to the eyestalk will be considered in the discussion.

3. The Musculature.

The musculature of the eyecup is complex and the joint between the eyecup and the eyestalk, unlike other joints of the body, is not limited to movement in one plane by closely fitting skeletal portions. The attachment of the eyecup to the eyestalk by the eye muscles and the articular membrane allows the eye to move in any direction within the physical limits imposed by the eye socket.

The eye movements of optokinetic nystagmus are accomplished by 10 muscle blocks which have their origins on the distal end of the eyestalk and insert with the eyecup (figure 10 and 11). In addition to these, muscle blocks attached to the median plate of the eyestalk assembly rotate the eyestalk and eyecups about their longitudinal axes causing upward or downward gazing (figure 8 and 14).

Two small skeletal portions, or sclerites, incorporated in the arthrodial membrane of the eyecup play an important role in the movement of the eyecup in relation to the eyestalk (figure 12). Sclerite 1 is attached firmly to the distal end of the eyestalk and extends into



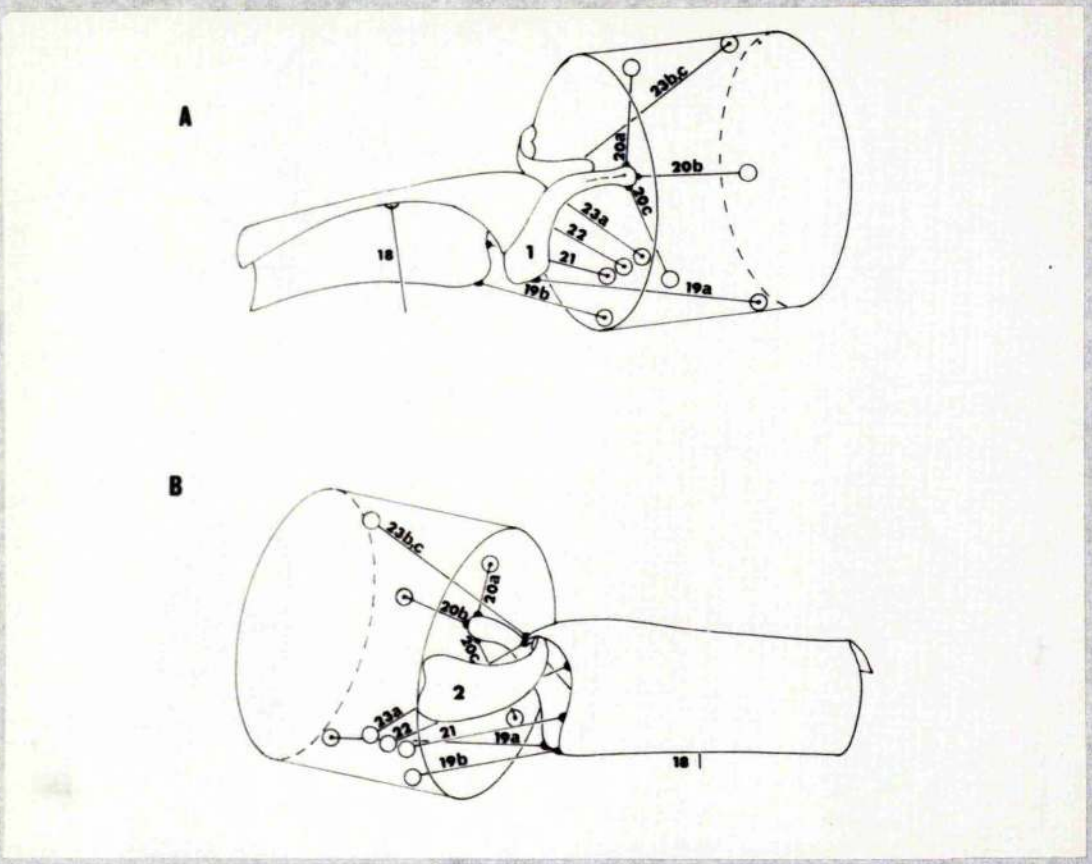


Figure 12. A diagrammatic representation of the posterior (A) and anterior (B) views of the animals right eyecup and eyestalk, to show the interaction of the muscles and the sclerites which bring about the movements of the eyecup relative to the eyestalk. The eyecup is shown as a transparent cylinder and the muscles are represented by straight lines. The origins of the muscles on the eyestalk are shown as solid hemispheres and their insertion on the eyecup nearside is designated by a circle, and on the far side by a circle and dot. Muscles 20a,b, and c move the eye away from the midline; 19b, 21 and 22 interact with sclerite 2 and swing the eye towards the midline. 23a, b, and c extend the eye and 19a retracts it. Muscle 18 attaches the eyestalk to the main body skeleton and reinforces the action of the retractor muscle by forcing the eye into its socket.

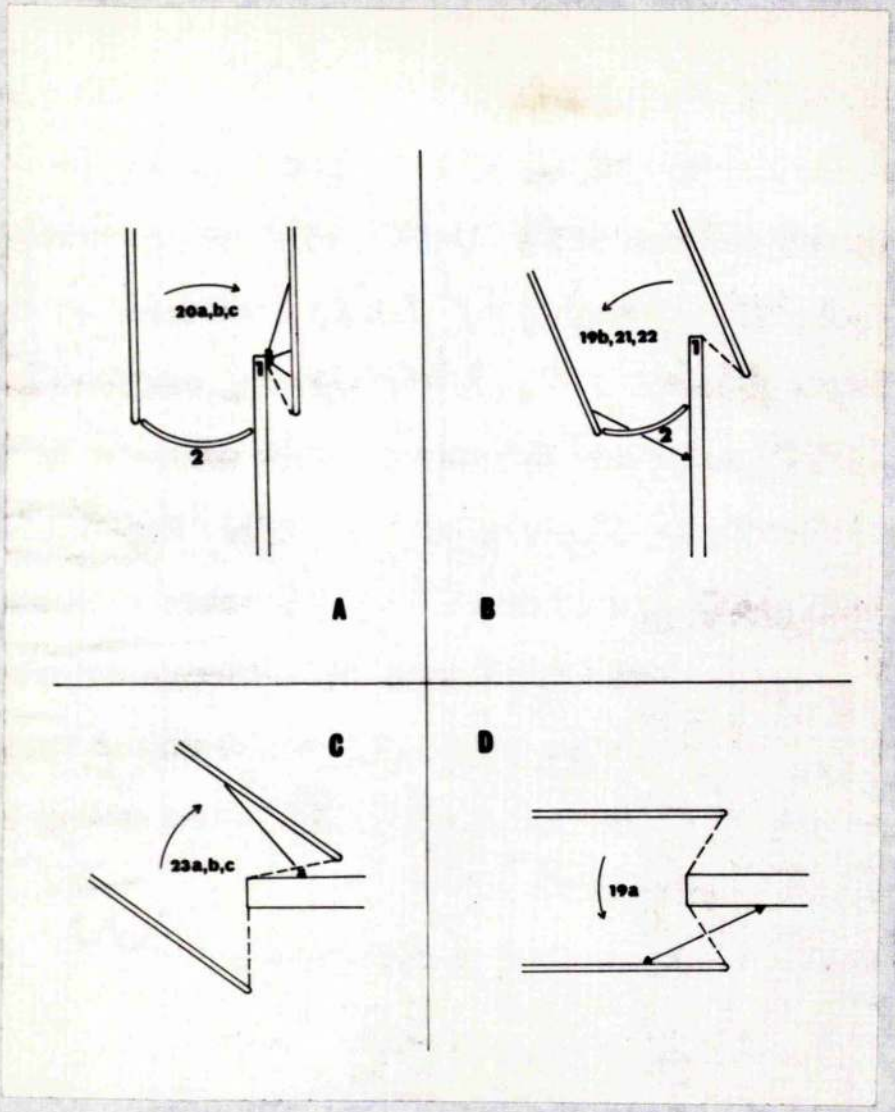


Figure 13. A diagrammatic representation of the dorsal (A,B) and lateral views (C,D) of the eyestalk to show the possible effects of the contractions of the eye muscles.
A, dorsal aspect, muscles 20 a,b, and c induce a movement of the eyecup away from the midline.
B, dorsal aspect, muscles 19 b, 21 and 22 interact with sclerite 2 and move the eye towards the midline.
C, lateral aspect, muscles 23 a, b and c produce the extension of the eye.
D, lateral aspect, muscle 19a getracts the eye.
In all cases the arthrodial membrane (broken line) is important in the translation of the muscular contractions into the angular deflection of the eyecup. Without the restraining action of the membrane the muscles would merely force the eyestalk further into the eyecup.

the eyecup (figure12A). Sclerite 2 is held in the arthrodial membrane between the anterior surface of the distal portion of the eyestalk and the rim of the eyecup (figure 12B). Contractions of the muscles which are attached to sclerite 1 (20a, b, c) produce a movement of the eye away from the midline (figure 13A). Alternatively, contraction of the muscles 19b, 21 and 22 and their interaction with sclerite 2, tends to swing the eye towards the midline, (figure 13B). The remaining muscles (23a,b,c and 19a) produce either the extension or retraction of the eyecup (figure 13 c and d). Muscle 18, although attached between the eyestalk and the body, has a pronounced effect during retraction of the eyecup in that it tends to force the eyecup more securely into its socket.

Postural changes of the eye, induced by displacing the animal about the horizontal axis, are also brought about by the ten eye muscle blocks. The versatility of the joint and the complexity of the eye movements control system is demonstrated by the ability of the eyes of an animals which is tilted to one side, to perform optokinetic nystagmus, even though under these conditions the eye moves in a new plane and when stationary maintains a different position relative to the eyestalk. The efferent commands for optokinetic nystagmus must be either centrally or peripherally integrated with the input from the statocysts which set the new postural zero for the eyes. The fast and slow phases of the eye movement in optokinetic nystagmus suggest that the muscle blocks must at least have a dual innervation which adds to the intricacy of the system.

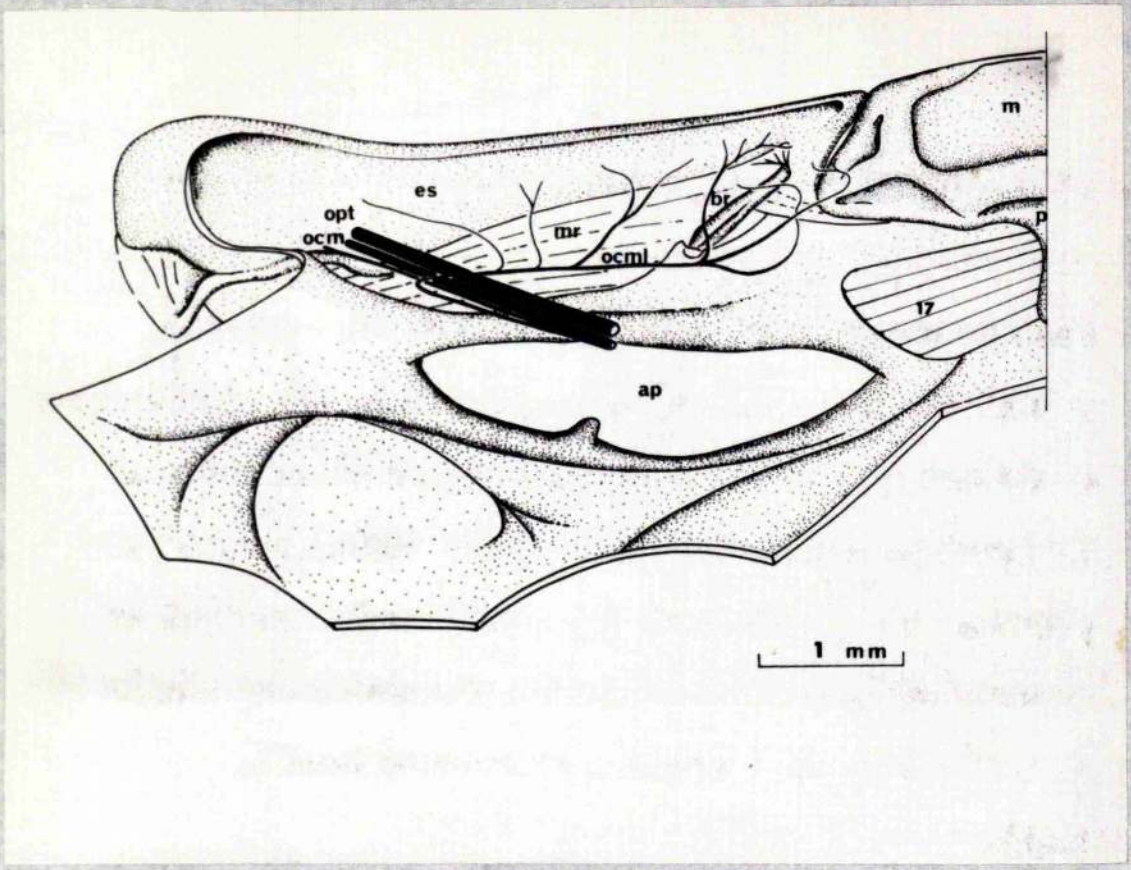
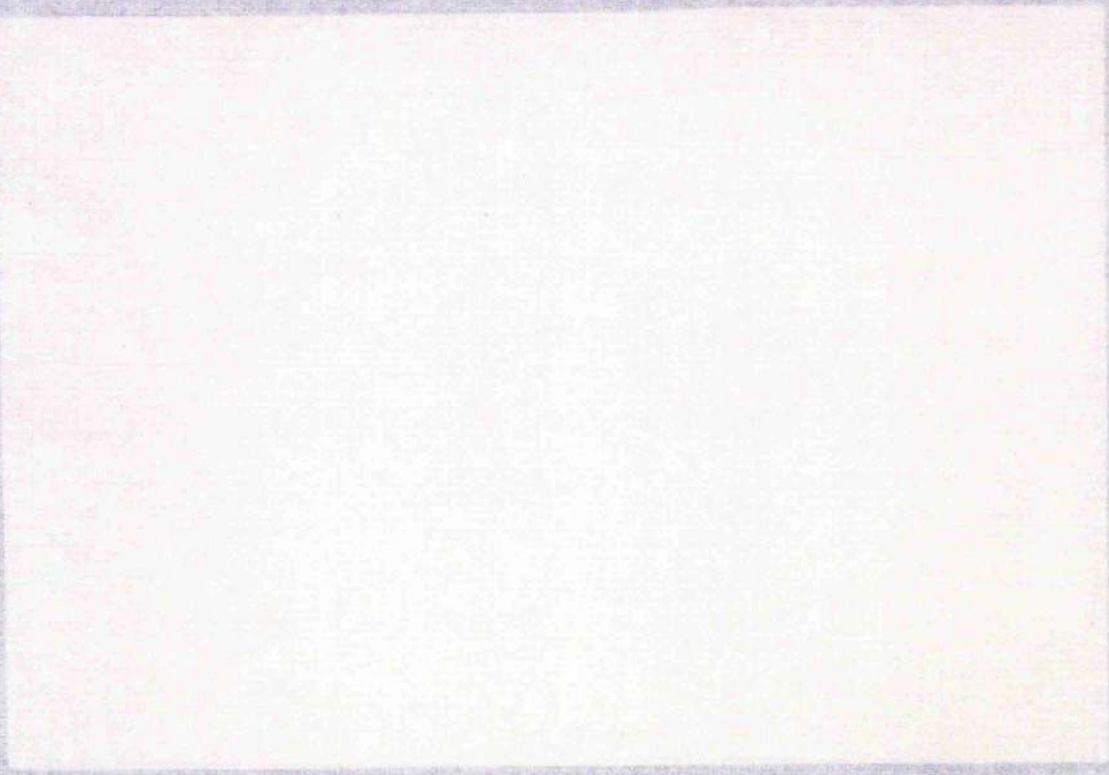


Figure 14. A posterior view of the inner surface of the left eyestalk to show the anterior ramifications of the lower branch of the oculomotor nerve. The eyestalk (es) is attached ventrally by a membrane (mr) and by a small skeletal bar (br) which projects from the main skeleton. A membrane also attaches the upper edges of the eyestalks to the adjoining exoskeleton. The nerves from the brain to the antennae and the antennules pass out through an aperture (ap) in the skeletal framework below the eyestalk assembly. The brain and posterior median plate muscles have been removed showing the muscle 17 of Cochran. This is attached to an anterior projection (p) of the median plate (m) and brings about transverse horizontal rotation of the eyes and eyestalks, so causing downward gazing. The branches of the lower oculomotor nerve (ocml) run from bipolar sensory cells in the tissue surrounding the skeletal bar (br) and the eyestalk, and back over the optic tract (opt) and upper oculomotor nerve (ocm). Scale = 1.0 millimetres.

Electrical recording from the muscles show that 18 and 19a are active during the fast retraction of the eyecup but conclusive results could not be obtained in this way for the other muscles. It is probable that the eye movements are produced by the simultaneous interaction of all the muscle blocks and electrical stimulation of the whole optic tract or oculomotor nerve (Bethe 1897a) cannot produce useful results. The analysis of the neuromuscular mechanisms of the eye movements can only be done by the stimulation of single axons which have been separated from the main nerve bundle.

4. The Innervation

No previous detailed account of the innervation of the head of Carcinus is available. Each eyecup is supplied by two main nerve bundles from the brain . The thicker and more anterior optic tract has some side branches but runs a relatively uninterrupted course to the optic lobe. The oculomotor nerve divides into two branches soon after leaving the brain. The upper branch runs to the eyecup, where it innervates a variety of cuticular receptors and the eye muscles. The lower branch of the oculomotor remifies in the connective tissue and cuticle which surround the eyestalk and the joint between the eyestalk and the eyecup (figure 14). That this lower branch consists mainly of sensory axons is shown by its distribution to the cuticle only and it may be entirely sensory because when cut, stimulation of the peripheral end produces no muscular contractions.



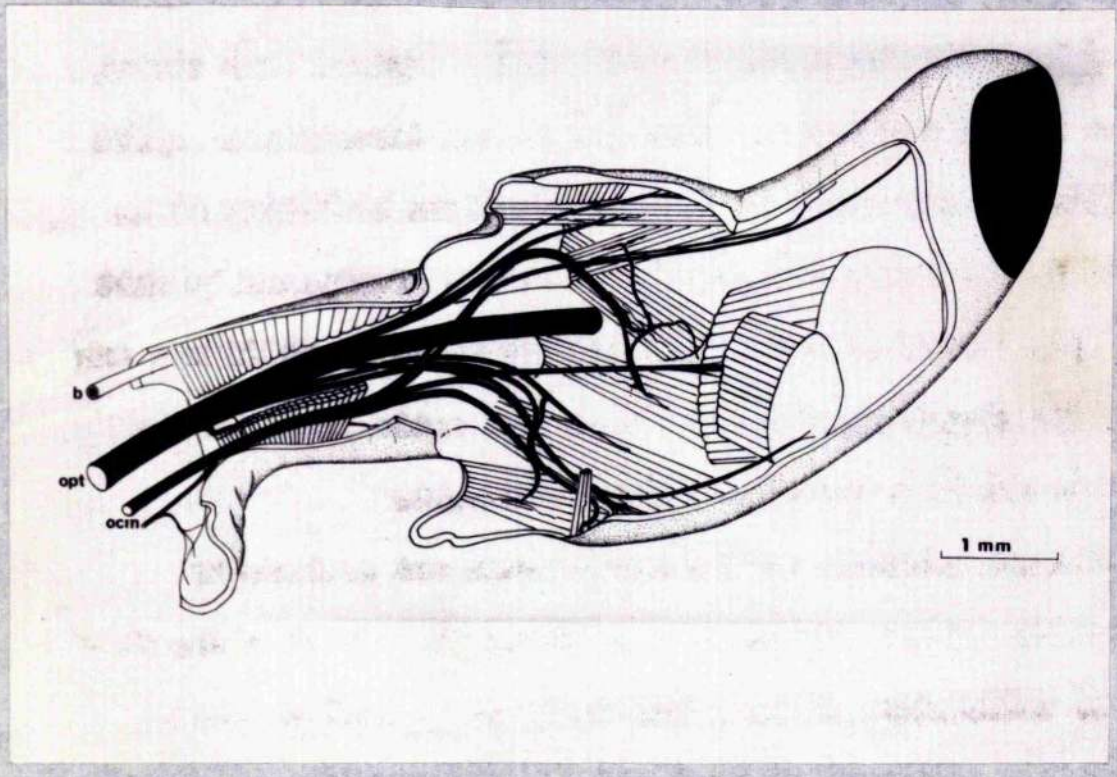
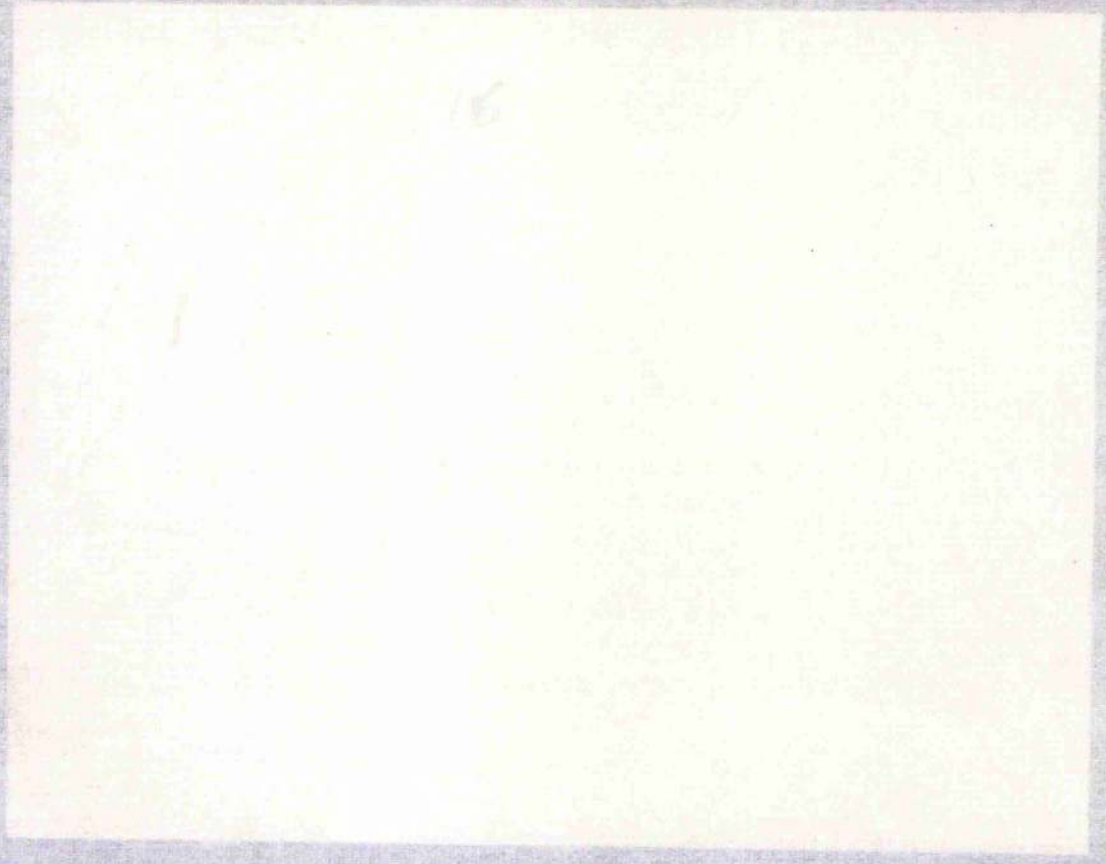


Figure 15. The eyecup opened to reveal the distribution of nerve bundles to the various muscle blocks. The number and function of the axons cannot be given in detail but it is clear that all the muscle blocks are innervated from both optic tract (opt) and oculomotor nerve (ocm). No special proprioceptive organs have been found. The small branch below the oculomotor nerve runs from cuticular sense organs at the joint between the eyecup and the eyestalk. Cuticular organs on the dorsal surface were supplied only by a branch from the oculomotor nerve although records from the optic tract showed that a number of cuticular sense organs have their axons in the optic tract. Care was taken in the preliminary recording experiments to preserve the blood vessel (b) as otherwise the optokinetic response rapidly deteriorates. Scale = 1.0 millimetres.

All the muscle blocks in the eyecup are supplied from branches of both the optic tract and the oculomotor nerve (figure 15). This has been shown by following axons stained with methylene blue through the connective tissue and fascia which run in all directions. Apart from the large obviously motor axons with polytomic branching it is not clear whether the axons are sensory or motor. Peripherally most axons of the optic tract disappear into the optic lobe and do not take up the stain. No direct connection between the optic lobe and the oculomotor nerve has been revealed although sought.

Thin transverse sections of the optic tract and oculomotor nerve show that the larger fibres tend to be on the dorsal side. These are presumed by their size and position to be motor axons. Other fibres in the optic tract are either visual afferent fibres or the interneurones (Wiersma Waterman and Bush 1961). The oculomotor nerve has a greater number of large, presumably motor fibres and less small sensory axons although methylene blue studies have shown that the eye muscles are supplied from both the optic tract and the oculmotor nerve. ~~The lower branch of the oculomotor nerve.~~ The lower branch of the oculomotor nerve contains a number of relatively large fibres which is surprising considering that the anatomical and electrophysiological studies suggest that this nerve is entirely sensory. The classification of nerves into sensory and motor axons merely by their relative diameters is probably misleading.



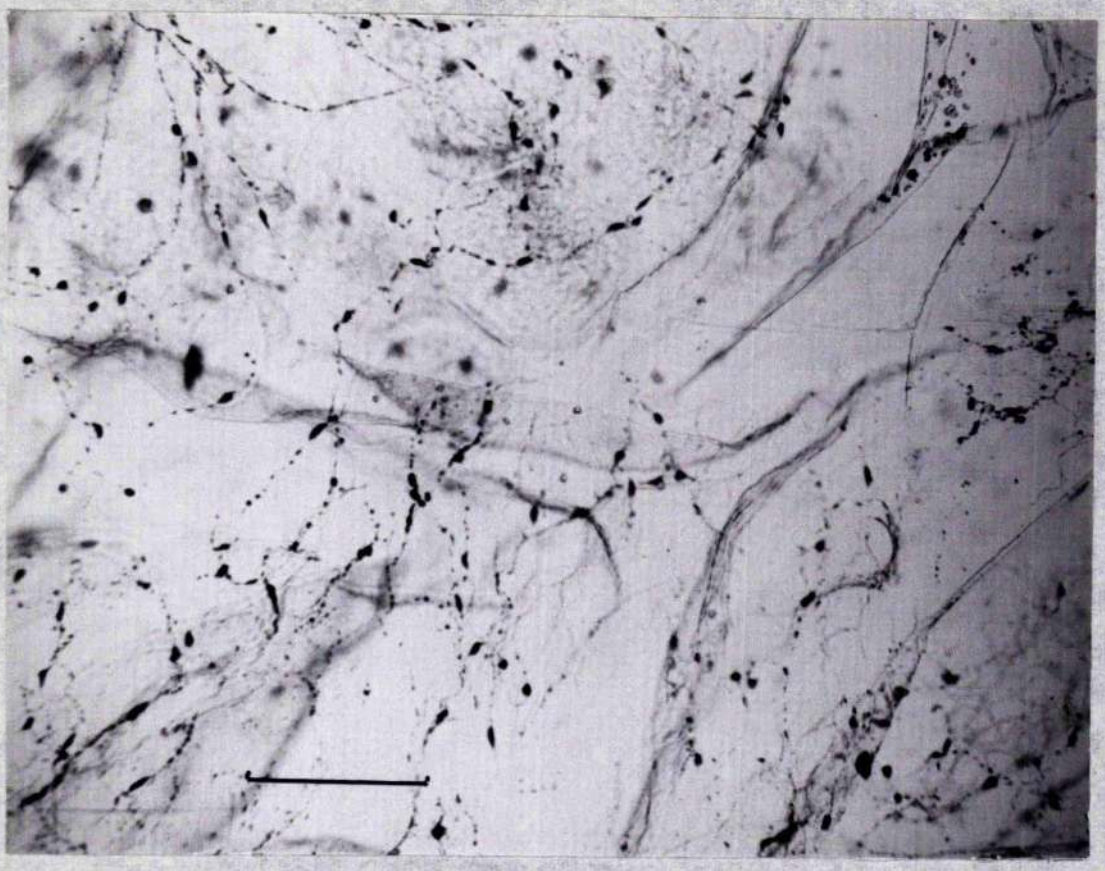


Figure 16. Bipolar sensory cells in the arthrodial membrane of the eyecup revealed by vital staining with methylene blue. The fine axons and dendrites, beaded by the methylene blue stain, ramify in all directions over the inside of the arthrodial membrane. The bipolar cell bodies (Larger black dots) have their axons in the oculomotor nerve. Attempts to record from these cells were unsuccessful and no response was observed when the membrane was distorted although the cells would seem to be in a position to be stimulated by this. The cells and their dendrites were never seen to form a network. Scale = 100 microns.

Figure 17. Bipolar sensory cells in the connective tissue surrounding the skeletal bar which atacches the eyestalk to the body, revealed by vital staining with methylene blue. The cells are distributed along the eyestalk and around the edge of the bar in A, and can be seen in B to form a branched plexus. The dendrites appeared to end in the connective tissue and were never seen to extend to cuticular structures. Like the bipolar cells of the arthrodial membrane (figure 16) they never formed a closed network. Scales = 100 microns.

5. Proprioceptors

Obvious proprioceptors, nerve cells or proprioceptive organs such as elastic strands at the eyecup joints or muscle receptor organs in the eyecup have not been found and no evidence of them has appeared either from behavioural or electrophysiological studies.

Peripheral sensory neurons, with their axons in the oculomotor nerve and single distal dendrites embedded in the arthrodial membrane between the eyecup and the eyestalk are revealed in methylene blue preparations (figure 16). Similar bipolar cells have been reported from other arthrodial membranes of many different types of crustaceans. The cells and axons never form a peripheral network, confirming Alexandrowicz (footnote to page 9, 1957). It is not known what function these undoubted sensory cells form at this critical joint. Larger bipolar cells arranged in a similar fashion to those which Alexandrowicz (1957) found situated on the pleural plate of Squilla are abundant in the tissue which surrounds the enclosed eyestalks. Electrical recordings from the lower branch of the oculomotor nerve which supplies this region, show responses to distortion of the connective tissue where the dendrites are situated (figure 17) and to forced movements of the central portion of the eye assembly. Movements at this joint do not occur during optokinetic nystagmus but protective retraction and rotation of the eyestalks about their long axes must stimulate these cells.

Section II

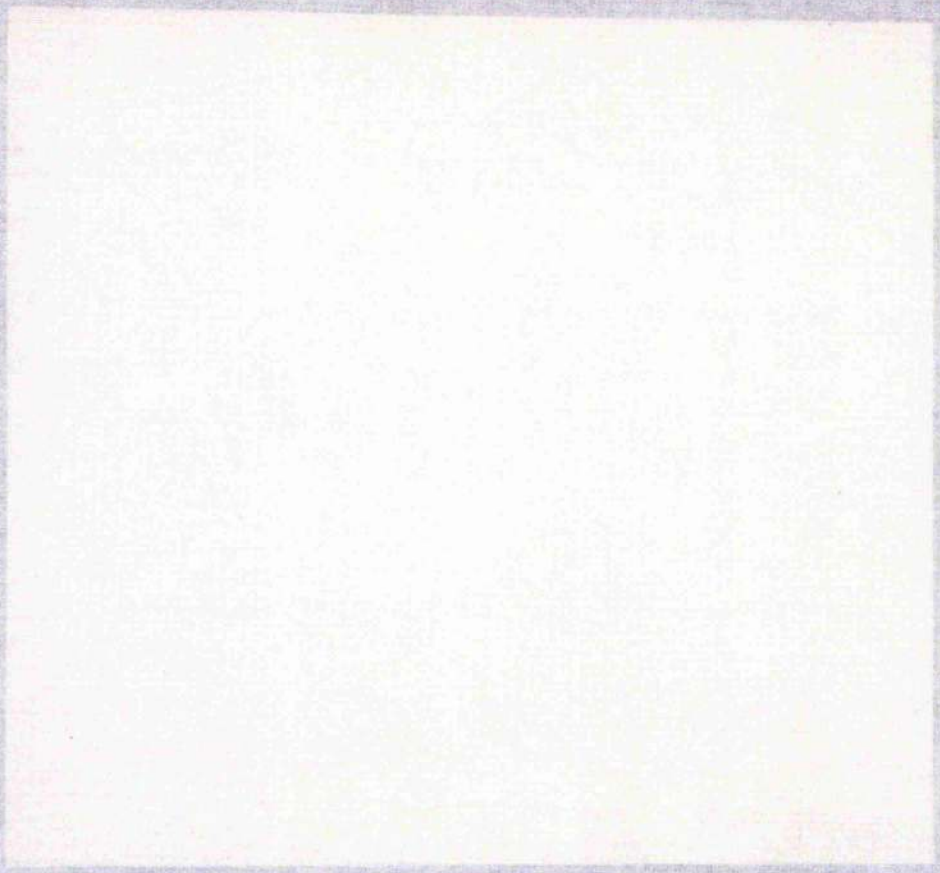
The Retraction Reflex

1. Surgical experiments

Mechanical stimulation of the eyes and certain areas of the carapace produces the reflex retraction of the eyecup (Bethe 1897a and confirmed in this investigation). A mechanical stimulus to cuticular receptors which have axons in the tegumentary nerve, the optic tract or the oculomotor nerve, can elicit the rapid eye withdrawal. It is most typically produced by roughly touching the carapace anterior to the cervical groove. Eye retraction in hurt or frightened animals can be produced by stimulating any part of the body, but this is probably due to the low threshold of the response in disturbed animals and also to an effective increase in the sensitivity of the cuticular receptors on the eyes and anterior carapace.

Cutting the tegumentary nerve abolishes the withdrawal response elicited by tactile stimulation of the carapace or the eye socket. The two eyes retract independently and the areas innervated by the tegumentary nerves meet in the midline. The area innervated by the brain is bounded posteriorly by the cervical groove, (using the terminology of Snodgrass (1952). Posterior to this groove, sensory nerves from the carapace run to the ventral cord.

Cutting through the optic tract abolishes the fast retraction reflex, wheras cutting the oculomotor nerve leaves it unchanged. Therefore sufficient fast fibres for the production of the rapid closure of the eye run in the optic tract. The eyecup can still be



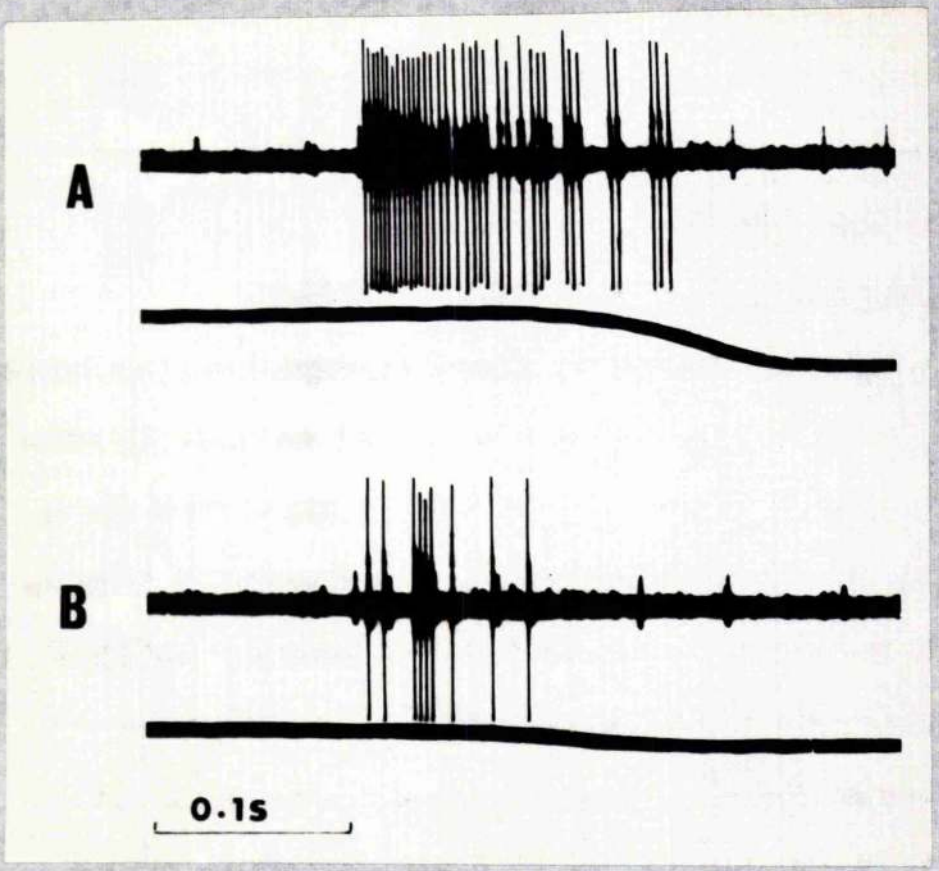
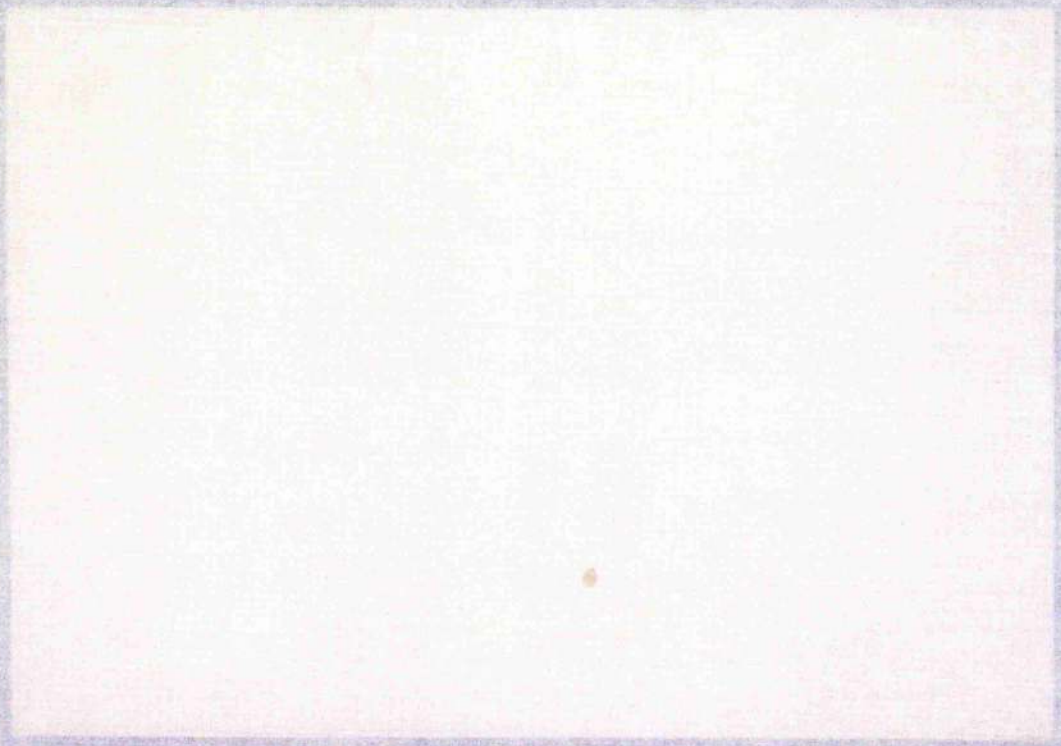


Figure 18. Large impulses of fast motor axons in the optic tract of an animal during partial and complete retraction of the eye. A, a full and B, a partial retraction showing the different numbers of spikes (upper trace) and corresponding movements of the eyecup (lower trace) caused by mechanical stimulation of the carapace. The records were obtained with stainless steel microelectrodes.
Scale = 0.1 seconds.

withdrawn and held in the retracted position after the optic nerve has been cut through, but the withdrawal is now a slow one although it is produced by the same or stronger mechanical stimuli which normally elicit the fast withdrawal of the eye.

2. The Electrophysiology of the Protective Retraction.

The fast retraction of the eye is always accompanied by a burst of impulses in the optic tract. Retraction is not necessarily complete, and the number of impulses is less for a partial than for a complete withdrawal, as shown by a comparison of figure 18A with B. The activity of several different axons can sometimes be distinguished in the efferent burst at retraction, especially when recording with silver electrodes which tended to record from a larger area than the stainless steel micro-electrodes. Single units sometimes fire at frequencies of 500/sec. but this frequency is not maintained for the complete burst which itself lasts for only approximately 200 millisecs. The burst of motor impulses can be elicited regardless of the eye position, or even its presence; if the eye is cemented into its socket with plasticine or fixed in an extended position, or completely removed, the same characteristic burst of efferent impulses follows tactile stimulation of the carapace or eye socket. There is therefore no prior or simultaneous proprioceptive or visual modification of the form of the response from the effector. In addition to this the retraction reflex completely over-rides a possibly simultaneous optokinetic movement of the eyecup. No evidence of a peripheral neuromuscular inhibition of these fast motor axons has appeared, in that no one ever finds impulses in them without movement occurring.



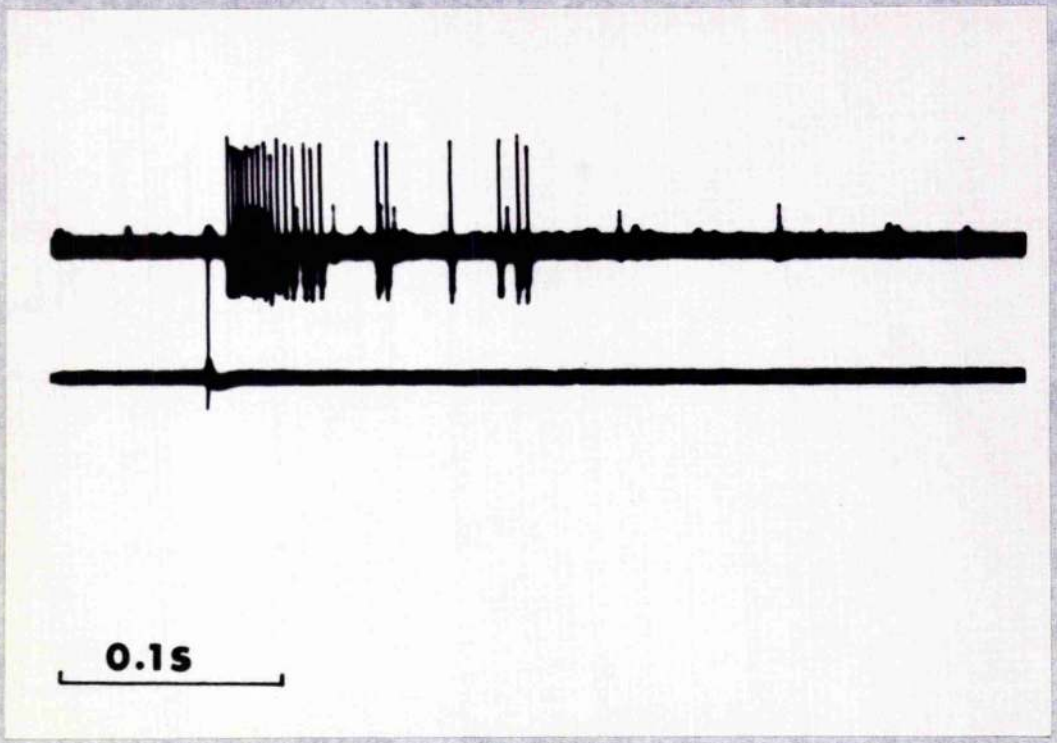
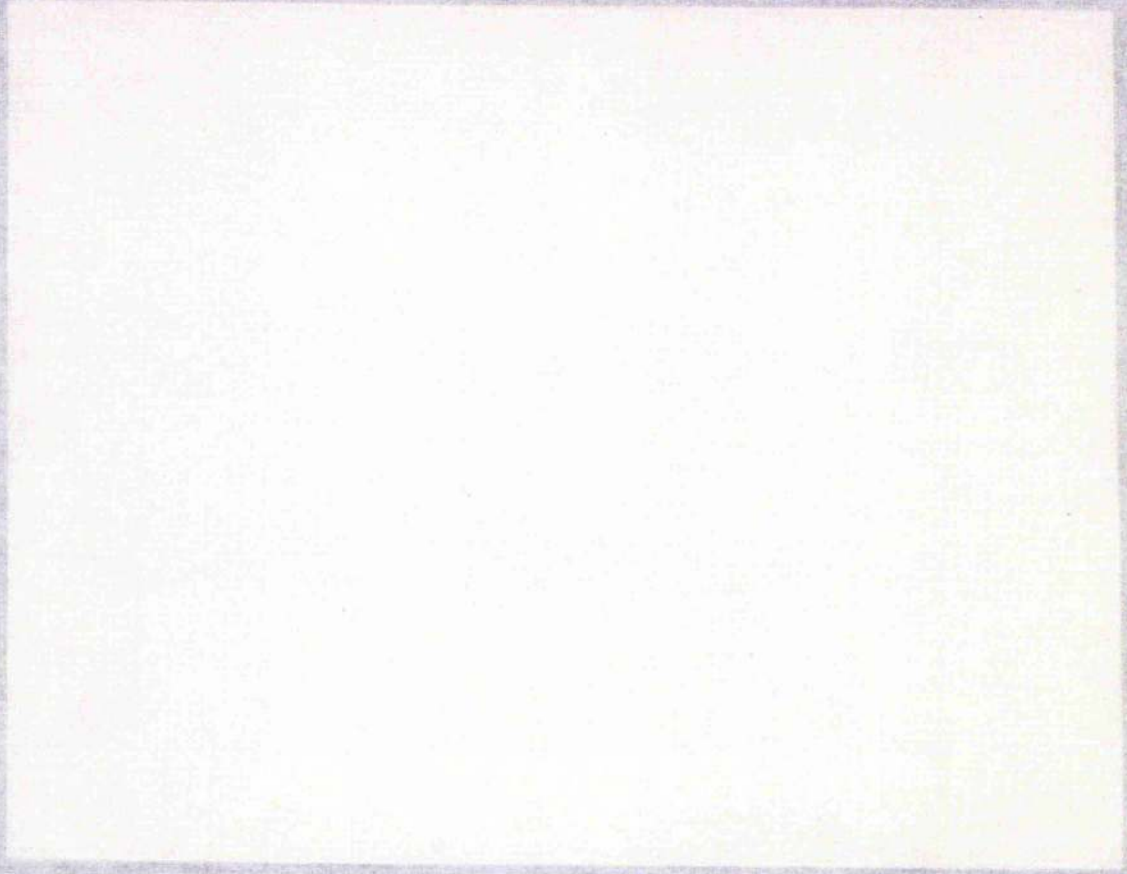


Figure 19. Large impulses of fast motor axons in the optic tract of an animal following electrical stimulation of the tegumentary nerve. The stimulus (lower trace) was a square pulse of 0.1 milliseconds. The 5 millisecond latency of the response suggests a reasonably direct connection from the sensory nerve to the fast motor axons of the optic tract. The maximum frequency of spikes is about 500 cycles/sec. but this is maintained for only a few milliseconds. The decrease in amplitude of the spikes at high frequencies confirms that they are of a single unit. Records were obtained with stainless steel microelectrodes and the stimulus was applied through platinum wires, hooked beneath the exposed tegumentary nerve. Scale = 0.1 seconds.



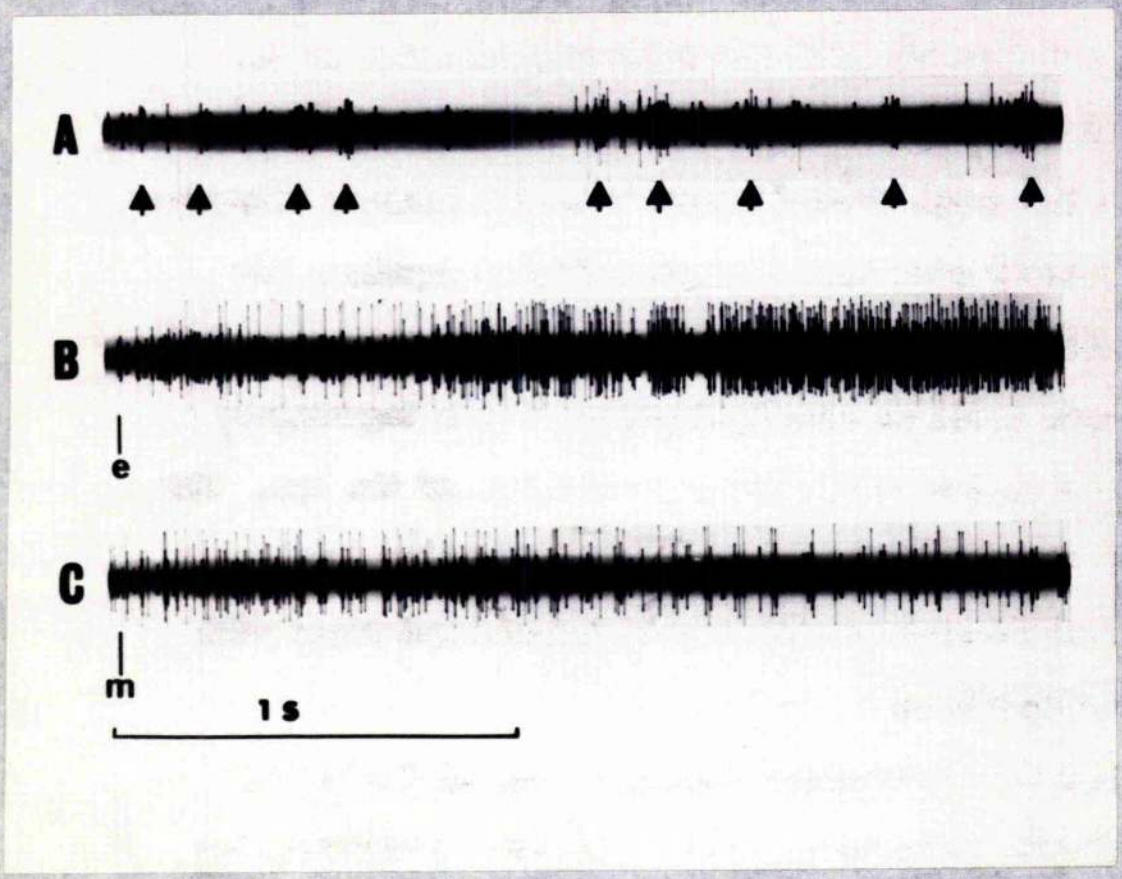
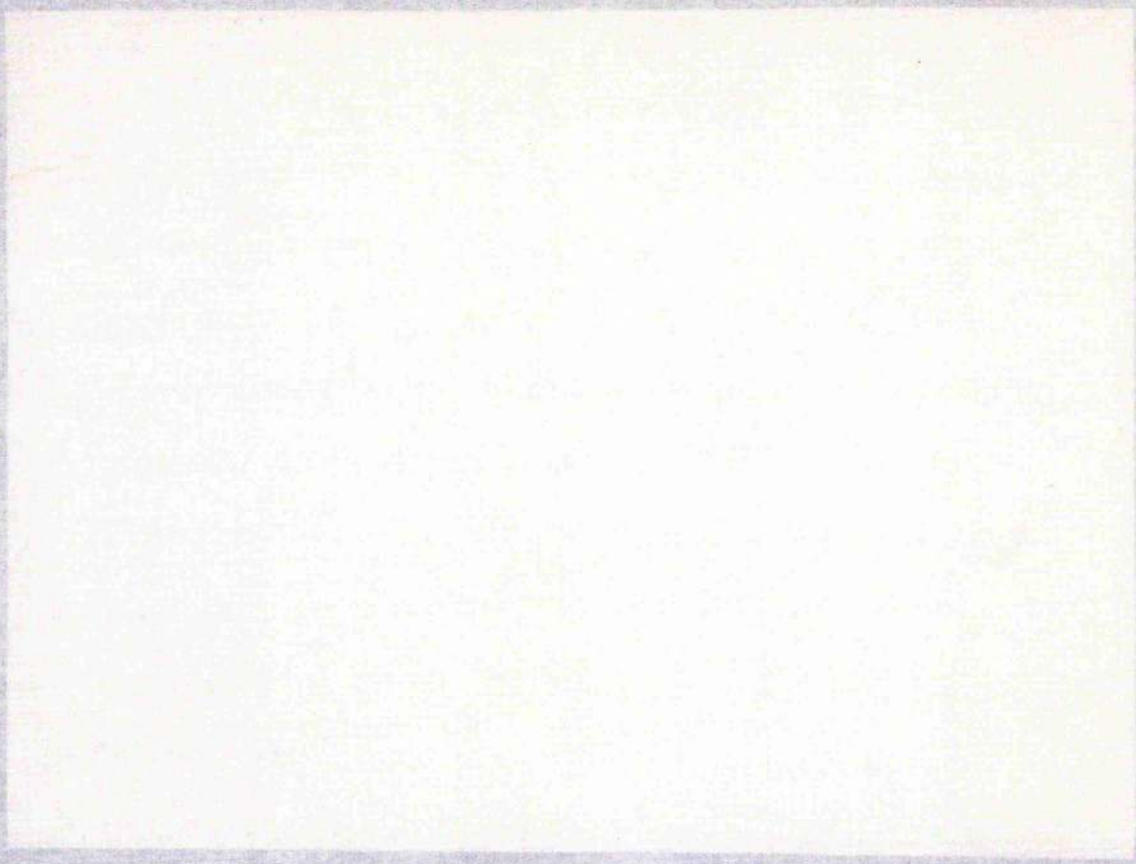


Figure 20. Efferent impulses in the oculomotor nerve during the extension of the eye. The eye is retracted to begin with and the bursts of impulses indicated by the arrows in A are the result of mechanically stimulating the legs. Large units in B correspond with the extension of the eye which commences at e. The eye is then held in the extended position, C, and the large efferent units continue to fire although movement of the eye ceased at point m. The records were obtained with silver electrodes. Scale = 1.0 seconds.

A single electric shock of 0.1 millisec. duration to the tegumentary nerve is also adequate to produce a complete pattern of impulses in the optic tract (figure 19). The minimum effective stimulus is probably more than a single afferent impulse, but careful mechanical stimulation of a single hair in the eye socket (which produces a train of sensory impulses in the tegumentary nerve) can often produce the complete retraction of the eye. The central threshold, below which no burst of retracting impulses emerges, certainly varies with different animals and rises with handling and repetition.

Nerve fibres in the oculomotor nerve transmit trains of impulses while the eye is held back in its socket following the retraction of the eye and in crabs with the oculomotor nerve cut the eye is not held in but is immediately extended after the reflex retraction. From this evidence it is suggested that slow motor axons in the oculomotor nerve activate muscles which hold the eye in the socket once it is retracted. It is not known whether there is also inhibition of the antagonistic muscles. Extension of the eye, induced by gently moving the animals legs, is always accompanied by extensive and separately identifiable efferent impulses in the oculomotor nerve (figure 20). Some of these units which are silent when the eye is retracted, fire continuously and at a constant frequency as long as the eye is extended and held in one position (figure 20A compared with C).



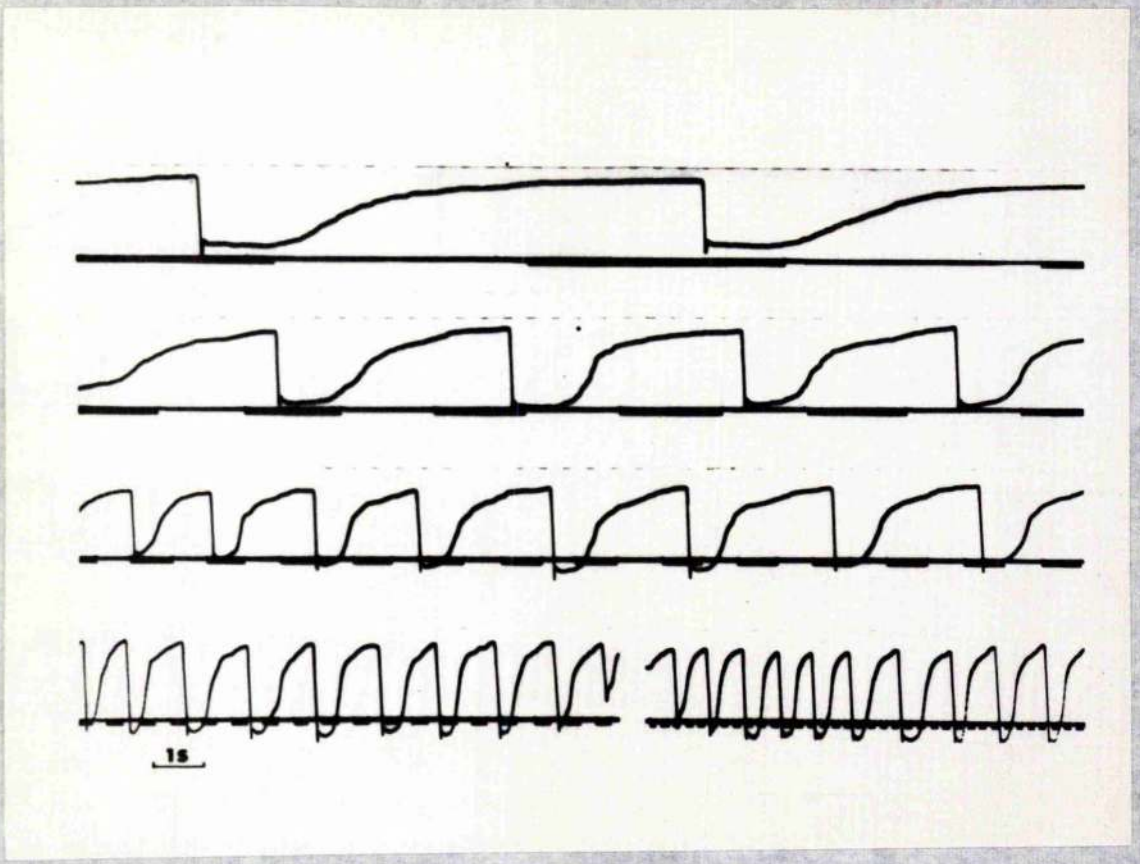
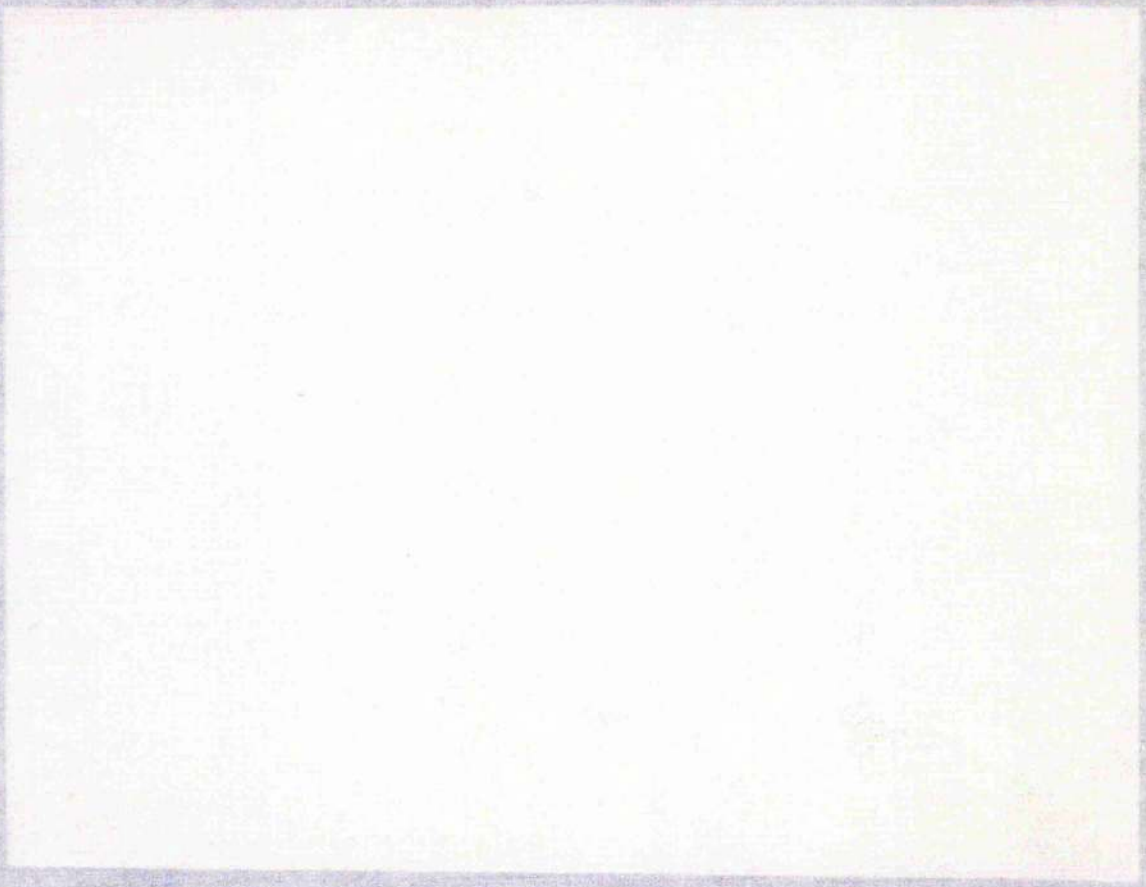


Figure 21. Records of the optokinetic response (upper trace) which corresponds with different speeds of the optomotor drum (lower trace). These records are no more than a indication of the activity of the eye muscles and of the frequency and consistency of the response, because the measuring system imposed upon the eye a load which increased with deflection and the recording system did not give a proportional response. The vertical scale is not linear and is omitted. Horizontal scale = 1.0 seconds.



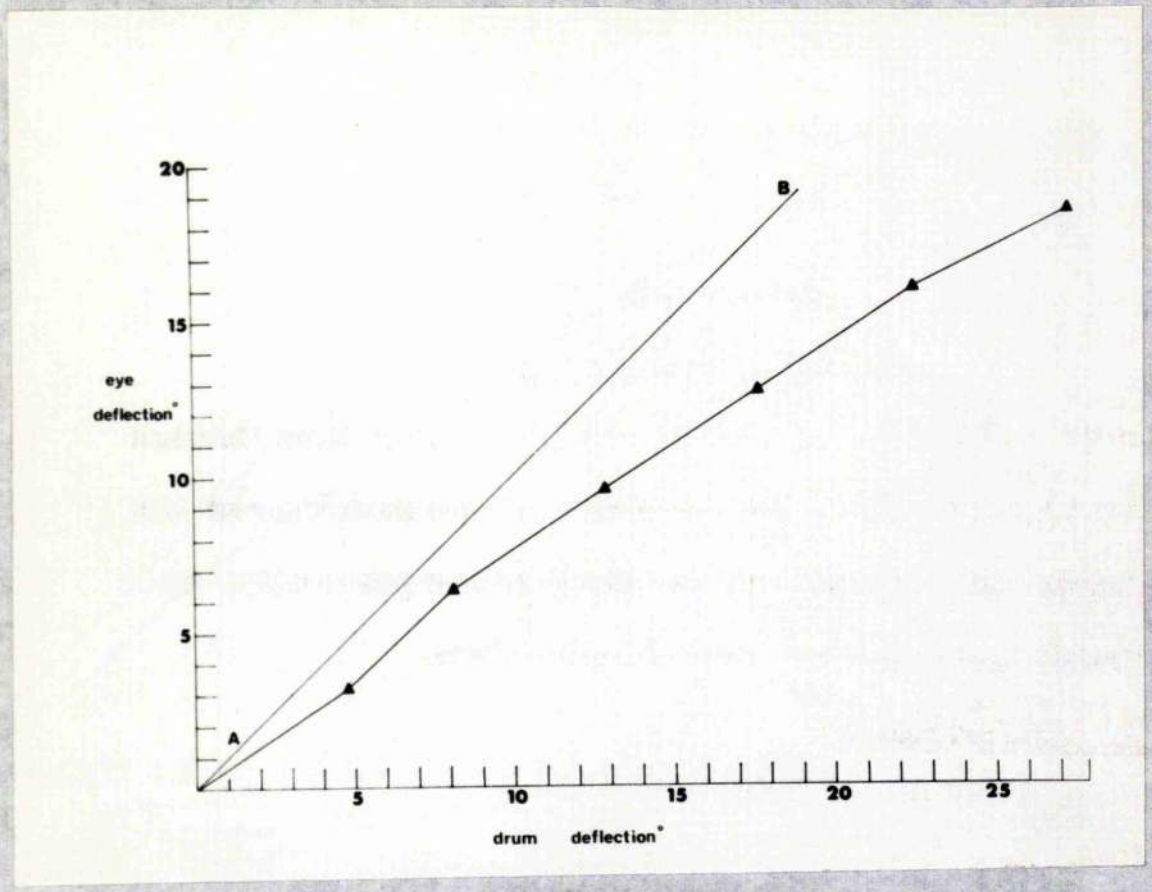


Figure 22. The angular deflection of the eye during one complete slow phase of optokinetic nystagmus, plotted against the angular deflection of the drum during the same period. The line A-B represents a relation between eye deflection and drum deflection of 1:1. The triangles represent the actual deflection of the eye and show that the eye lags increasingly behind the drum. This continual increase in lag, termed the slip, is the effective stimulus for optokinetic nystagmus.

Section III

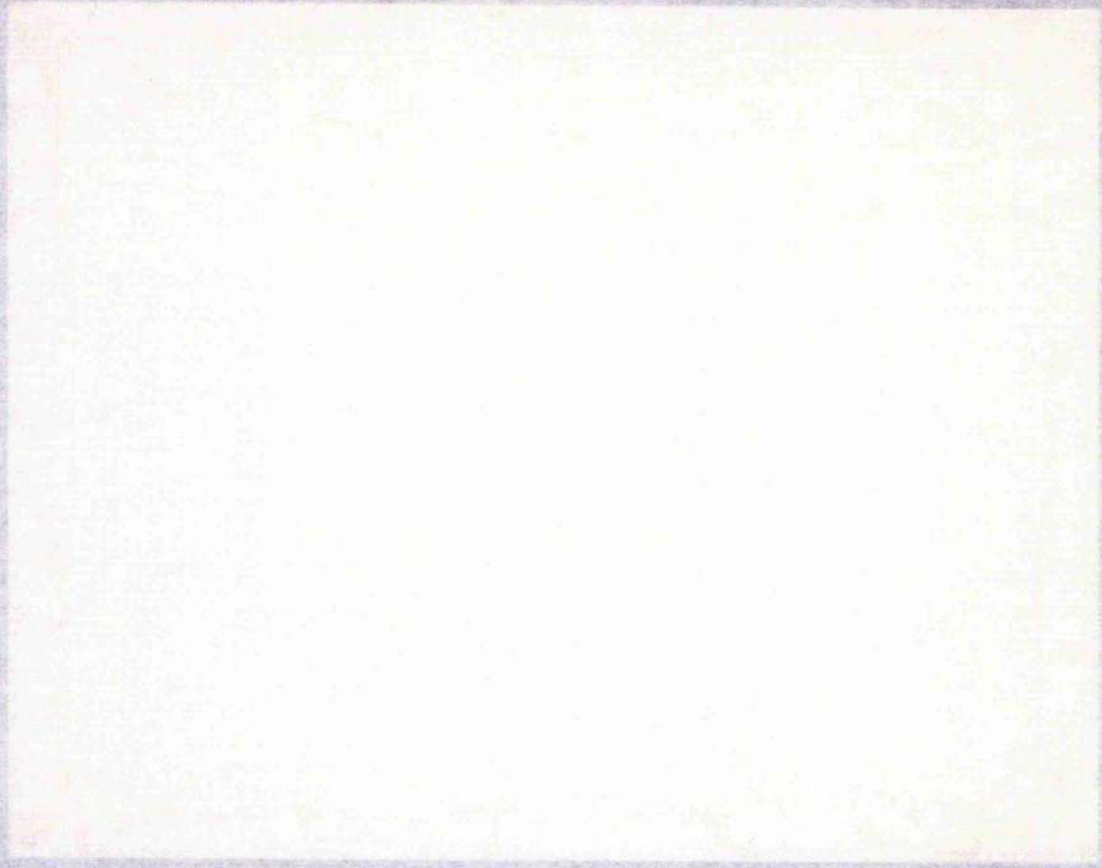
Optokinetic Nystagmus

Optokinetic nystagmus consists of two phases. A slow forward phase when the eyecups follow the direction of the rotation of the environment around the animal, and the fast return phase when the eyecups are flicked back in the opposite direction.

1. The Form of the Response.

Both the slow and fast forward ~~and~~ return phases of optokinetic nystagmus produced by various drum speeds are shown in figure 21 while data from measurements of the angle through which the unrestricted eye moves are shown in figures 22,23 and 24.

The stimulus which elicits optokinetic nystagmus is the movement of the stripes of the drum across in front of the ommatidia. The eye moves in the same direction as the rotating drum but lags increasingly behind it as shown by plotting the angular deflection of the eye during the slow phase against the corresponding angular deflection of the drum during the same period (figure 22). The effective stimulus is therefore the difference between the drum speed and the eye speed during the slow phase. This is termed the slip speed or the rate of increase of lag.



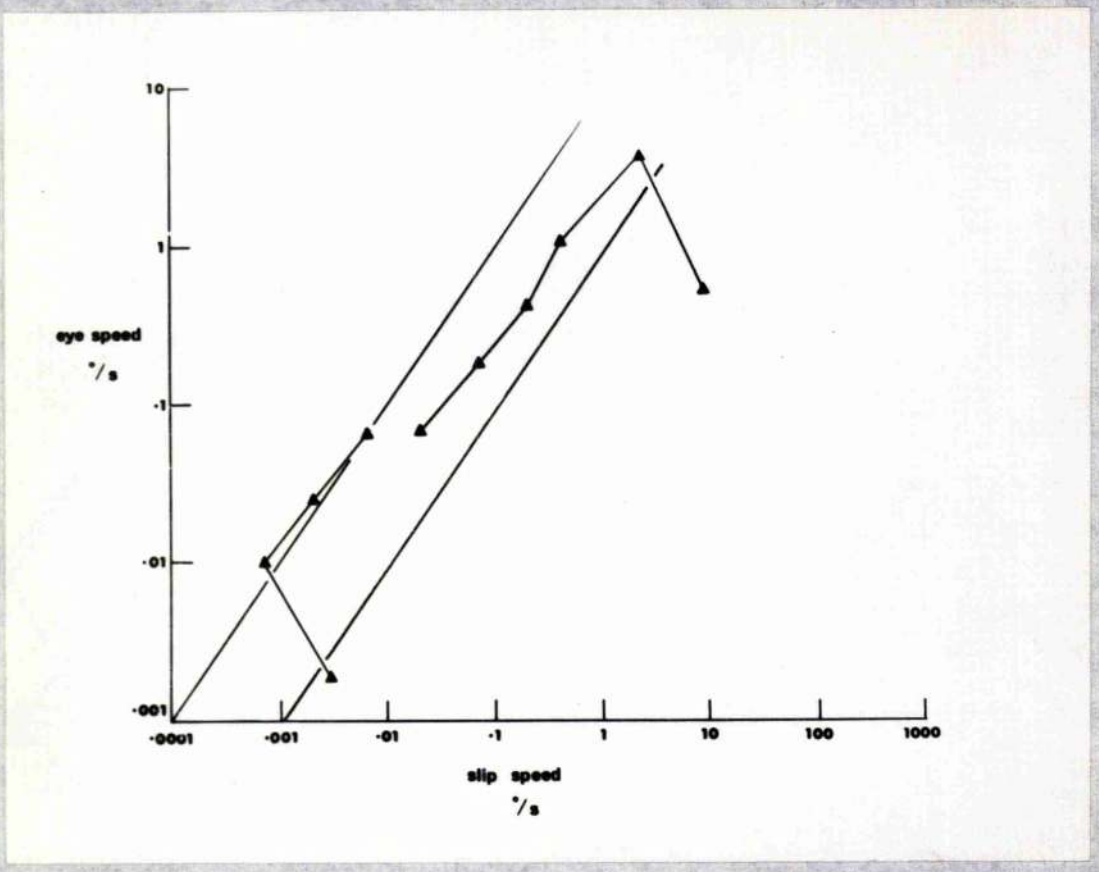
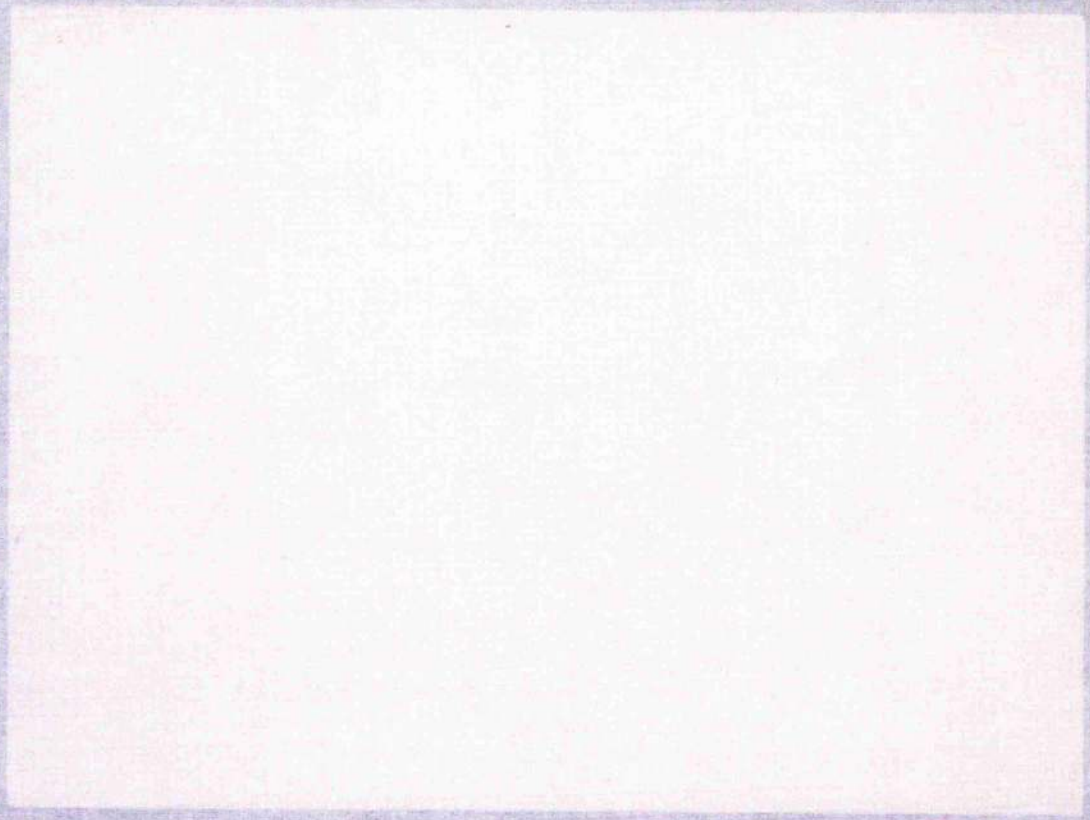


Figure 23. The stimulus, (slip speed) plotted against the response (eye speed), showing the upper and lower limits of the response. To the right of its lower limit the response increases with the increase in stimulus until the upper limit is approached at drum speeds of approximately 7°/sec. Some response is obtained even at 70°/sec. but not at 140°/sec. Results are from two different animals to avoid taking a complete series with one animal over the long periods of time which are necessary at the low drum speeds. The relation of the response to the stimulus is not proportional as shown by a comparison of the graph with the two straight parallel lines. The upper of the two parallel lines represents the propotional ratio of response to stimulus of 10.1 and the lower line represents a proportionality of 1:1.



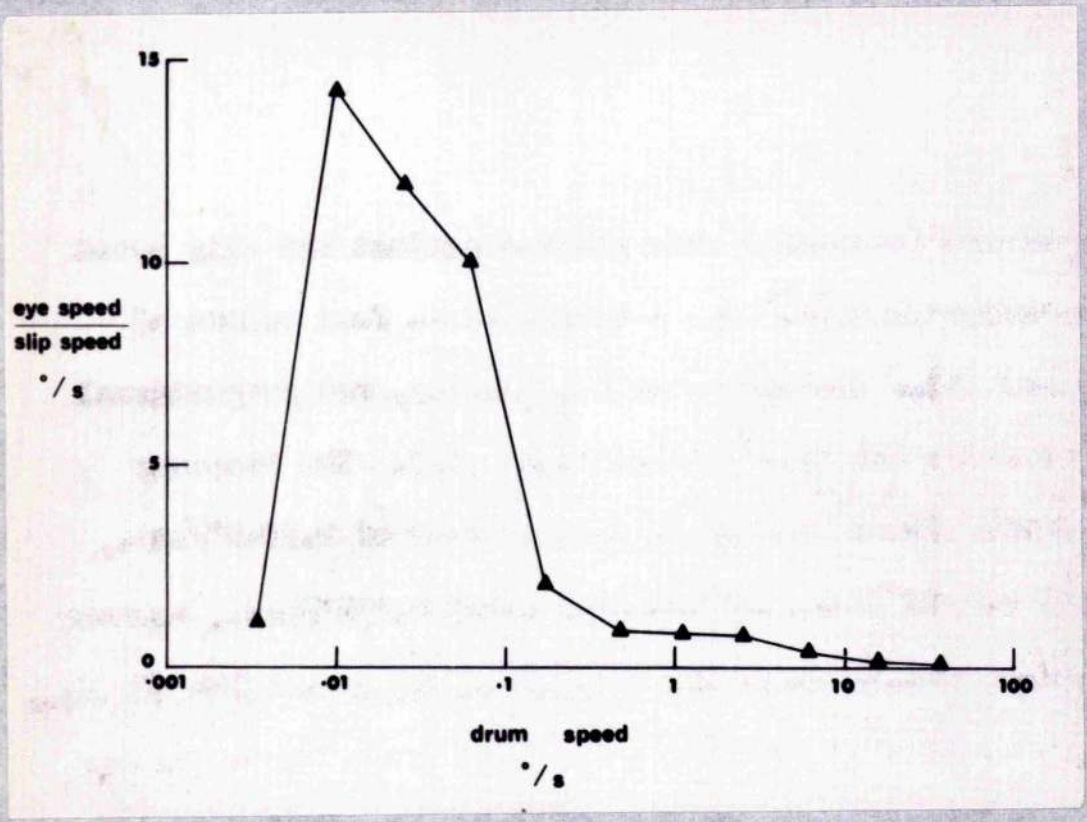


Figure 24. The relation of the eye speed to the slip speed expressed as gain, for different drum speeds. The gain at drum speeds of 1°/sec. to 10°/sec. is relatively low and the graph shows the response to be approximately proportional to the stimulus at these stimulus velocities. At very slow drum speeds the gain increases rapidly until the response fails at the lowest drum speed. The increase in gain corresponds with the approach of fixation of the eye on the moving stimulus. If fixation occurred, the slip speed would become zero and the gain infinite.

The speed of the eye (response) when plotted against the slip speed (stimulus) follows a straight line relation over about four orders of magnitude (figure 23). The eye speed is, however, not proportional to the slip speed for all drum speeds (figure 24). The response fails at a definite lower limit. At a drum speed of 0.0048°/sec., the eyespeed is 0.0018°/sec. and the slip speed 0.003°/sec., however at a slightly faster drum speed the slip speed falls to 0.00073°/sec., suggesting that at lower speeds the stimulus is not fully effective in exciting the central co-ordination mechanism. There is therefore a lower threshold of drum speed, below which the optokinetic response rapidly falls off and this is interpreted not as a failure of vision but as arising from the inability to move the eye so slowly. The upper limit of the response is demonstrated by its failure at drum speeds of more than 5°/sec. The significance of the range over which the response occurs and the factors which contribute to the upper and lower limits of the response will be considered in this discussion. The optokinetic response of unilaterally blinded animals is similar to that of normal animals. An eye covered by a screen or painted over

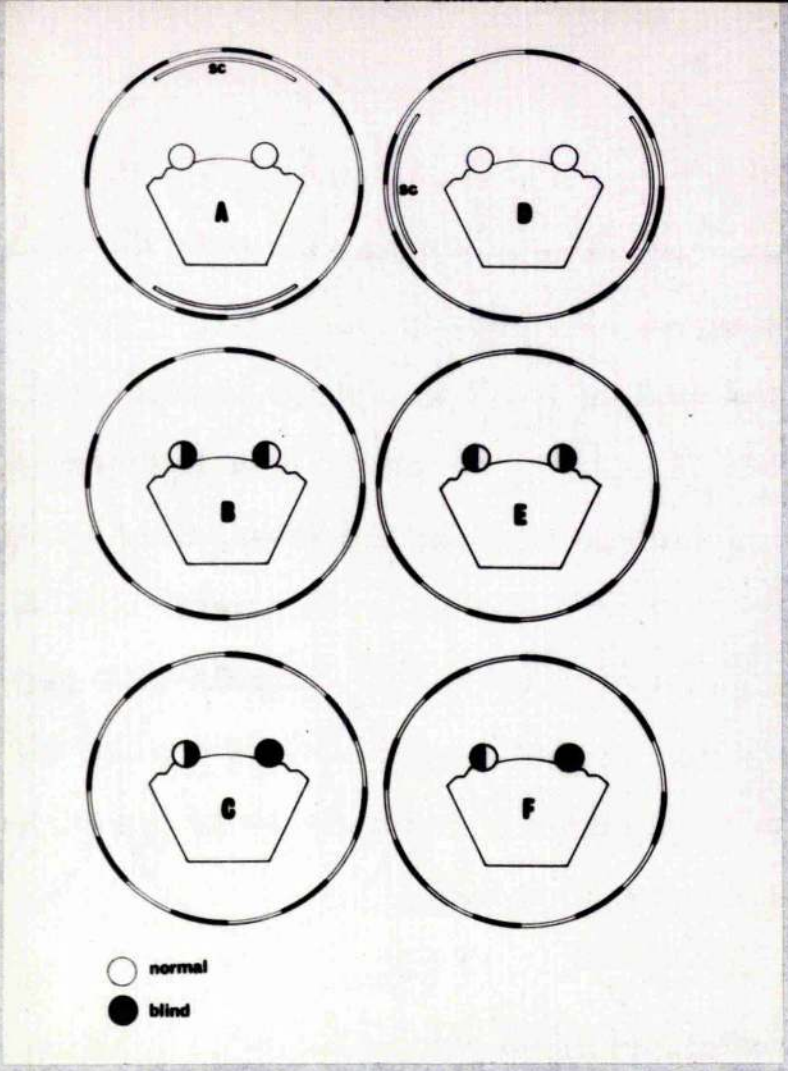


Figure 25. The suppression of the optokinetic response by partially blinding the eyes with black paint or restricting the visual field with screens (sc) interposed between the animal and the rotating drum. Optokinetic nystagmus occurs in A,B and C but not in D,E and F. Functional exclusion of the anteriorly facing ommatidia, as in A and B, does not prevent optokinetic nystagmus, but exclusion of the outer halves, shown in D and E, does prevent the response. The presence of the outer half of a single eye was sufficient to produce optokinetic nystagmus, C compared with F. It is suggested that the various areas of the eye are differentially sensitive to movement. Whatever the mechanism, optokinetic effects which may have been induced by the animal walking sideways, are eliminated.

or otherwise unable to see any sharply defined feature of the environment, executes the slow and fast phases in synchrony with the normal eye. This is termed driving the blind eye by the seeing eye.

Partially blinding the eyes by painting over particular areas of the corneal surface with black paint or restricting the animals view of the striped drum by interposing opaque screens, shows that the optokinetic response cannot be produced unless the outside half of at least one eye remains uncovered (figure 25). Animals with only anteriorly facing halves of the eyes uncovered did not exhibit any optokinetic response. This point will be returned to in the discussion in connection with sideways walking in crabs.

2. Surgical Interference with the Response.

A crab blinded by cutting through both optic tracts shows compensatory eye movements during its own active turning and these may be simulated to a certain extent by rotating the legs beneath the crab while holding the carapace still (Dijkgraaf 1956). Therefore in the experiments described the proprioceptive influences of the legs have been excluded by making observations only when the legs are stationary. The resting position of the legs is found to be of no importance.

Cutting through the oculomotor nerve completely abolishes optokinetic nystagmus and other compensatory eye movements where the eyecup is moved in relation to the eyestalk, although as described above, the retraction reflex can still be carried out by the fast motor axons of the optic tract. It does not follow however that all the efferent axons necessary for the production of the eye movements

are confined to the oculomotor nerve. The movements may have been prevented by the loss of necessary proprioceptive information passing from the periphery along the oculomotor nerve and which may be essential for the co-ordination of the various eye muscles. However this possibility can be eliminated by the use of crabs with the oculomotor nerve cut on the one side and the optic tract cut on the other side. This preparation shows an intimate link between the visual information received by the immobilised seeing eye and complete optokinetic nystagmus with slow and fast phases, carried out by the blinded eye. The oculomotor nerve therefore transmits to the blinded eyecup sufficient information for optokinetic nystagmus although the seeing eye is stationary and there is no possibility of a proprioceptive control of the movement of the seeing eye or of visual control of the moving eye itself. This phenomenon will be considered in more detail in the discussion.

Experiments following cutting the optic tract or oculomotor nerve are somewhat complicated because there is a small disorientation of the eyecup on the same side as the operation. As a precaution, and to examine this effect more closely, thin glass fibres were attached to the eyecups of a freely moving crab in such a way as not to interfere with eye movement or vision. The angles which the fibres made with each other and with a stripe painted down the midline of the carapace of the crab, were measured as accurately as possible. In the intact animal the eyes are almost always at a constant angle to one another but the angle between the eyes and the median stripe

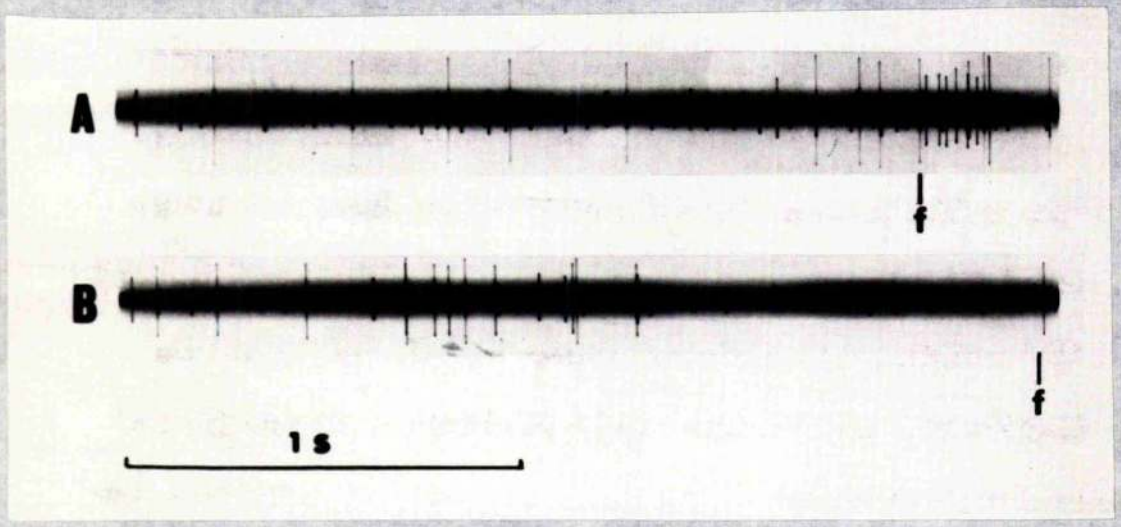
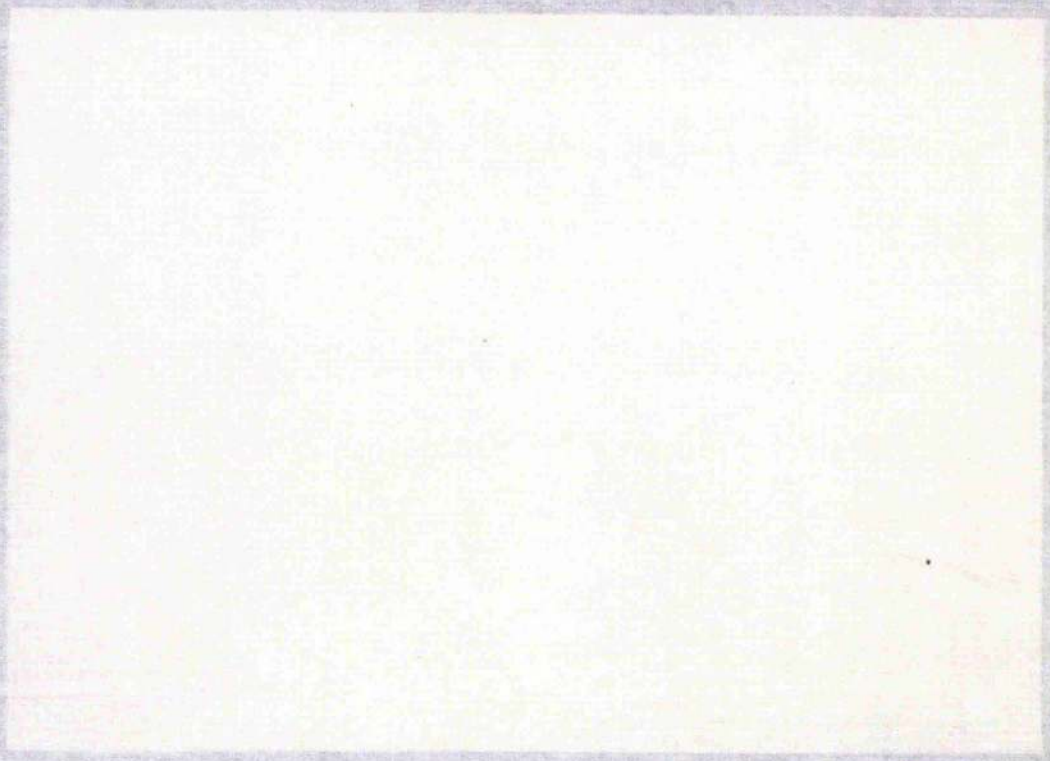


Figure 26. Afferent impulses from mechanoreceptors, recorded from the optic tract during optokinetic nystagmus. A similar increase in the activity of these nerve units could be obtained by mechanically stimulating the eyecup with the animal in the dark. In A, the smaller unit, also afferent, fires only during the fast phase (f). B, a similar nerve unit in a different preparation showing the characteristic irregularity of the response obtained from the mechanoreceptors during optokinetic nystagmus. The recordings were made with silver electrodes. Scale = 1.0 seconds.

on the carapace varies with the slightly different position assumed after the animal turns of its own accord. Cutting the optic tract changes the position of the eye on the operated side. However the new angle between the eyes is maintained when the eyes change their position relative to the midline as the animal moves itself or after optokinetic nystagmus. It is not possible to say whether the initial disorientation is due to operational trauma or the prevention of proprioceptive or motor information which normally travels along the optic tract. The disorientation does not arise from the loss of vision because crabs blinded with black paint hold their eyes at the normal angle to each other and to the midline. Cutting through only the oculomotor nerve produces a change in the normal position of the extended eye; it now remains in constant relation to the carapace during the optokinetic movements of the other eye, or during active turning of the animal.

3. Electrophysiology of Optokinetic Nystagmus

In the optic tract the nerve impulses which are most easily recorded are from the large efferent axons during the retraction reflex, and the massive discharge of afferent spikes caused by passing a shadow across the eye. Afferent units with response to the movements of the visual field in one direction were individually distinguished in micro-electrode recordings. By gently moving the eyecup in the light and in the dark with the electrode in the same position, these impulses are established as being visual and not from mechanoreceptors which are excited by the movement of the eye



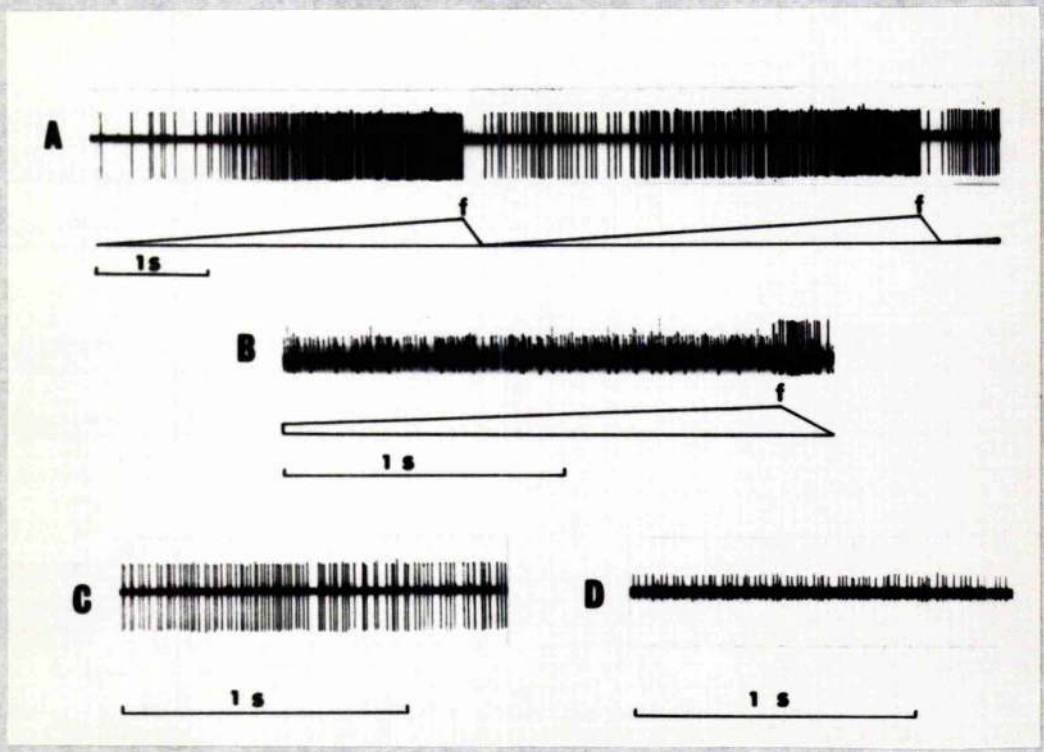


Figure 27. Oculomotor nerve impulses which are correlated with optokinetic nystagmus. The relative movements of the eyecups in A and B are shown beneath the recordings. A, the increase of frequency of efferent impulses at progressively larger angles of deflection during the slow phase of optokinetic nystagmus, and the central inhibition during the fast phase (f). B, efferent impulses which are active only during the fast return phase (f). C and D the response of two efferent units of the same type which are described in A, to opposite movements of the visual field. The recordings in C and D were made from the same preparation and without moving the electrode; the different spike heights of the functionally distinct nerve units are caused by circumstances at the recording tip. Scale = 1.0 seconds.

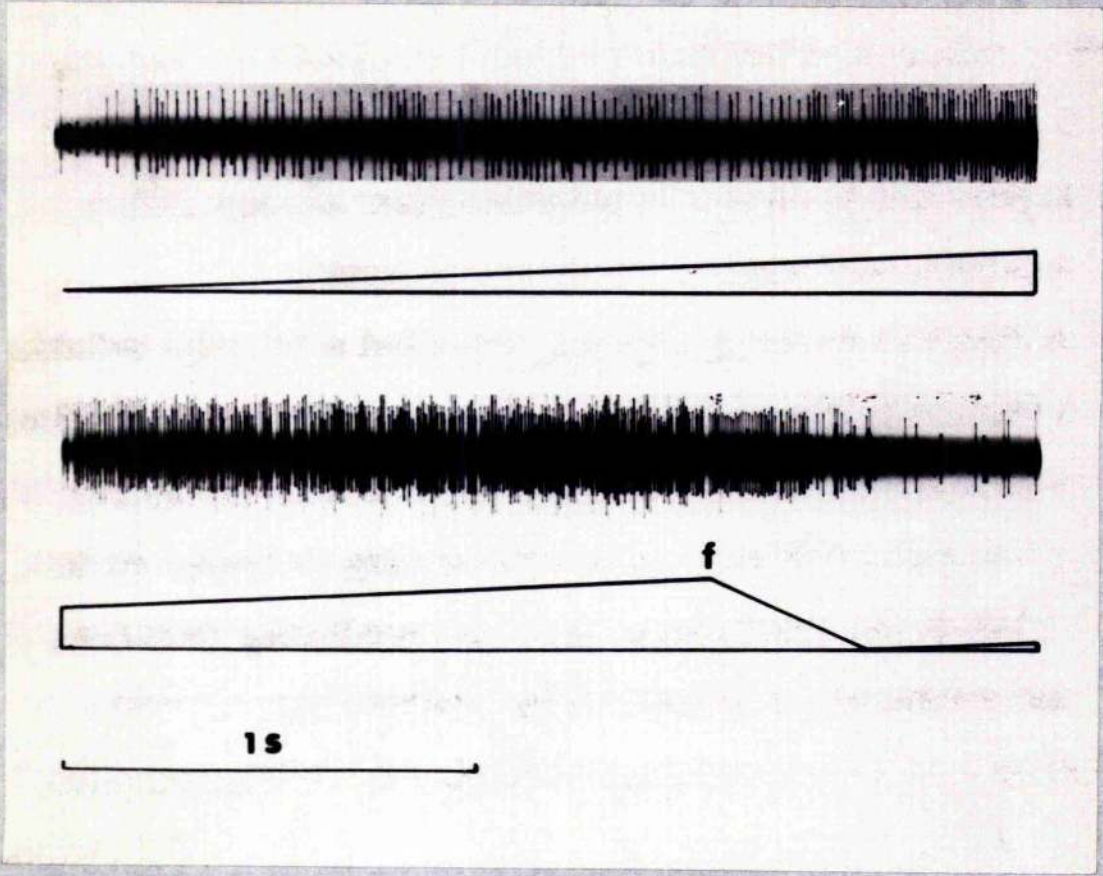
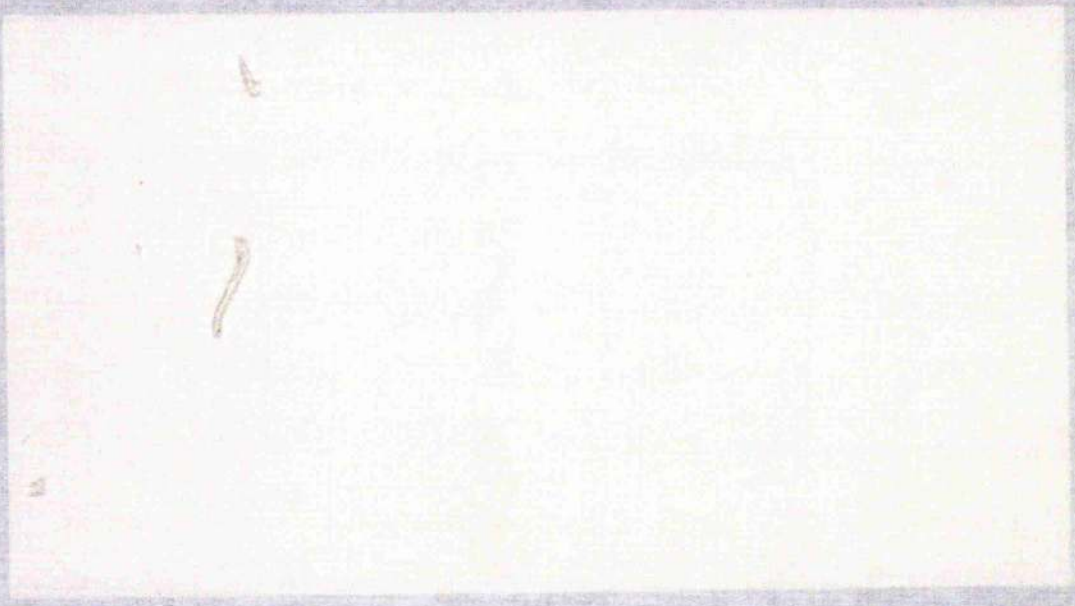


Figure 28. Recordings showing the sequence of impulses in the oculomotor nerve which are correlated with the slow and fast phases of optokinetic nystagmus. The relative movement of the eye cup is shown beneath the records. The frequency of a number of efferent units increases with the progressively larger deflection of the eye during the slow phase of optokinetic nystagmus. These impulses are inhibited during the discharge of the fast phase (f) efferent fibres. Relatively few neurones fire during the fast phase. The recordings were obtained with silver electrodes. Scale = 1.0 seconds.

during optokinetic nystagmus (figure 26). The visual response to moving shadows was subdued but not completely inhibited by forcing the eye into its socket with no nerves cut. It is not known whether this slight suppression is caused by proprioceptive sensory inflow or by the mechanical screening effect of the carapace.

Efferent impulses in the oculomotor nerve had a definite relation to the eye movements during optokinetic nystagmus. The nerve impulses most often recorded, fire at a slow irregular rate when the eyecup is stationary but more regularly and with increasing frequency as the eyecup moves through the slow phase. They are completely inhibited during the fast return phase (figure 27A). Another type of nerve unit, apparently a fast motor axon , is active only during the fast phase, when it discharges a rapid burst of impulses at high frequency, as in figure 27B. The consecutive discharge in the same nerve bundle is recorded with the silver electrodes (figure 28). A greater number of nerve units fire during the slow phase than during the fast phase and it is suggested that not only do the eye muscles have separate slow and fast motor innervation, but those eye muscles which collectively produce the fast phase may share a common fast axon. Both the fast and slow phase types of neurone have been reported in Grapsus and other decapods (Waterman and Wiersma 1963).

The efferent impulses in the oculomotor nerve are specific to the direction in which the eye moves as would be expected of motor impulses to the ten muscle blocks of the eyecup (figure 27C and D).



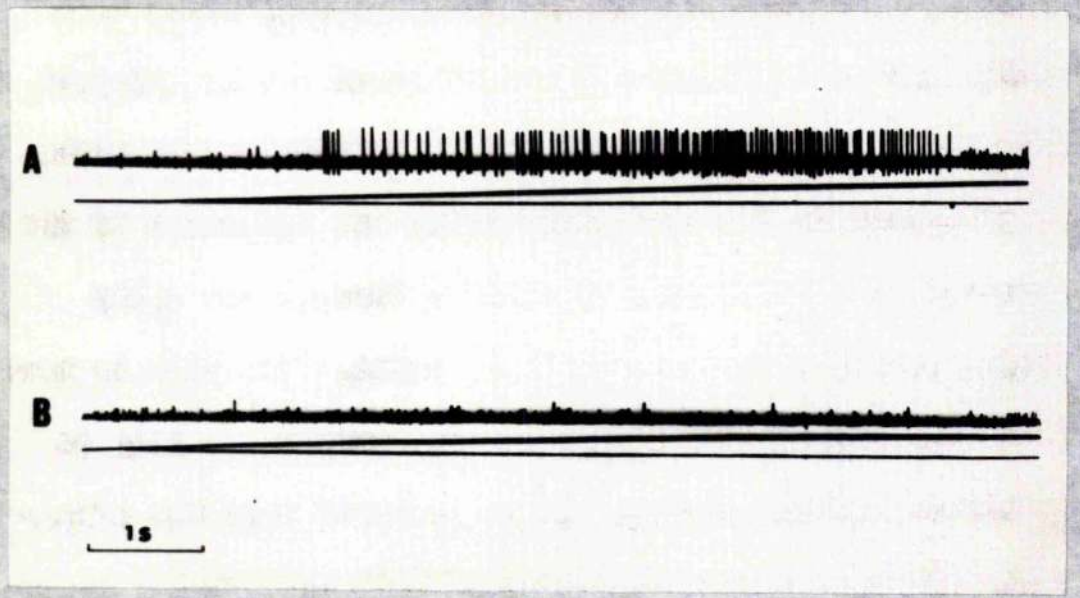


Figure 29. Efferent impulses (upper trace) recorded from the oculomotor nerve of an eyecup which is forced to move relative to a stationary contrasting visual field. A, the response with the visual field illuminated, B, the same in the dark. The records were taken from the oculomotor nerve of the seeing eye of a unilaterally blinded animal. A stainless steel microelectrode was used and the imposed movement of the eyecup (lower trace) was monitored by the apparatus described in figure 7. Scale = 1.0 seconds.

Also these units are silent when the eye is moved back and forth in the dark (figure 29A and B). This result and the fact that visual responses are never recorded from the oculomotor nerve, shows that the impulses illustrated in figures 27 and 28 could not be afferent, a fact which is useful in the analysis of records from intact crabs.

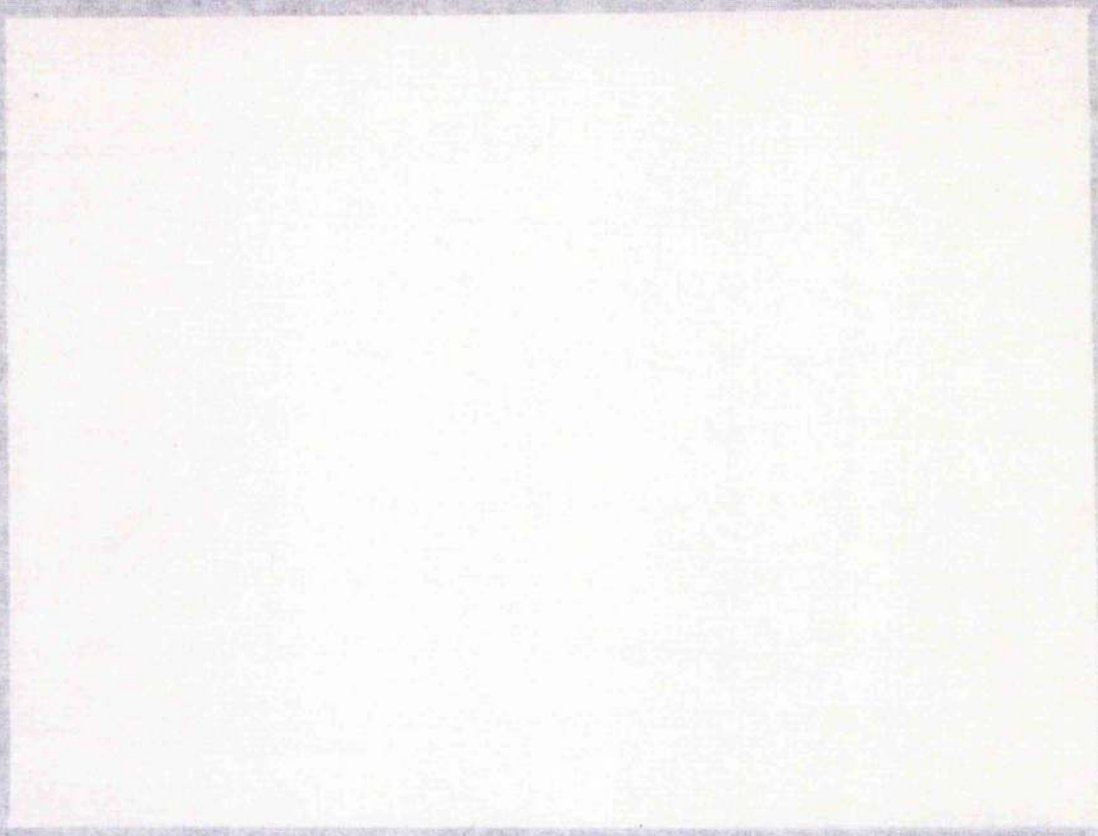
Efferent responses in the oculomotor nerve are unchanged if the eye on the recorded side is blinded by cutting through the optic tract or painting over the cornea with black paint. The same is true if the eyecup on the driven side is completely removed, so long as the other eye has functional vision. It is inferred that the efferent commands for the optokinetic movements of both eyes form a pattern which is centrally initiated and is maintained by the flow of purely visual stimuli from either eye, without preference to any other receptors. The visual input alone is transformed to a motor output in relatively few motor axons, over about four orders of magnitude of stimulus velocity. It must be remembered that there are ten eyecup muscle blocks on each side and that during the precise optokinetic movements the two eyecups move in the opposite directions relative to the midline. Since the motor axons to these muscles originate in the brain, and the optic tract has so far yielded only responses from interneurons sensitive to movement of the visual field it is suggested that final integration takes place in the brain. This point will be raised again in the discussion with reference to figure 47.

and the consideration of the overall neural mechanism of optokinetic nystagmus.

4. Initiation of the Fast Return Phase.

The fast phase of optokinetic nystagmus occurs when the motor impulses driving the slow phase reach a certain frequency. This frequency is different in different preparations because of the number of separate muscle blocks and different neurones involved. The stimulus for the onset of the fast phase does not depend on muscle tension or on the position reached by the eye, as shown by the continuation of the normal flow of efferent impulses when the eyecup of a driven eye is completely removed or prevented from moving or even forced in the opposite direction. The progressive increase in frequency of impulses, followed by a brief pause during which other neurones give a rapid burst of spikes, remains exactly as before. These experiments eliminate proprioceptors as possible indicators of the appropriate time or place for the flick back but other cues which can indicate the eye position will be considered.

The fast phase always occurs at approximately the same eye deflection although both the eye speeds and slip speeds are different for different drum speeds. If the rotating drum is stopped with the eye in the middle of a slow forward phase, the fast phase cannot be induced by the movement of a single object across the field of view or even by gently moving the drum back and forth. However if the drum is stopped when the eye is very near the point at which the fast phase occurs, the flick back can sometimes be elicited by a variety of seemingly unrelated stimuli, such as rapidly turning a



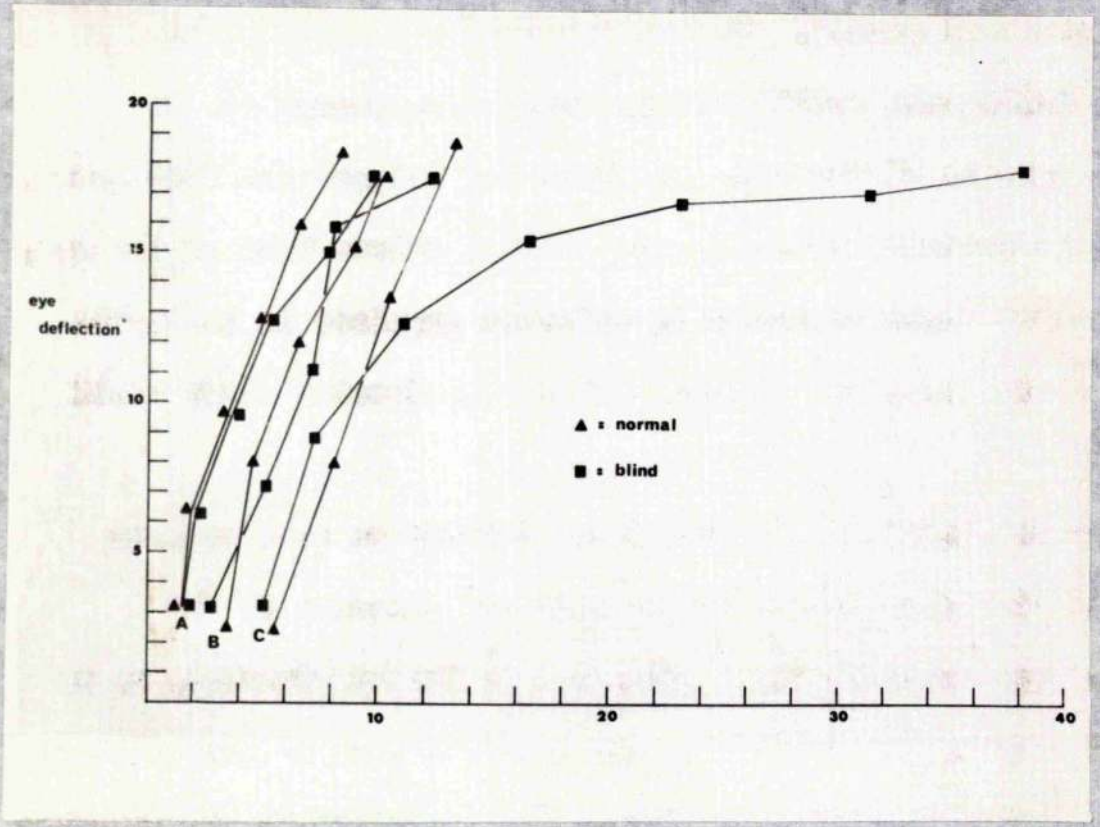


Figure 30. The contrast between optokinetic nystagmus at various drum speeds of an animal which is normal and then unilaterally blinded with paint. The angular deflection of the eye is plotted against the total lag of the eye behind the drum in degrees. Three pairs of lines A, B, C represent the results obtained for drum speeds of 0.19/sec., 0.49°/sec., and 1.2°/sec., respectively. In all cases the measurements were made over one complete slow phase of the response; the fast phase occurs immediately after the greatest deflection shown by the highest point. Towards the end of the response the eye movement slows down so producing an increase in the lag behind the drum. This delay is more pronounced in the unilaterally blinded animal, and at high drum speeds.

a light on or off, moving the legs, or gently touching the carapace behind the cervical groove. In response to these stimuli the eyes of normal animals make small scanning movements, thought to be partial retractions of the eye, and these may trigger the fast phase. However if the scanning movements are partial retractions of the eye, the eye movement would be caused by efferent impulses in the optic tract and the frequency of discharge in the oculomotor nerve would be unchanged.

Whether the onset of the fast phase depends on some measure of the visual stimulus to the eye or upon some measure of the frequency of the motor impulses going out to the eye muscles, or is influenced by both, can only be tested by alteration of the relation between the stimulus and the response. This relation is changed when one eye is blinded by painting it over with black paint, or by cutting through its optic tract - these operations have the same effect, showing that the continuous activity in the optic tract is not necessary for the execution of optokinetic nystagmus by the driven eye. The optokinetic response of an eye of a normal crab and the response after blinding the eye from which the measurements were taken, is shown in figure 30. At slow drum speeds, the relation between eye deflection and overall lag is little changed by blinding, and the onset of the fast phase occurs after the same eye deflection in each. At higher drum speeds the eyes of a unilaterally blind crab fail to keep up with the drum, the lag increases to a much greater

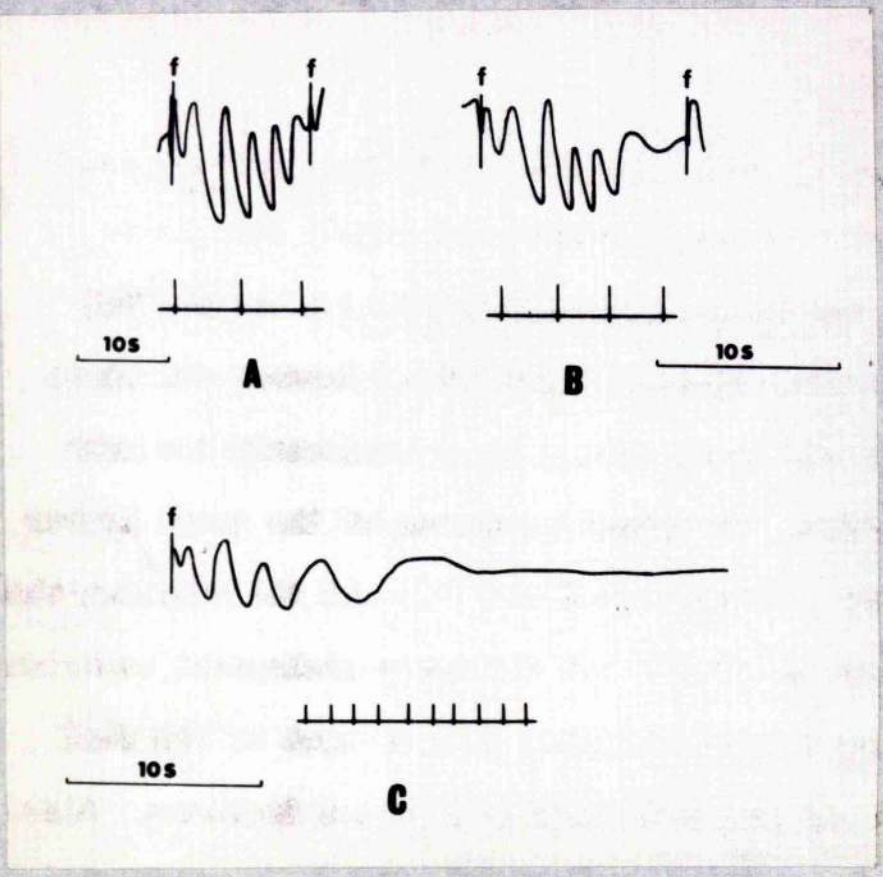


Figure 31. The movement of the unrestrained eyecup of a normal animal during the slow phase of optokinetic nystagmus. The single slow phase (progressing from left to right on the record) is bounded by two fast phases (f) and is divided by the recording mechanism into a number of peaks. The distance from the summit of one peak to the summit of the next represents an eye deflection of approximately 2 degrees. Each division of the stimulus marker (lower trace) corresponds to the boundary between the black and white stripes on the drum. A, the eye moves with approximately constant velocity throughout the slow phase. B, the onset of the fast phase (right side of record) is delayed at a higher drum speed. C, at high drum speeds the initial portion of the slow phase takes place but the fast phase does not occur, the eye being held in the direction of the moving stimulus by the animal. Scale =10.0 seconds.

extent during the last part of the slow phase and the fast phase is delayed. The onset of the fast phase in normal animals is delayed in the same way as in unilaterally blinded animals but at relatively higher drum speeds (figure 31). However the onset of the fast phase in all cases occurs at approximately the same angle of eye deflection. Therefore a measure of the total number of stripes which have slipped past the eye is not the stimulus which produces the fast phase. In all the electrophysiological experiments, the only factor which could be related to the onset of the fast phase was the increased frequency of the efferent impulses. Blinding an eye or increasing the drum speed are both operations ~~with~~ which reduce the effect of the stimulus causing the response and results in the delay of the fast phase. A similar delay of the fast phase occurs after many repititions of the optokinetic response elicited by slow drum speeds, but this may be due to a rise in the threshold of the fast phase trigger mechanism.

The above evidence points to a central fast phase initiating mechanism which is sensitive to the frequency of the efferent impulses going to the eye muscles. There are however certain neuromuscular anomalies which arise out of the theory that a critical frequency of discharge in the oculomotor nerve is the trigger for the fast phase and these will be considered in the discussion.

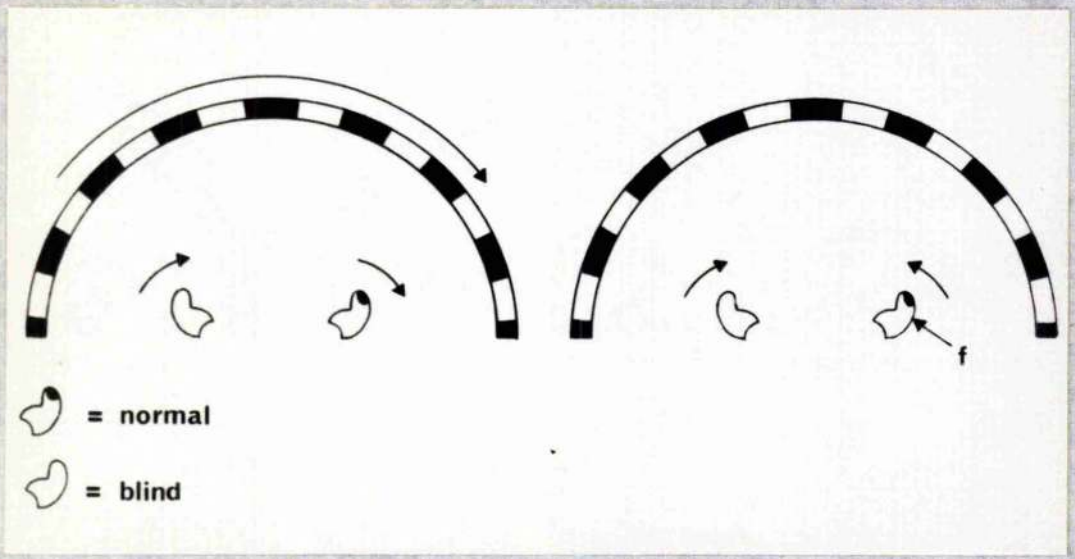
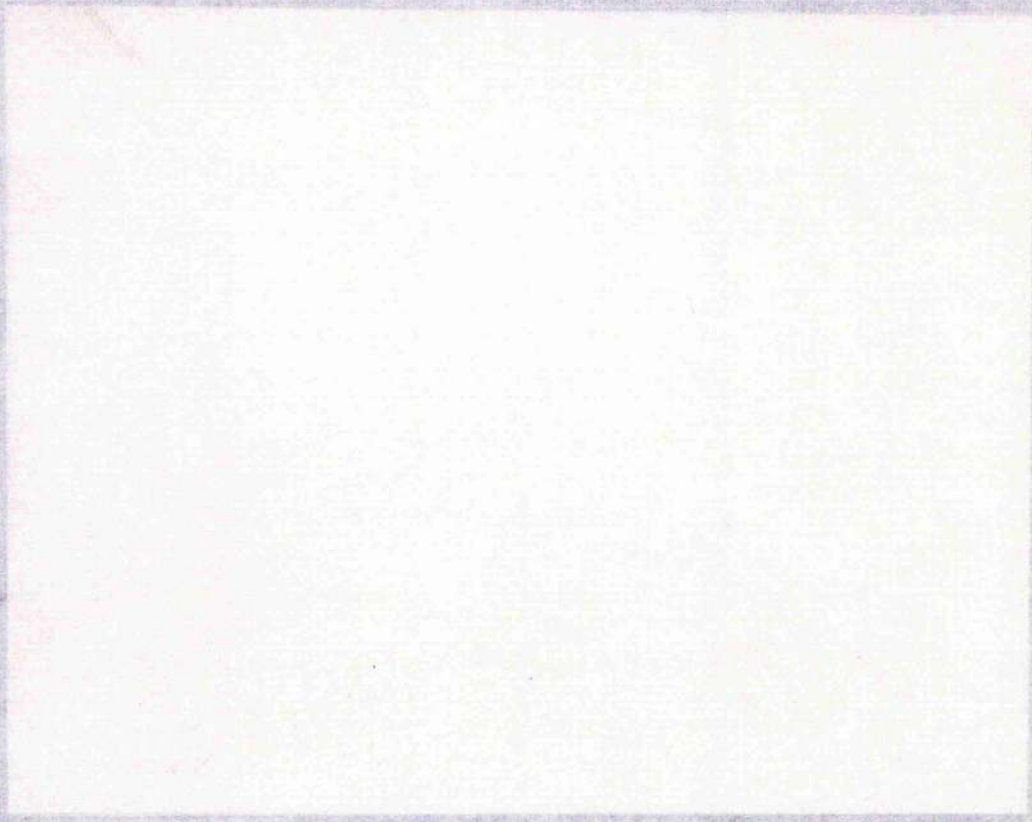


Figure 32. A, eye movements which are performed by an animal which is unilaterally blinded on its left side in response to a striped drum which rotates around it from its left to its right. B, the drum is now stationary and the normal right eye is forced (f) to the left. The blind left eye responds as though it perceives a relative movement to the right. The directions of the eye movements are shown by the small arrows.



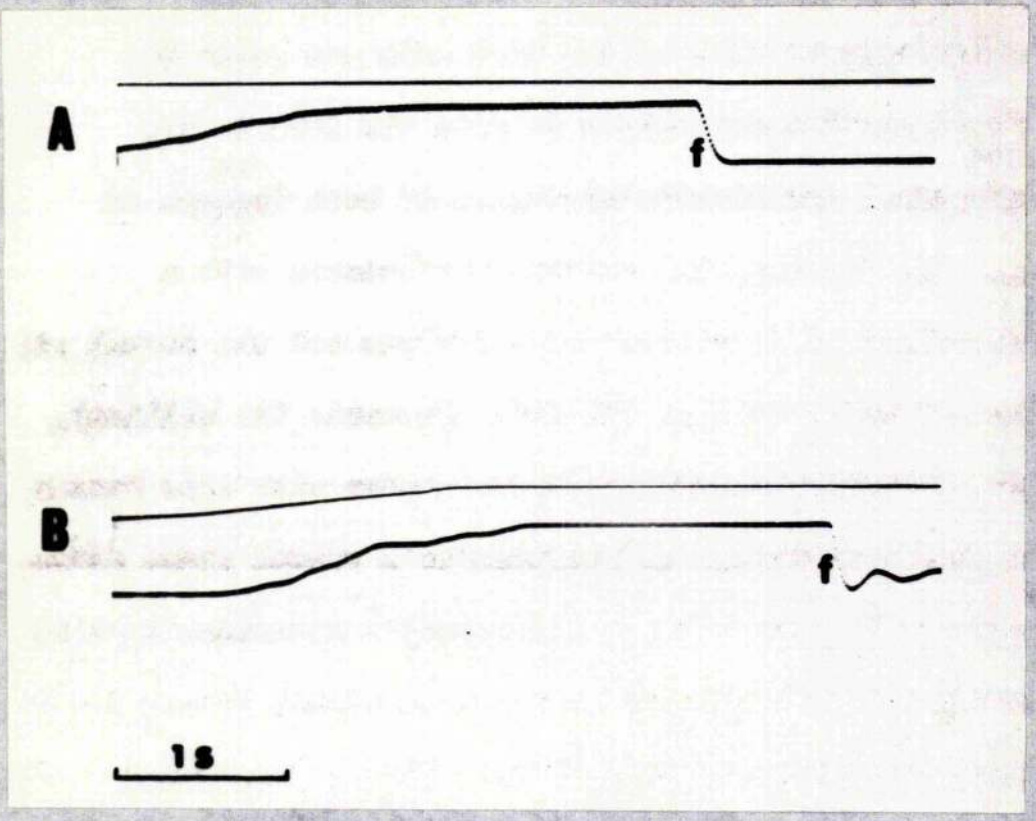


Figure 33. Optokinetic nystagmus of the blinded eye of a unilaterally blinded crab. A, movement of the blinded eye (lower trace) in response to the normal eye following a striped drum which is moving in a clockwise direction. B, movement of the blind eye in response to forcing the normal eye (upper trace) in an anti-clockwise direction in front of a striped stationary visual field. The eye movements were monitored using the lever recording system described in figure 5 which shows the slow and fast (f) phases of the optokinetic nystagmus. The uneveness of the record of eye movement during the slow phase is due to the imperfect articulation between the eyecup and the monitoring lever.
Scale = 1.0 seconds.

Section IV

Forced Movement of the Eyecup.

1. The response to forced movement.

A crab unilaterally blinded on the left side and presented with a visual field which moves around it from its left to its right side makes normal optokinetic nystagmus of both eyecups at low drum speeds. If, instead, the animal is presented with a stationary visual field of black and white stripes and the normal right eye is gently and slowly forced to the left, (towards the midline), the blinded left eye executes optokinetic nystagmus with slow forward and fast return phases as though in response to a visual field moving to its right, and the eyecups move in the opposite direction so that the animal squints. The arrangement is shown in figure 32 and 33A and B. The explanation lies in the fact that the visual information which normally produces the response is the relative movement of the black and white stripes around the eye. Evidently in this situation the eye cannot distinguish between movement of the environment to the right and movement of itself to the left relative to the carapace. Any other non-visual sensory input from proprioceptors or mechanoreceptors of the eyecups, statocysts or legs, which might have given a clue to the central nervous system as to the true movement of the eyecup, appears to be completely disregarded. In a similar unilaterally blinded animal the seeing eye can be stopped in the middle of the slow phase by a vertical peg held in its path. When this happens the blinded eye increases its speed in accordance with the new slip speed (Figure 34).

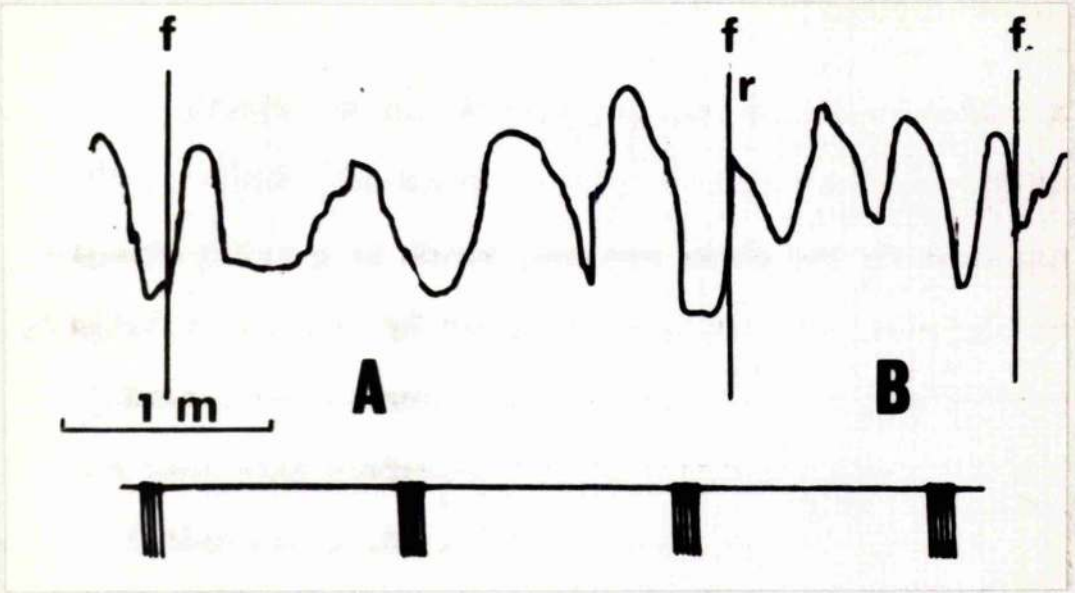


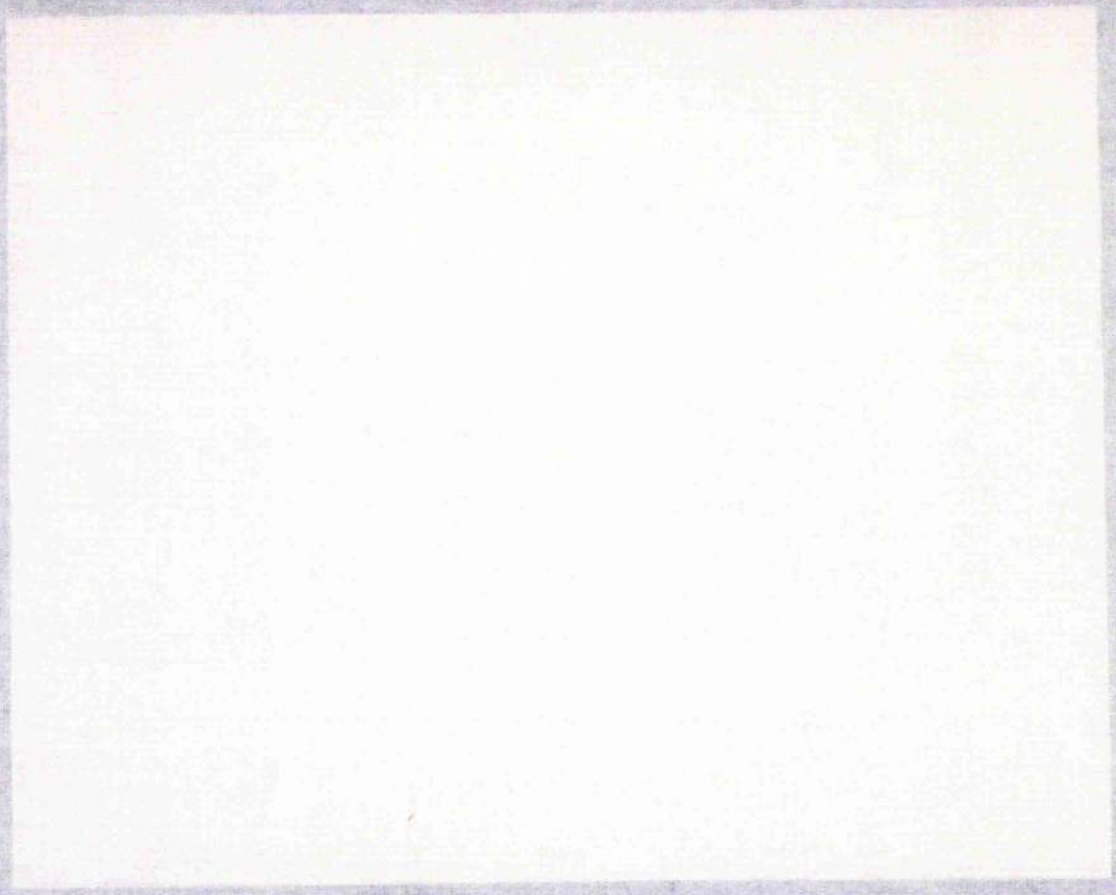
Figure 34. The change in the velocity of the movement of the unrestrained blind eye of a unilaterally blinded crab, in response to preventing the movement of the seeing eye during the slow phase of optokinetic nystagmus. Two complete slow phases (progressing from left to right on the record) and three fast phases (f) are shown. The slow phases are divided into a number of peaks by the recording mechanism and the distance from peak to peak represents an eye deflection of approximately 2 degrees. A, the movement of the blind eye when the seeing eye is not restricted and B the movement of the blind eye showing the increase in its velocity after restraining (r) the seeing eye; the drum speed remains constant throughout. The increased velocity of the blind eye in B can be explained by the increased slip speed caused by not allowing the seeing eye to move in the same direction as the drum and so reduce the apparent movement of the drum. No account is taken of proprioceptive cues which could inform the animal that the seeing eye was motionless. Scale = 1.0 minutes.

showing again that proprioceptive information about the rate of movement of the seeing eye relative to the carapace is not taken into account.

In normal animals with contrasting objects in the visual field, a forced displacement of one eyecup causes only small opposite displacement in the other eye cup, which is quickly brought back to its resting position followed sometimes by small oscillations. However, if the passive eye (the one not being forced) is placed inside a portion of a table tennis ball and therefore only sees a blank field, it moves in the opposite direction (i.e. clockwise) to which the forced eye is being moved (i.e. anticlockwise), in the same way as the blinded eye described above, and the animal squints. Therefore, the suppression of the optomotor response in normal crabs during forced movement of one eye is by visual not by proprioceptive information, and occurs only when there are stationary contrasting objects in the visual field. However, as emphasized in the discussion, a slight scanning movement and small oscillations of the blind eye are not suppressed.

2. Visual suppression of optokinetic nystagmus

Visual suppression of optokinetic nystagmus can also be shown electrophysiologically. An electrode is placed in the oculomotor nerve on the operated side of a unilaterally blinded crab and the intact opposite eye is moved slowly in one direction (i.e. clockwise) in front of a stationary visual field. The ensuing efferent impulses recorded from the oculomotor nerve of the blinded eye are those normally recorded when the environment moves in the direction opposite to the forced



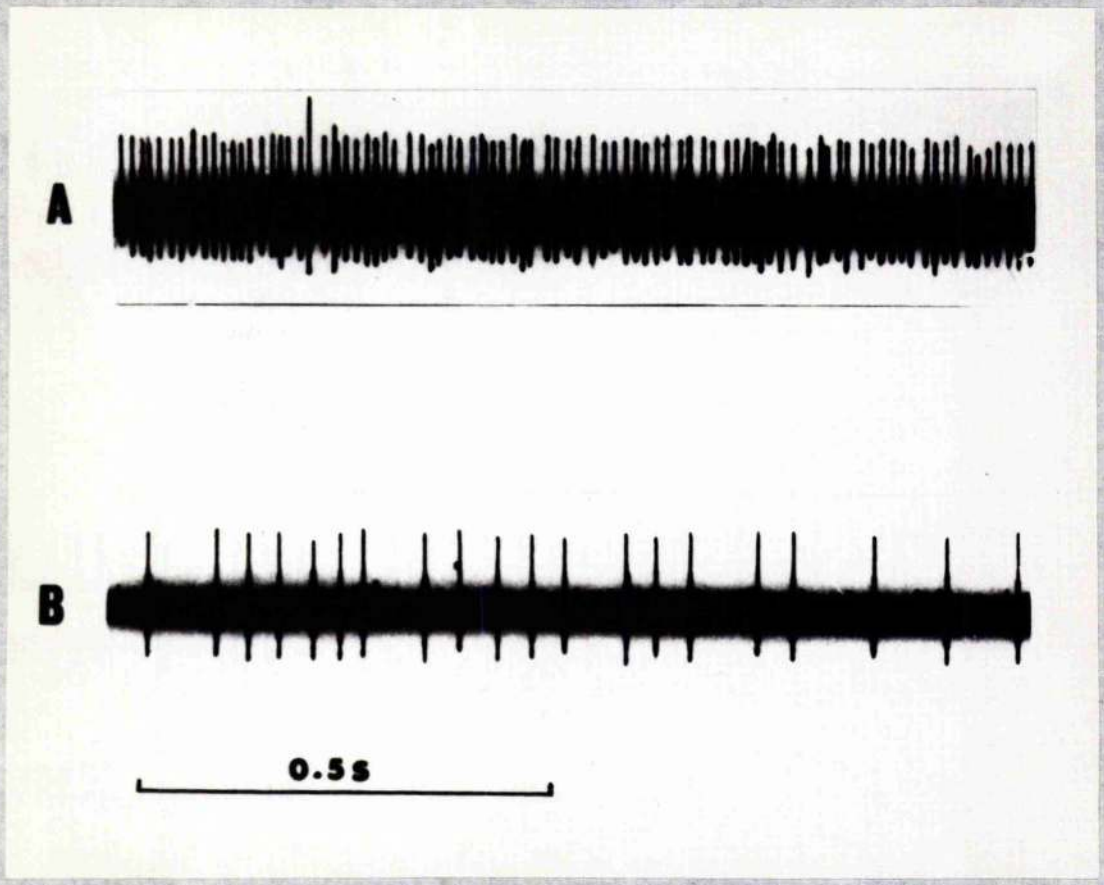
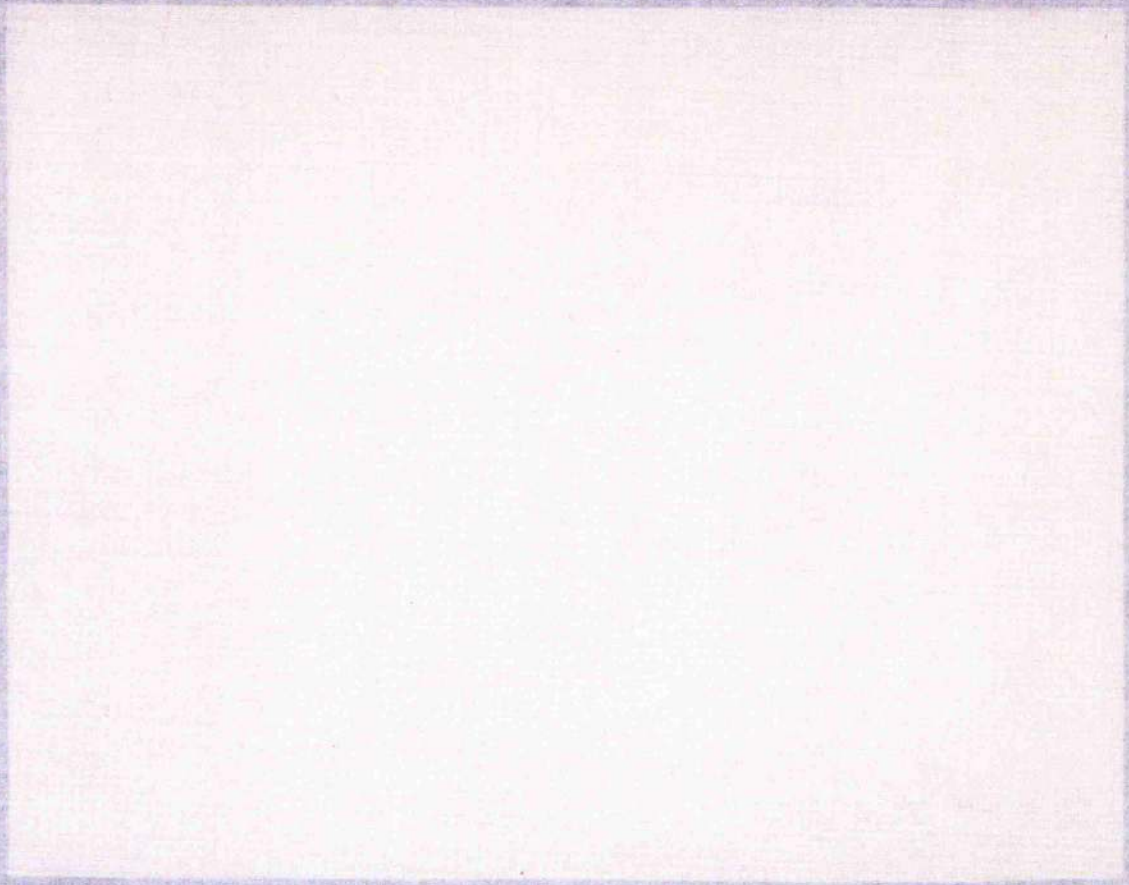


Figure 35. Oculomotor nerve impulses of a unilaterally blinded crab during forced eye movement. A, efferent impulses from a blinded eye during the forced movement of the normal eye. B, records from the same eye when both eyes are able to see, the efferent activity is now depressed. Scale = 0.5 seconds.



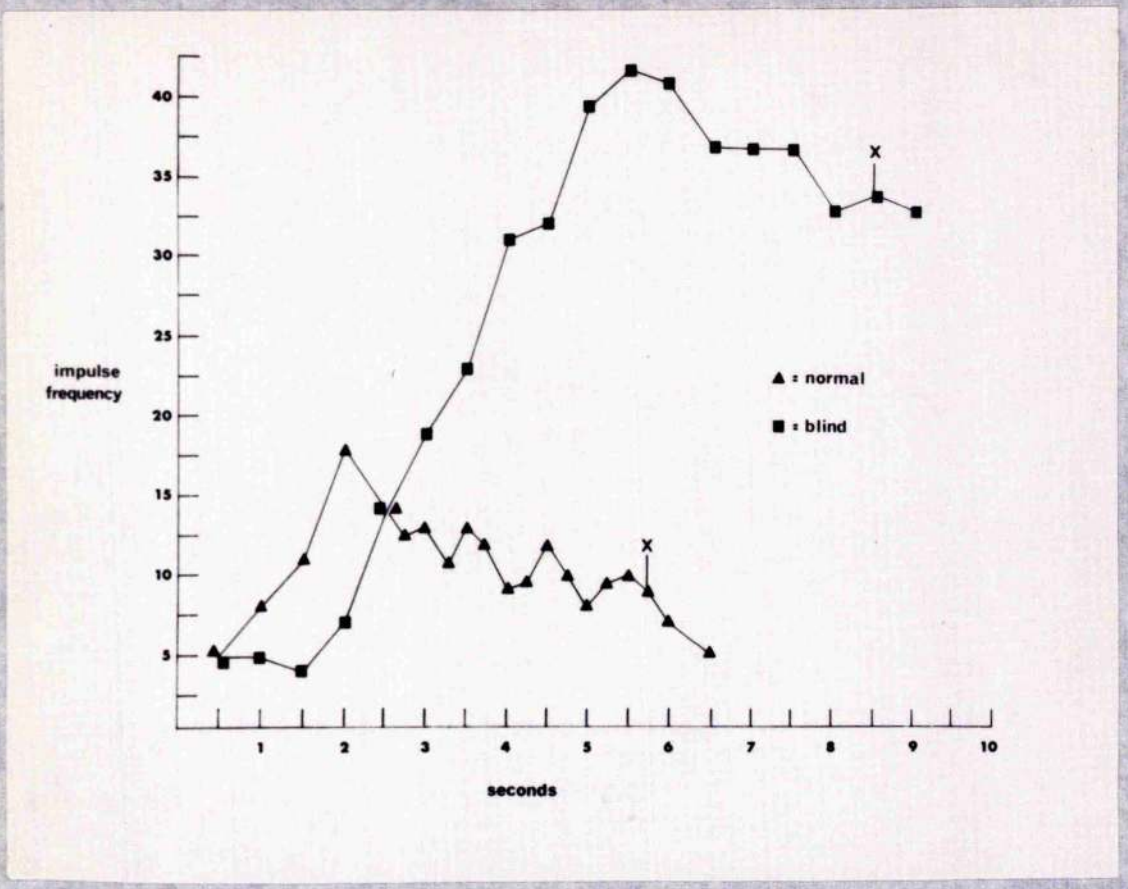
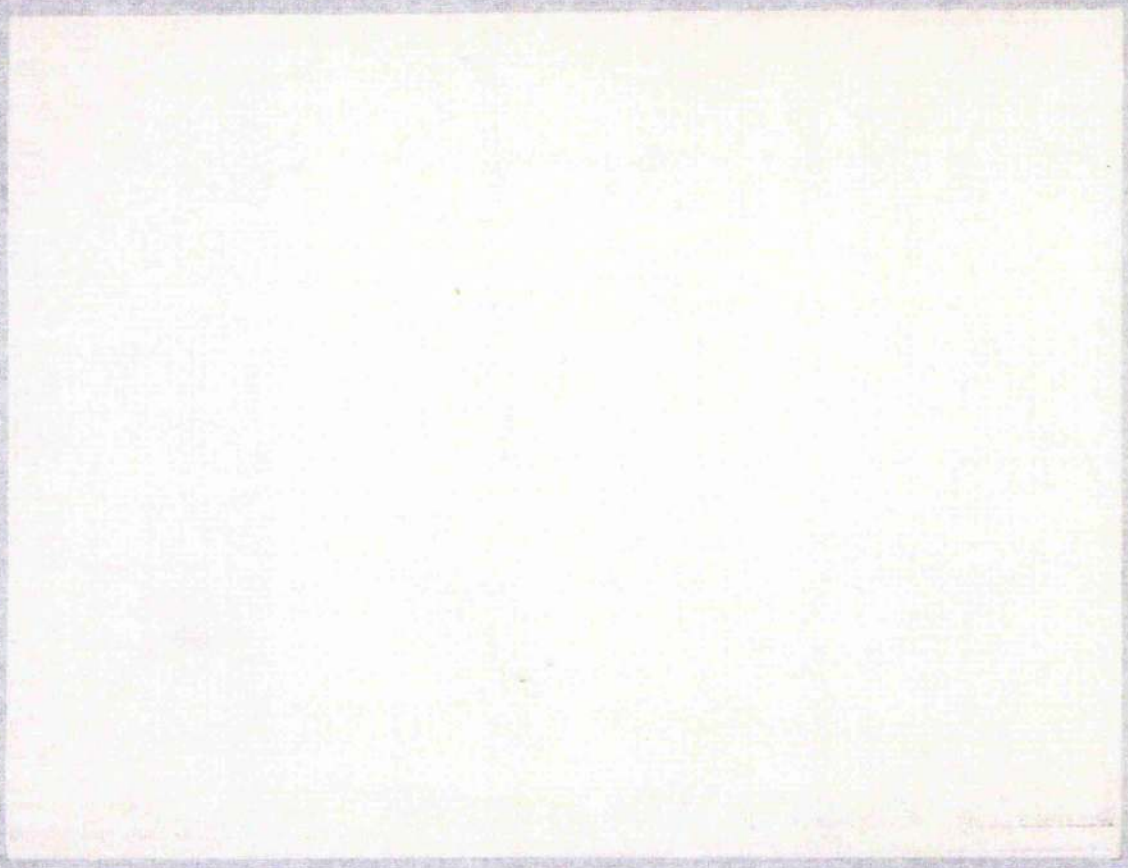


Figure 36. Inhibition of the optokinetic efferent impulses by visual input from the ipsilateral eye, as in A of figure 38. A measure of the frequency is obtained by counting the impulses over the half second periods ending at the points. The response of the unilaterally blinded animal is characteristic in that the impulse frequency arises as the slow phase of optokinetic nystagmus progresses. In contrast, the response in the normal animal falls off after the first two seconds of imposed movement and becomes irregular. In both curves the point X indicates the removal of the forcing peg and the consequent reversal of the direction of movement. The actual cessation of the forced movement and of the moving visual stimulus occurs at about the peak of the response of the unilaterally blinded animal.



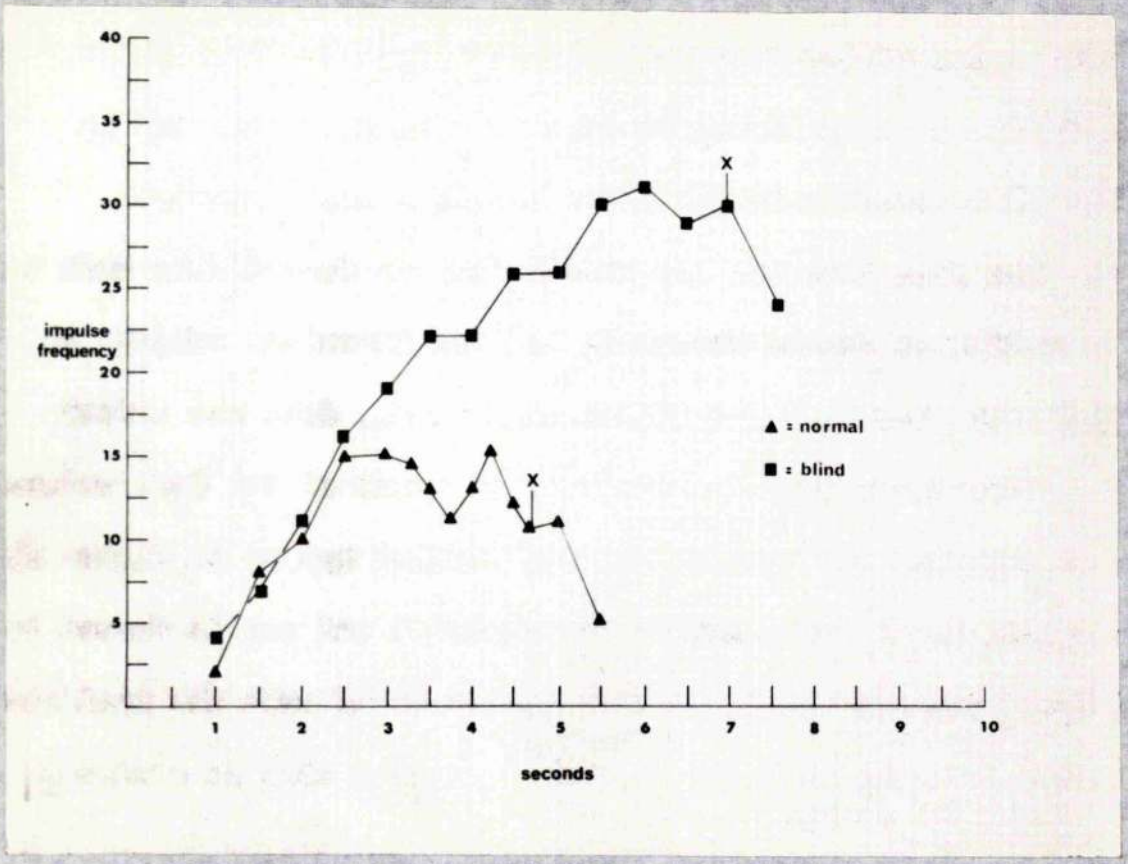
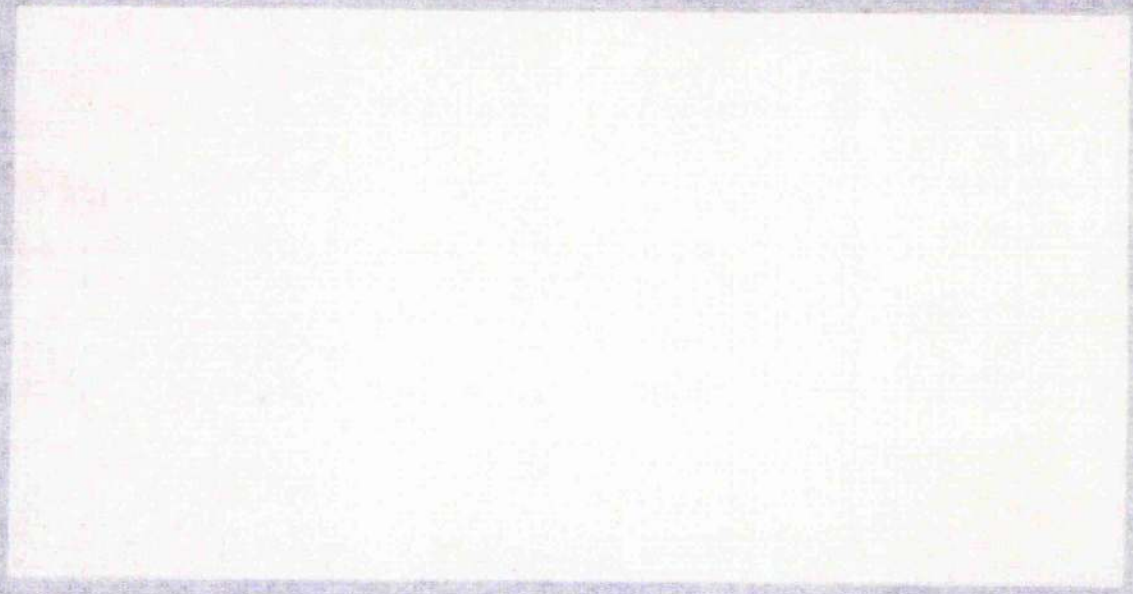


Figure 37. Inhibition by visual input from the contralateral eye as in B of figure 38. The response of the normal animal is again suppressed, as in ipsilateral inhibition but this ~~is~~ now has its origin in the opposite eye. Because the forcing speed is less the progressive rise in frequency occurs more slowly than in figure 36. In the normal animal there is the same irregularity as in ipsilateral inhibition even though the inhibiting visual information is relayed from the contralateral unforced eye. Forced movement ends at the peak of the curve and the point X marks the removal of the forcing peg so that movement in the opposite direction can occur. Frequencies are calculated as in figure 36.

eyecup movement (i.e. anticlockwise). The same apparent movement of the visual field occurs in both cases, as explained in figure 32 and 33. Before the eye is reversibly blinded, the impulses are suppressed (figure 35B). The fact that the eye muscles on the forced side tend to oppose the direction of forced movement, and are therefore subject to far greater tension than during a normal slow phase, does not affect the optokinetic nystagmus impulse rate nor the onset of the fast return phase in the oculomotor nerve of the other, blinded eye as in figure 29.

If both eyes see a field containing contrast and one is forced to move, the efferent activity in the oculomotor nerve of both the ipsilateral (forced) and the contralateral eye is much less than that in a normal optomotor response of the same rate as the forced movement, as shown by the frequencies in figures 36 and 37. Normal efferent discharges can be again elicited merely by holding the passive eye closed in its socket or by surrounding it by a table tennis ball, both of which treatments reversibly blind the eye in these experiments. The experiments show that in one case of inhibition, here called ipsilateral (figure 36), which is the more pronounced, the relative movement across the right eye which perceives a moving field sets off a right eye optokinetic nystagmus which is counteracted by different visual information from the left eye. Similarly in the other form of inhibition, here called contralateral (figure 37) the left eye sees a moving field and initiates optokinetic nystagmus but the conflicting visual information from the right eye inhibits the efferent commands to itself and to the moving left eye so that optokinetic nystagmus is not maintained. The two types of suppression are shown diagrammatically



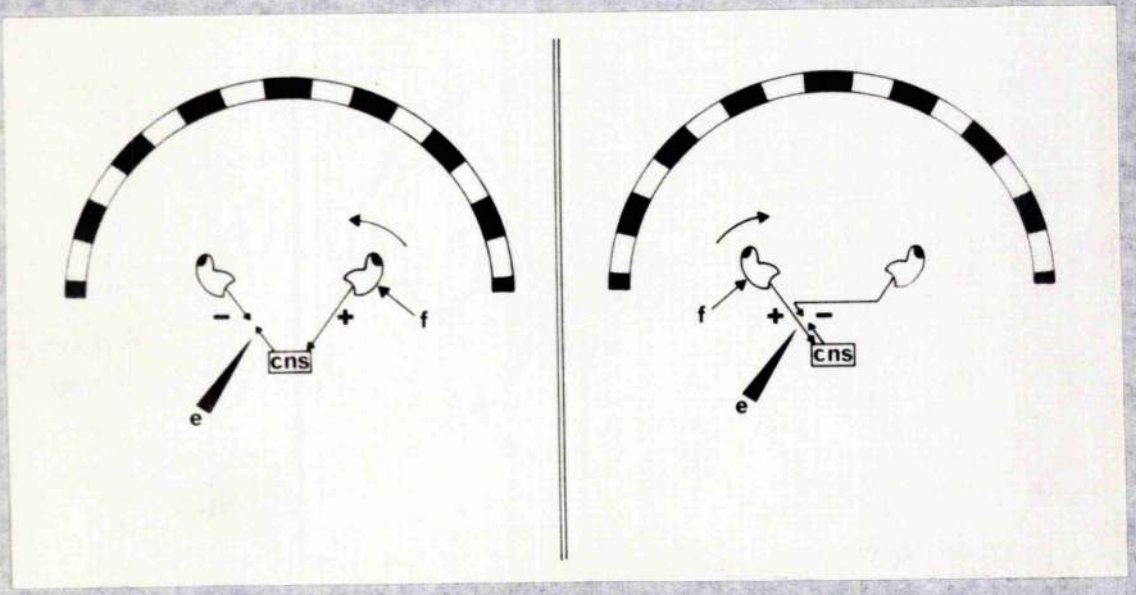


Figure 38. Ipsilateral and contralateral inhibition of the slow phase of optokinetic nystagmus. A, efferent impulses in the oculomotor nerve are inhibited (-) by visual information from the same eye (ipsilateral inhibition). The initial excitatory signals (+) come from the contralateral forced eye (f). B, the eye from which the recording is made is now the forced one (contralateral inhibition); the inhibitory visual information (-) is now issued by the contralateral (right) eye which not only inhibits its own movement but also that of the forced eye (f). In all cases arrows from the eyes to the brain (CNS) indicate afferent visual excitation and arrows from the brain indicate the optokinetic efferent impulses. The electrode (e) records from the same oculomotor nerve and from the same optokinetic nerve units in both experiments.

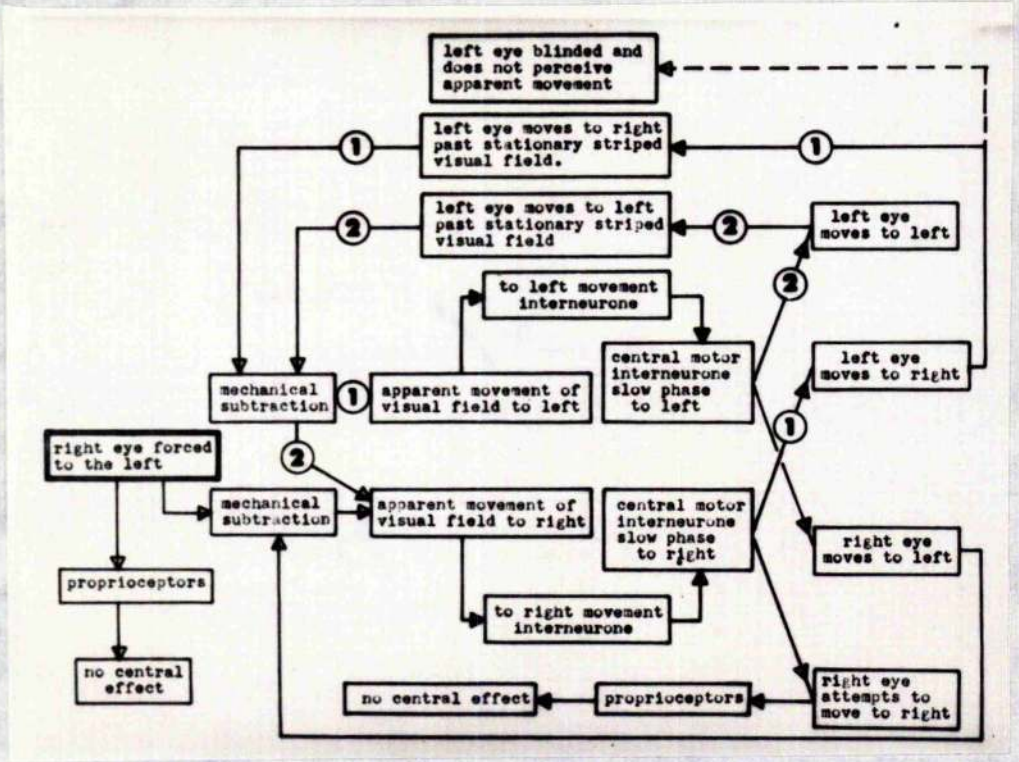
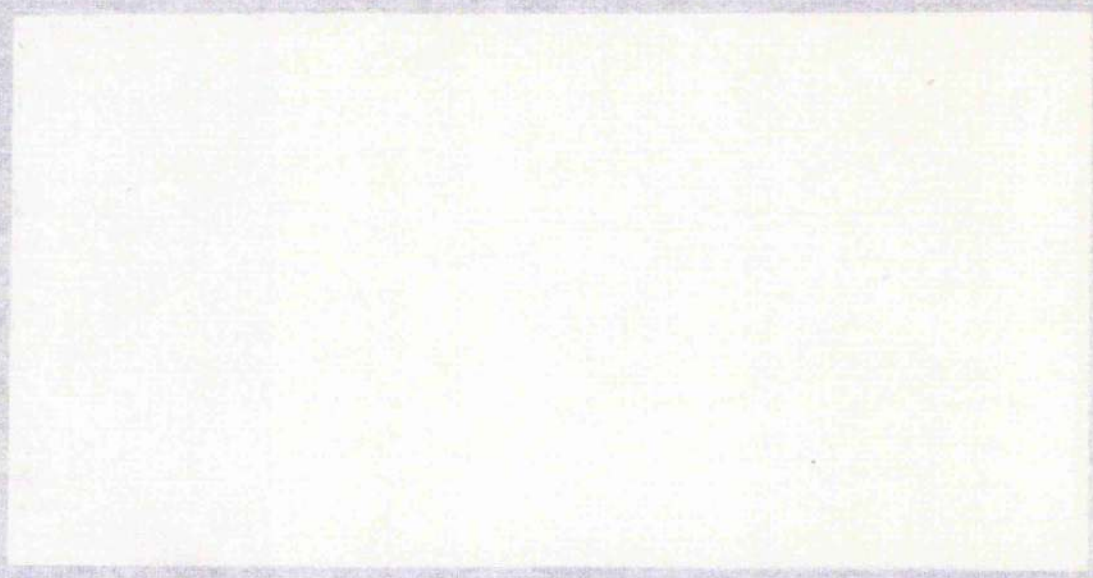


Figure 39. The inferred neural mechanism involved in the suppression of optokinetic nystagmus by an eye which perceived a stationary visual field. In the scheme the right eye is forced to the left which induces an apparent movement of the visual field to the right. This sets off the slow phase of optokinetic nystagmus which tends to drive both eyes to the right. The left eye begins to move to the right past the stationary striped visual field. (1) inducing an apparent movement of the field to the left. An opposite optokinetic response is initiated and the left eye now begins to move to the left past the stationary striped visual field (2) which reinforces (2) the instructions of the right eye. If the left eye is blinded (broken lines) or is not allowed to move it does not initiate an opposite optokinetic response when moving past the stationary visual field. Proprioceptors appear to play no part.



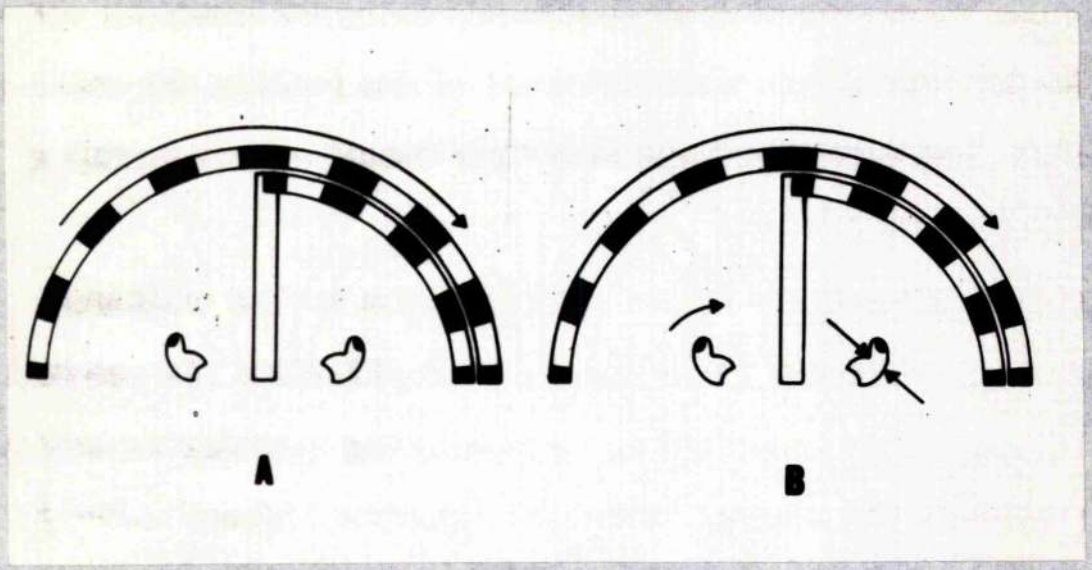


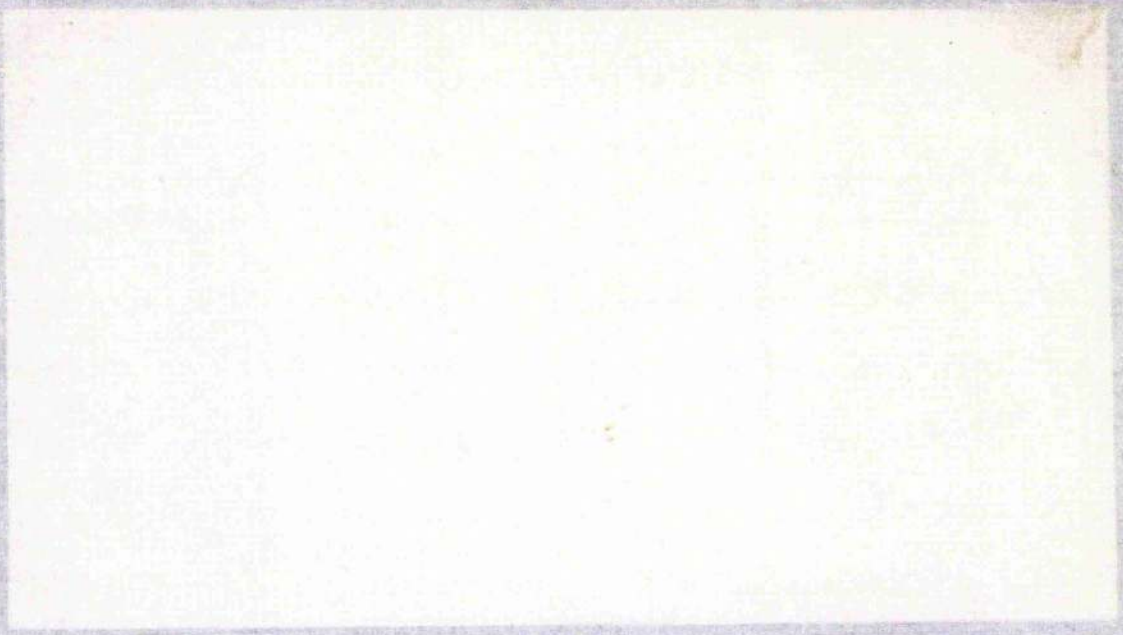
Figure 40. The effect of a stationary visual field. A, the animal's left eye is subjected to a moving visual field but its optokinetic response is suppressed by the right eye viewing a stationary visual field. B, the right eye is prevented from making small incipient movements in relation to the stationary environment and the animal's left eye now executes optokinetic nystagmus in response to the moving stimulus.

in figure 38.

A stationary contrasting field can therefore exert an inhibitory effect, but this does not mean that patterns which are stationary relative to the eye initiate visual impulses. Electrophysiological analysis shows that the efferent impulses which cause movement of the passive eye are inhibited only after they have fired and therefore caused some movement of the eyecup, as in figures 36 and 37.

The irregular discharge of the efferent impulses in the inhibited eye may be a sign of oscillation although rapid oscillations are prevented by the neural inertia which damps eye movements during optokinetic nystagmus. The initial movement of the eyecup facing the stationary visual field is small and barely perceptible but it is sufficient to show that the environment which is stationary relative to the one eye is not sufficient stimulus to prevent the other seeing eye from following a moving visual field. It is therefore suggested that the passive eyecup begins to obey the efferent commands initiated by the forced eye, but as soon as it moves in the direction dictated it perceives the environment moving in the opposite direction. As the passive eye now corrects its mistake, the correction movement produces an environmental shift agreeing with that seen by the artificially moved eye. This stops the suppression of the efferent information and so immediately re-introduces the opposite visual input. The inferred mechanism is shown in figure 39.

The same phenomenon can be shown behaviourally by allowing a normal animal to view a stationary contrasting field with one eye and a rotating visual field with the other (figure 40). The optokinetic response of both eyes is suppressed. If the eye watching the stationary field is prevented



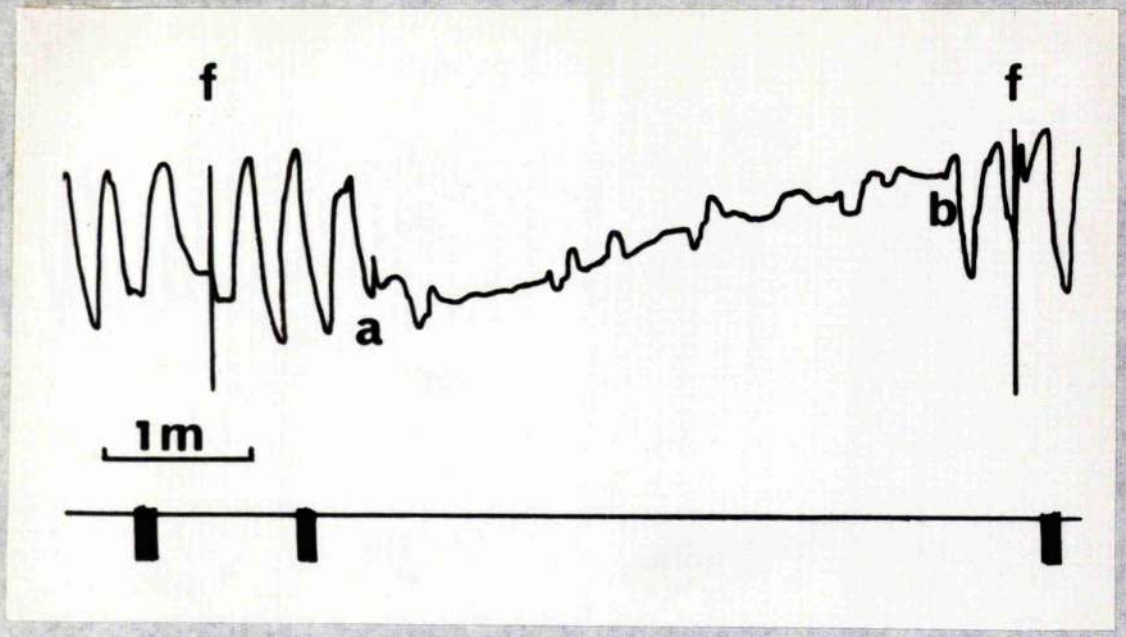
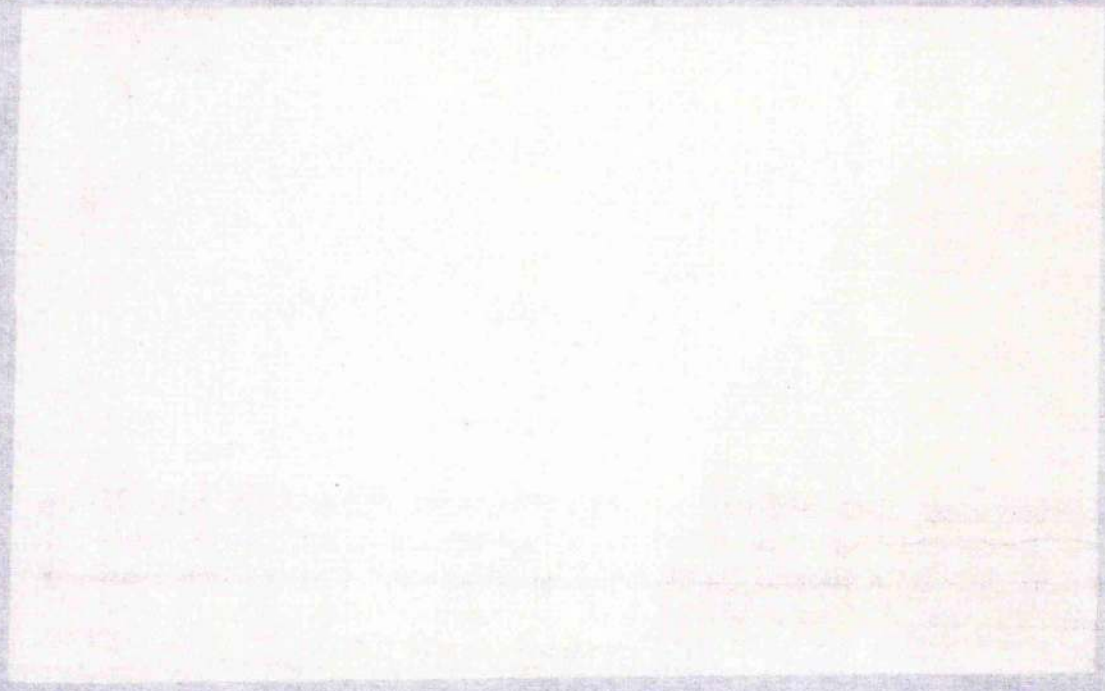


Figure 41. The effect of stopping the drum half way through the slow phase. The drum is stopped at a after the eye has moved through approximately 8 degrees of a complete slow phase, and the eye is held stationary by the animal but begins to drift slowly back. Rapid drift movements of the eye in either direction are immediately checked because any movement of the eye across the stationary striped visual field excites the movement receptors which produce the optokinetic response. Restarting the drum (b) enables the eye to complete the 12 degrees traverse of the slow phase and return to its original position after the fast phase (f). The slow phase progresses from left to right in the record and the movement of the drum is indicated by the marks on the lower trace. Scale = 1.0 minutes.



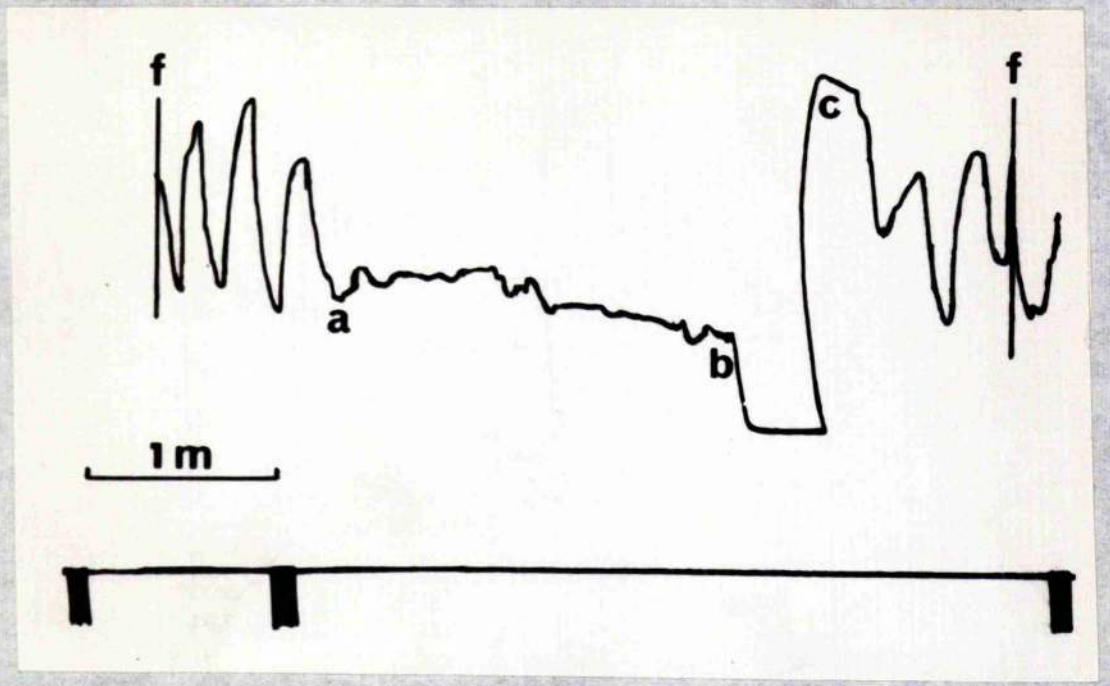
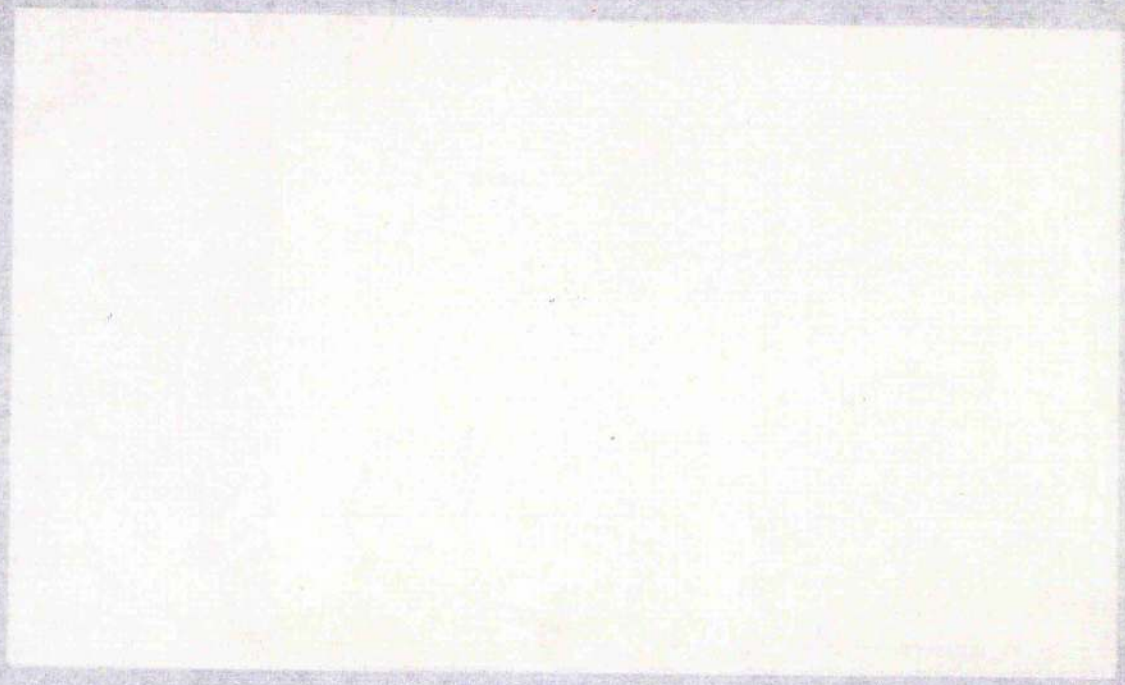


Figure 42. The effect of stopping the drum half-way through the slow phase and then momentarily switching off the light. The eye is allowed to move through 8 degrees (i.e. four peaks) of a 12 degree slow phase before the drum is stopped at a. Small incipient movements are made by the eye which prevents it from returning to its original position. Switching off the light (b) for a short time results in the eye moving back towards its original position shown by the fact that the eye travels through 6 degrees before the onset of the fast phase (f) when the drum is restarted at c. The slow phase progresses from left to right in the record. Scale = 1.0 minutes.



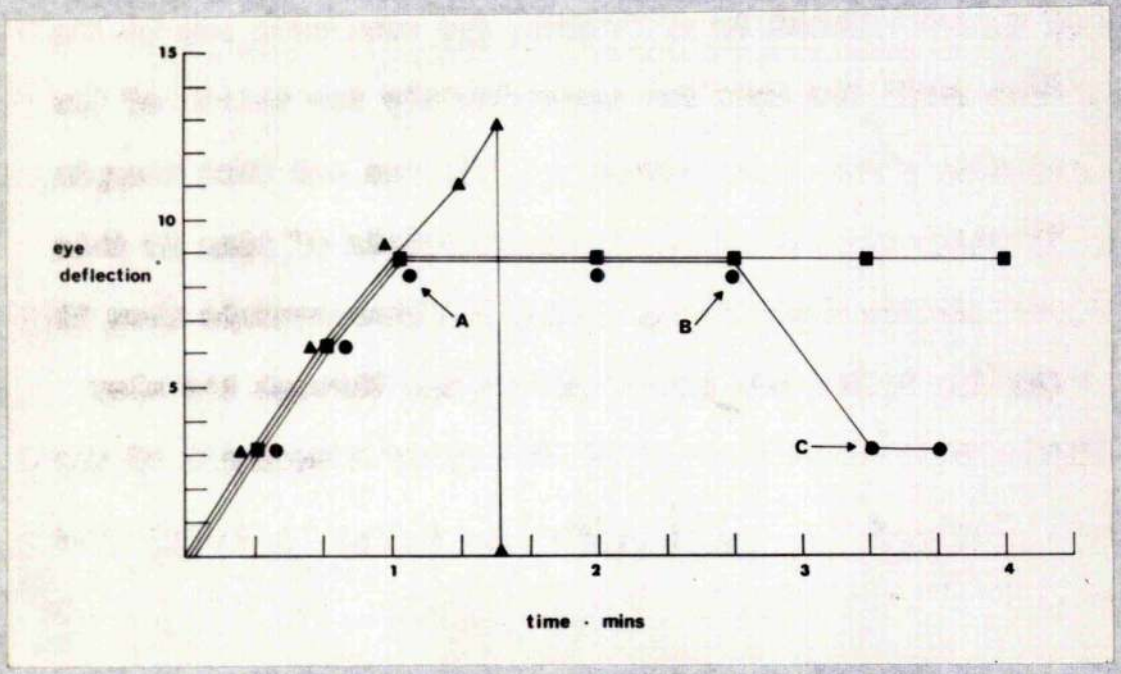


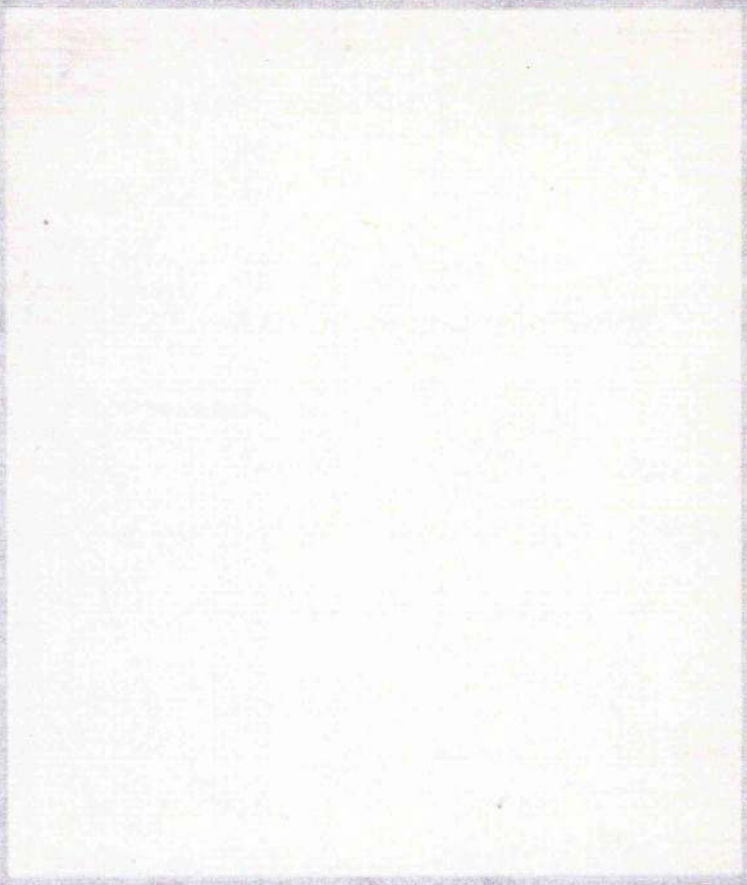
Figure 43. Angular deflections of the eye showing the effect of stopping the drum half way through the slow phase of optokinetic nystagmus. The triangles show the normal eye deflection during the slow forward phase ending in the fast return phase. At point A the drum is stopped and the eye is visually locked in this position (circles and squares). At point B the light is switched off and the eye moves back towards its normal position (circles), until at point C the light is switched on again and the eye movement is arrested.

from making small movements by holding it tight to the carapace without impeding its vision, there is now no inhibition of the optokinetic nystagmus of the eye which views the moving field.

3. Prevention of eye movements by visual stimuli.

The role of visual stimuli in preventing eye movements can be shown by rotating the drum until the eyes are approximately two thirds of the way through the normal slow phase of optokinetic nystagmus and then stopping the drum abruptly. The eyes are then held for long periods of time in this position by the animals own mechanisms. Sensitive measurements show that the eyes, when visually locked two thirds of the way through the slow phase, repeatedly begin to move slowly back but after a movement of about 0.2° returns each time to the same, or almost the same, "held over" position (figure 41). The explanation of these small eye excursions lies in the fact that any slow movement of the eyecup, caused by the fatigue of the eye muscles, immediately induces an environmental movement in the opposite direction and a subsequent optokinetic response. When the lights which illuminate the stripes of the stationary drum are switched off, the eye returns at once to its normal position (figure 42 and 43). However with the lights on the drift of the eye back to its normal resting position is not so slow as the slowest movement of the drum which can produce an optokinetic response.

The above response provides an interesting example of the animals own movements causing an optokinetic response and will be further discussed in connection with the principles of the re-afference theory.



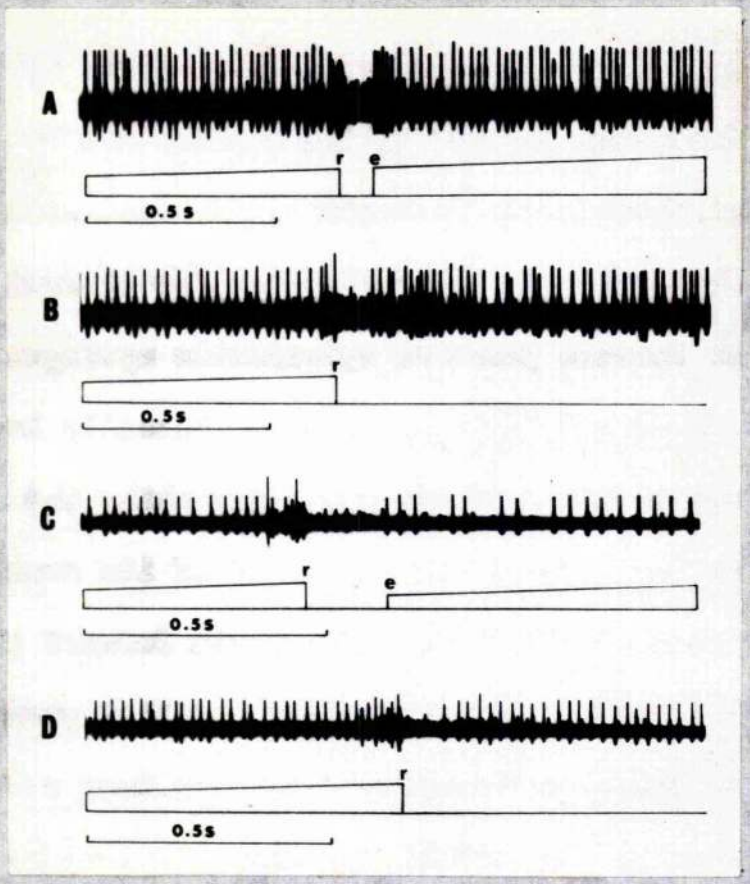


Figure 44. Impulses in the oculomotor nerve showing the inhibition of the optokinetic motor impulses during the retraction reflex. The corresponding movements of the eyes are shown beneath the records. A and B, responses from a unilaterally blinded animal. Activity was recorded from the oculomotor nerve of the blinded eye, which was also the eye induced to retract. In A the eye was again extended immediately after the retraction, but in B it was retained within the socket by the animal. In each case the eye position and the frequency of the optokinetic impulses are approximately the same before as after the retraction. C and D, responses as in A and B but from a normal animal. When the eye is extended immediately after the retraction, as in C, there is a partial suppression of the optokinetic response. In D, after retraction the eye was held closed into the socket by the animal's own mechanisms. The optokinetic impulses are resumed at the same rate as before but are inhibited peripherally. A constant drum speed is maintained throughout the experiment.

In the above experiments the eye is retracted in a direction opposite to the rotation of the drum, so that its movement during extension induces an apparent slowing down of the drum and suppresses the optokinetic stimulus. Rotation of the drum in the opposite direction would be expected to give the opposite effect. Scales = 0.5 seconds.

Section V

The Interaction of the Responses.

One of the most interesting aspects of the interaction between the retraction reflex and optokinetic nystagmus is demonstrated in the following way: The eyes of a unilaterally blinded animal are allowed to travel half-way through the slow forward phase of optokinetic nystagmus and then the drum is stopped, at which point the eye becomes visually locked onto the drum. The blinded eye is now induced to retract while the seeing eye remains unaffected. When the blinded eye comes out of its socket it returns to its previous position half way through the forward phase. All information indicates that this position is not controlled proprioceptively from the position of the seeing eye but that there has been a temporary central block of the centrally determined frequency of motor impulses which determine the position of a blinded eye.

Electrophysiological recordings from the oculomotor nerve on the side where the eye retraction is induced, shows that after a brief but total central inhibition, the efferent impulses which produce the slow phase of optokinetic nystagmus resume their firing (figure 44A to D). The stimulus of moving stripes is maintained throughout the experiment.

The interaction of the reflexes of unilaterally blinded animals is different from that of normal animals. If in unilaterally blinded animals the blinded eye is induced to retract, after a pause the efferent optokinetic impulses are resumed at the same rate as before, or slightly faster, regardless of whether the eye remains retracted or is re-extended to its

position before retraction, as in figure 44A compared with B. In the intact animal the rate of firing decreases after a period of central inhibition if the eye is re-extended, but increases if the eye remains retracted, as in figure 44C and D. There is therefore a partial inhibition of the optomotor response caused by the re-extension of the normal eye, bcause its movement in the same direction as the drum effectively slows down or stops the nett visual stimulus from the moving drum.

Peripheral inhibition must be playing a part in animals which do not re-extend the eyes after the initial retraction because the optomotor efferent impulses reappear at the termination of the central inhibition but the eyecup does not move, (figure 44B and D). Inhibition of the movement of one eye by the conflicting visual information received by the other is again demonstrated by these experiments, and will be further considered in the discussion.

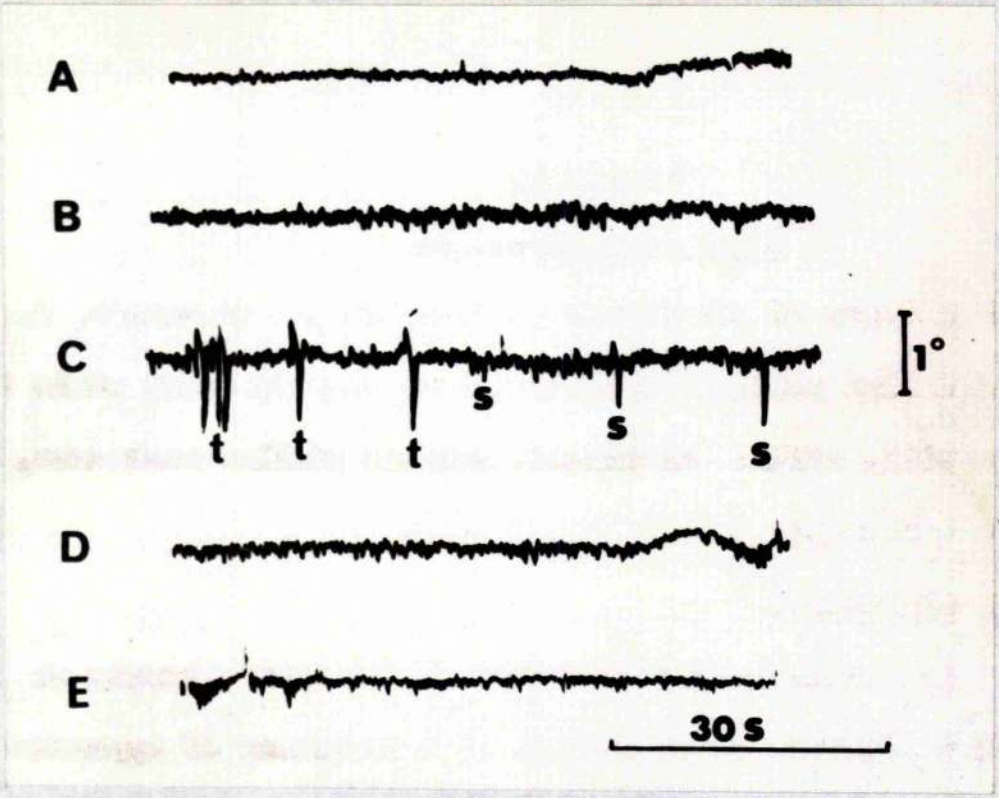


Figure 45. High frequency tremor and scanning movements of the eyecups. A, the combined noise level of the recording system. B, the movements of the eye when it is confronted with a plain white visual field. C, scanning movements (s) induced by the introduction of a 5 cm black disc into the visual field between the animal and the white backgrouns, and (t) by tapping the bench. The eye movements in response to the black disc were only produced by the introduction of the black disc and not by its removal from the visual field. The response rapidly adapts. The eye movements induced by tapping the bench also adapt if the taps are rapidly repeated. The scanning movements are thought to be partial retractions of the eye. D, partial suppression of the high frequency tremor when the animal is surrounded by a striped visual field. E, the record obtained with the flag of the recording apparatus attached to the carapace. The similarity of this record with A (the combined noise level of the system) indicates the extent of the eye movements in B, C and D. Horizontal scale = 30.0 seconds, vertical scale = 1.0 degrees.

Section VI

Other Eye Movements.

Three other types of previously undescribed eye movements, distinct from the slow and fast phase of optokinetic nystagmus, occur while the animals are perfectly still. As mammals exhibit similar movements, the same nomenclature has been used (Alpern 1962).

1. High Frequency Tremor.

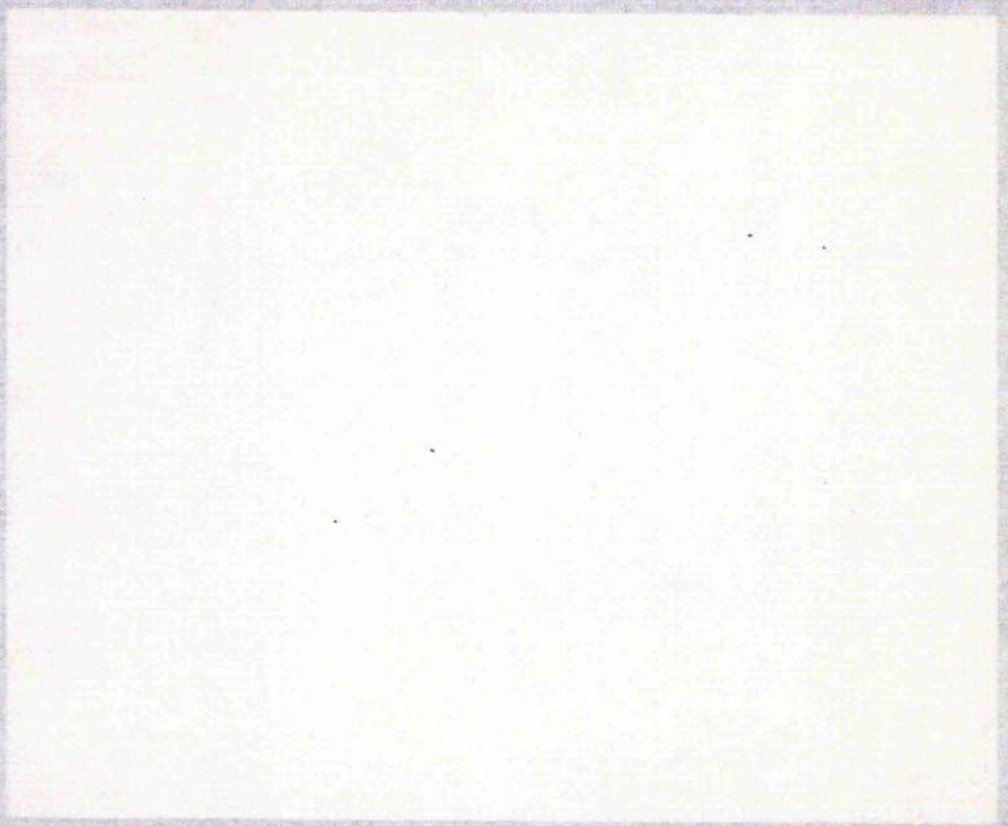
These are fine oscillatory movements of the eyecup having an amplitude of 0.05 degrees to 0.2 degrees at a frequency of approximately 2 cps. This movement can be demonstrated to be visually significant by providing the animal with different visual fields. Tremor movements of the eyecup are as much as 0.2° in a plain white environment but are reduced to approximately 0.05° when the animal is surrounded by a visual field of black and white stripes as shown by the comparison of B with C in figure 45. From this result we infer that there is a mechanism which could provide stalk-eyed crustacea with the means of perceiving contrasting objects in a stationary visual field.

2. Irregular Wandering Movements.

These are movements of approximately 0.5° in either direction. They are so irregular in their appearance and amplitude that it has not been possible to show whether or not they are related to vision. By their size it would seem that they must be, although the eye does not necessarily immediately return to its starting position after such a movement.

3. Scanning movements.

If an animal is presented with a plain white visual field and a



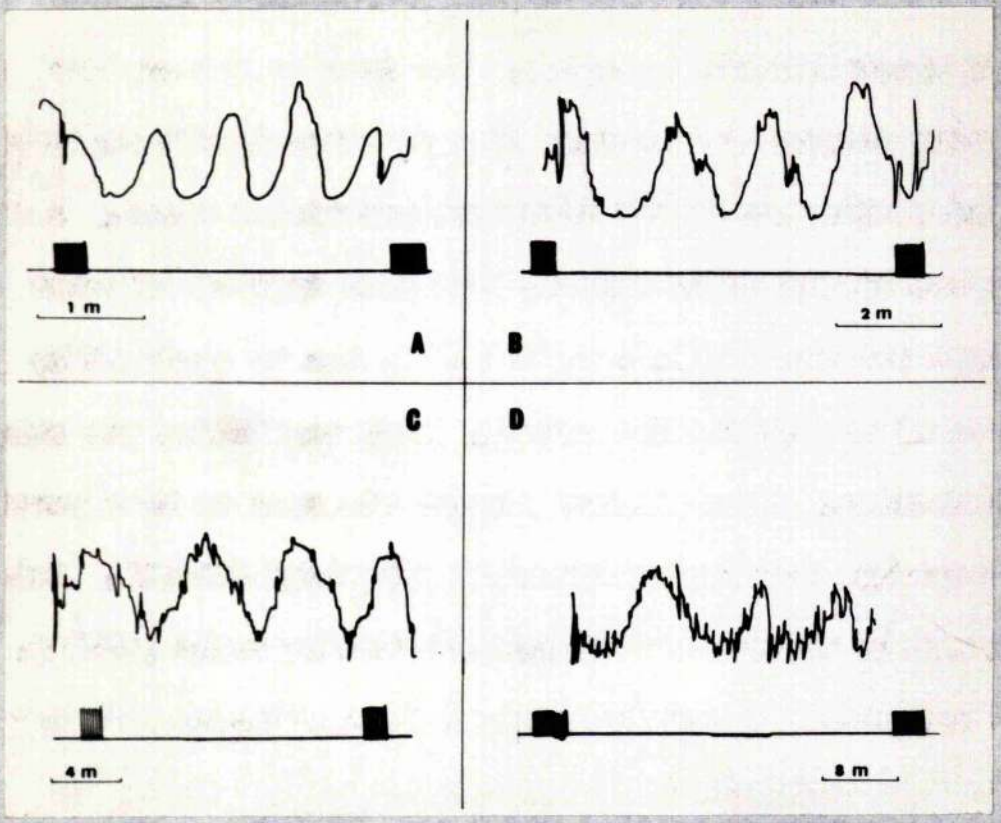


Figure 46. Scanning movements of the eyecup superimposed on the movements of the eyecup during the slow phase of optokinetic nystagmus at very slow drum speeds. A single slow phase is divided into a number of peaks as described in figure 31. The scanning movements become more pronounced with the corresponding decrease in the drum speed from A to D. The lower trace shows the movement of the drum. Scales in minutes.

2.5 cm diameter black disc is lowered into the visual field the eyes make rapid sideways scans away from the midline of between 0.5° to 1.0° and then return to their original position. The scan is not repeated when the object is rapidly removed and becomes less pronounced with repeated re-introduction and withdrawal of the disc from the visual field. A disc introduced slowly has little or no effect. The same type of sideways scan, sometimes more pronounced (i.e. up to 5.0°), can be produced by sharply tapping the clamp holding the animal. With repetition the stimulus again becomes ineffective. These scanning movements seem to be a partial retraction of the eyecup, induced by photic or vibratory stimuli. Retraction of the eye caused by photic stimuli was reported by Bethe (1897a). The visual significance of the scanning has not been assessed but that the scans cause apparent movement of the environment is suggested by the experiments on the initiation of the fast phase and also the interaction between the retraction reflex and optokinetic nystagmus.

4. Scanning movements during optokinetic nystagmus

Accurate measurements of eye movements produced by very slow drum speeds show that the eye frequently makes short excursions in either direction. These movements are superimposed upon the overall movement of the slow phase and become more pronounced at low drum speeds (Figure 46 A to D). The eye movements may indicate the limitations of the control system related to such low drum speeds and their significance is considered in the discussion.

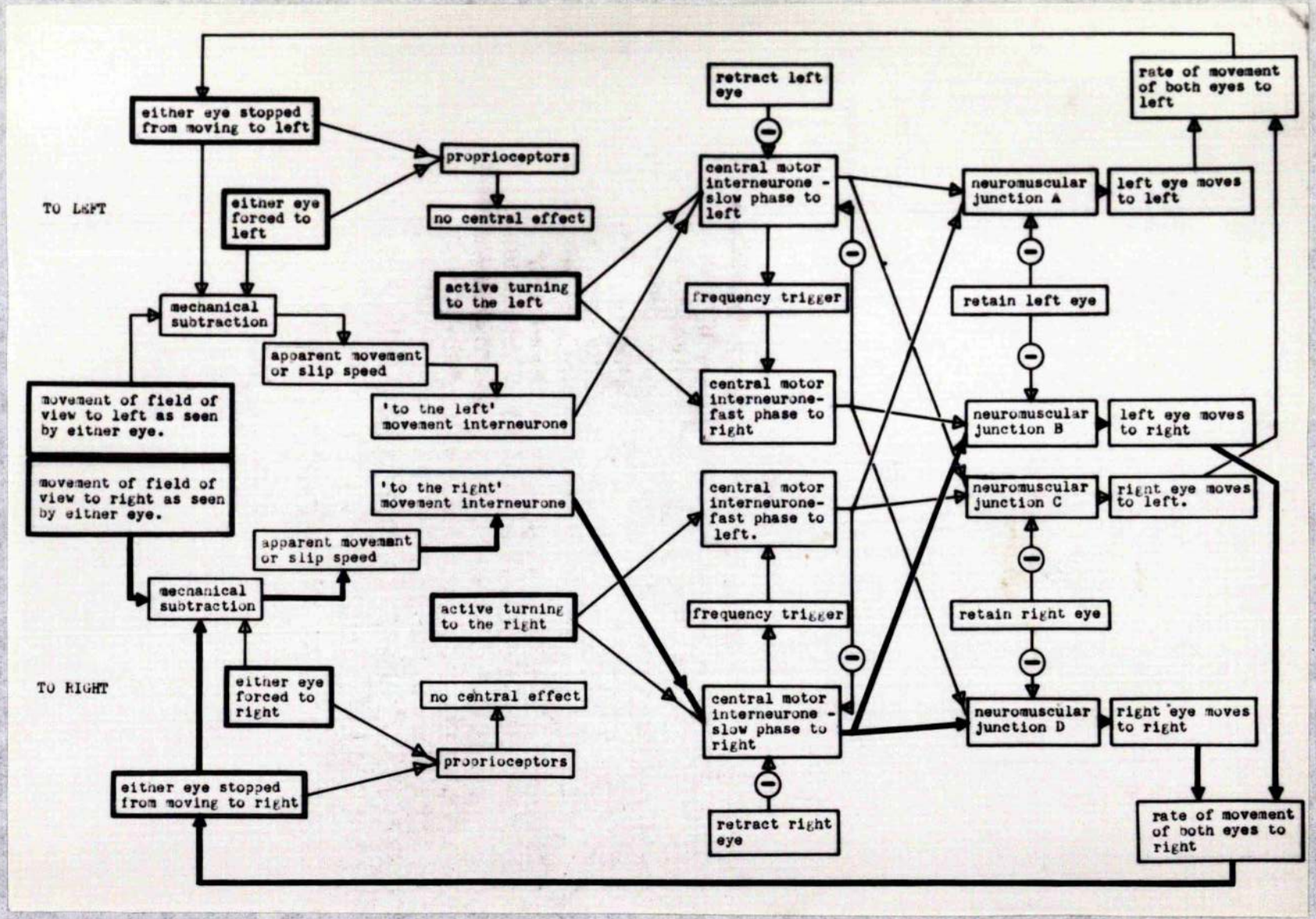

either eye stopped from moving to left
proprioceptors
TO LEFT
either eye forced to left
no central effect
mechanical subtraction
active turning to the left
apparent movement or slip speed
'to the left' movement interneurone
movement of field of view to left as seen by either eye.
movement of field of view to right as seen by either eye.
'to the right' movement interneurone
apparent movement or slip speed
mechanical subtraction
active turning to the right
TO RIGHT
either eye forced to right
no central effect
proprioceptors
either eye stopped from moving to right
retract left eye
central motor interneurone - slow phase to left
frequency trigger
central motor interneurone- fast phase to right
central motor interneurone- fast phase to left.
frequency trigger
central motor interneurone - slow phase to right
retract right eye
neuromuscular junction A
left eye moves to left
retain left eye
neuromuscular junction B
left eye moves to right
neuromuscular junction C
right eye moves to left.
retain right eye
neuromuscular junction D
right eye moves to right
rate of movement of both eyes to left
rate of movement of both eyes to right

Figure 47. (Opposite). A summary of the inferred relationships between entities which can be distinguished by the methods employed in this investigation, with emphasis on the neural mechanisms involved during the slow and fast phases of optokinetic nystagmus in the normal animal. The inhibitory relationship of the retraction and retention of the eye into the socket to the optokinetic mechanisms are also shown. The stimuli in the scheme are surrounded by a double line. In the stimulus situations where the seeing eye is, forced or prevented from moving, optokinetic nystagmus as shown by the plan will only be produced in unilaterally blinded crabs.. Eye movements during active turning are included; the initiation of these movements is regarded to be of central origin.

The formal structure of the control system.

The general plan of the control system inferred from the experiments on optokinetic nystagmus is outlined in figure 47. The movements of the eye in following the visual field reduces the apparent movement of the field and this is the only overall feedback loop which has been found. This closed loop feedback system (Mittelstaedt 1960) is quite different from the servo-mechanism systems which have been proposed for the optomotor responses of insects (Kalmus 1949), because in the crab the angular deflection of the eyes lag increasingly behind that of the drum. Sevo-mechanisms, characterised by a constant and not increasing lag between the eye and the target ~~may~~ occur in mammals where the eye fixates on the moving stimulus. An analysis of oscillatory movements of the human eye has shown (Fender and Nye 1961) that retinal and proprioceptive feedback loops play separate roles in the servo-mechanism controlling the eye movements, but there is still no direct evidence for the function of the proprioceptors in mammals (Whitteridge, personal communication, 1963). In crabs there is a constant relationship between the stimulus and the response of each eye over a wide range of drum speeds in spite of the fact that the many eye muscles of the eyecups move the two eyes in opposite directions through about 12° relative to the midline. There must be a consistent and precise central neural compensation for non-linearities which are inherent in the effector system.

The closed loop ~~system~~ of the crab eye control system is converted into an open chain system by cutting the optic tract on one side of the animal or by blinding one eye with black paint. Movement of the blinded eye does not now affect the stimulus input to itself. However the eye still moves in a controlled way, and the only noticeable difference is

that the onset of the fast phase is delayed. Optokinetically produced eye movements, therefore, appear to be controlled almost entirely by the integration of impulses from visual one way movement interneurones and do not depend upon proprioceptive feedback from the movements of the eyecup. More accurate measurements are needed from unilaterally blinded crabs before an estimate can be made of the importance of the visual feedback to a normal moving eye.

The fast return phase of nystagmus is not dependent on the duration or amount of eye deflection, or on the possible mechanoreceptors of the eyestalk assembly or eyecup. The response originates in the brain, independent of the presence of the eye and is thought to be set off by a threshold requency in the motor neurones which drive the optomotor response, and not at a fixed position or particular visual input. There is some evidence that the visual movement receptors of both eyes are important in determining the threshold of the trigger mechanism. The control system of the fast phase appears to have a separate internal feedback loop which briefly inhibits the slow system during the fast phase.

Reflex retraction is clearly an over-riding rapid response independent of the form of the input above certain well defined thresholds and also independent of the existence of the effector. The two sides of the animal act separately. The optokinetic responses are centrally suppressed during the fast withdrawal of the eye and in a unilaterally blinded animal the blind eye returns to the same place in the arc of the slow phase from which it retracted.

This shows that retraction involves only temporary suppression of the effects of the efferent outflow and not cancellation of it. Peripheral inhibition can occur if the eye is held in its socket after the initial retraction, while the contralateral eye continues the optokinetic response.

Apparent movement of the visual field during the fast protective retraction of the eye and the fast phase of optokinetic nystagmus does not initiate an optokinetic response because in both cases the slow efferent impulses are centrally suppressed. Thus even if there were visual excitation this would not be able to take effect. In addition to the central inhibition of the slow efferent impulses it is possible that the movements of the eyes are too fast during both retraction and the fast phase to produce an effective visual stimulus.

Forced movements of the eyecups cause a relative movement of the visual field and all experiments show that eyestalk proprioceptors play no part.

Eye movements during active turning of the animal are interpreted in figure 47 to be centrally initiated, because the fast phase occurs first and without the preliminary build up of efferent impulses in the oculomotor nerve which accompanies the slow phase. This will be considered in greater detail later.

Section II

The lack of evidence for proprioceptors.

Methylene blue staining of the eyecups of Carcinus does not reveal any special proprioceptive organs, although other nerves stain well. The lack of standard proprioceptors is not surprising because the joint between the eyecup and the eyestalk moves in all directions and could not be effectively monitored by muscle or tendon receptor mechanisms found in the many skeletal joints of Cructacea. The failure to reveal anatomical evidence for proprioceptors in the eyestalks and eyecups agress with the experimental evidence, which shows that movements of the eyes relative to the environment are always interpreted by the animal as movements of the environment regardless of any forced movements or restrictions imposed on the eye. Also forced movement of an eye which does not see because it is either shown a blank field or put in darkness, produces no movement of the opposite, blinded eye. Nor is there any change in the frequency of efferent impulses in the oculomotor nerve of the blinded eye under these circumstances. Muscle tension therefore, plays no part in the control system.

Movement of the eye both in the light and in the dark produces afferent discharges from the mechanoreceptors on the cuticle, but removal of bristles from around the eyes and from the eyecups of Carcinus has no effect on the positions maintained by the eyes or on the eye movement, although in these operations it was impossible to remove the hairpeg organs or the fine hairs which are distributed over the surface of the eye and both these sensilla types must be sensitive to movements of the eye and movements of the water surrounding the animal. As a mechanism for monitoring

the eye movement the hair peg organs would be limited because this type of organ is very sensitive to disturbances of the surrounding medium (Laverack 1962). They could not monitor the position of the eyecup relative to the eyestalk.

The cuticular receptors most likely fulfill a cleansing or protective function. The hair peg organs are situated only on the exposed surfaces of the eye and can produce the retraction of the eye in response to disturbances in the water around the animal. The bristles probably prevent foreign particles from entering the eye socket and they are so orientated as to sweep out the eye socket whenever the eye is extended. The functions of the fine hairs, the feather hairs on the surfaces of the eyecup and eyestalk, and the bipolar cells in the arthrodial membrane of the eyecup joint, are not known and there is no electrophysiological evidence available.

A system of control in which the movements of the eyes are deduced from visual cues is suggested by previous experiments on other Crustacea (Schöne 1952), and there is no evidence of the proprioceptive monitoring of the eye movements. In Carcinus tonic efferent impulses in the oculomotor nerve have been observed to fire with constant frequency for periods of up to twelve hours, provided that the eye is held by the animal in the same position. Also, eyes engaged in optokinetic nystagmus bear a more constant angular relationship to each other than to the carapace. This suggests that the positions of the eyes are governed by a central mechanism which sends balanced frequencies of nerve impulses to the eye muscles of the two sides, rather than by an error controlled mechanism

which monitors the actual position of the eyecup with relation to the head. Again, after reflex retraction, a blinded eye returns to its position half way through the slow phase of the optokinetic response where it had been previously locked by stopping the drum. This never happens if the seeing eye of the same animal is artificially brought to the same position half way through the slow phase. Therefore the return of the blind eye to the position optokinetically determined by the seeing eye does not depend on a proprioceptive monitoring system. It is suggested from this evidence that in Carcinus, as in other Crustacea, movements of the eyes are controlled by visual cues, and the positions of the eyes are governed by the frequency of the efferent commands in the oculomotor nerve which in turn are set off and maintained by the visual input.

There is also evidence of a central pacemaker system which is uninterrupted by the retraction reflex, and which acts reciprocally on paired motor centres which in turn operate the two sides, as illustrated by the separate points of inhibition in Figure 47. However in crabs in which the optic tract has been cut on the one side and the oculomotor nerve cut on the other, the control of the blinded eye may be by proprioceptors in place of the visual feedback. This possibility cannot be excluded.

Section III

The upper and lower limits of the response and the onset of the fast phase.

A definite upper and lower limit of the optokinetic response exists and it is of interest to consider what part of the control system breaks down and causes the failure of the response.

The lowest limit of the response is taken as being a slip speed of 0.0007°/sec. because below this point the relationship between the stimulus and the response is changed as shown in figure 24. An absolute threshold below which there is no response is not reached because this is beyond the capabilities of the apparatus. The eye responds, but does not complete a slow phase, at a drum speed of approximately 0.00025°/sec (i.e. one revolution in approximately 40 hours). A complete slow phase would take approximately two hours at this drum speed and this is probably beyond the ability of the neuromuscular system.

An interesting oscillation of the eye takes place at the low drum speeds. These oscillations are superimposed on the overall slow movement of the eye and are interpreted as the breakdown of the effector system. It is inferred from this that during the slow phase the eye muscles cannot move the eye forwards by such small amounts as would be necessary at low stimulus speeds. The eye is apparently

moved too far forwards and induces an opposite optokinetic stimulus by way of the visual feedback loop, and this opposite optokinetic stimulus returns the eye to its starting point. A drum rotating slowly clockwise will tend to decrease the optokinetic stimulus caused by the forward, clockwise, scan of the eye, and increase the optokinetic stimulus induced by the backward, anticlockwise scan of the eye. The scanning movements of the eye tend in this way to reinforce the stimulus from the moving drum. The natural tendency of the closed loop system to oscillate in this way at even higher speeds is prevented by the neural inertia of the optokinetic response which causes the eye to carry on moving for up to ten seconds after the stimulus has stopped. It would be interesting to compare the very slow eye movements of normal crabs with the slow eye movements of unilaterally blinded crabs because in the blinded crabs the feedback loop is open and forms a chain system. The movement of the blinded eye, if driven by a stationary seeing eye, would be expected to show less controlled movements at the slow speeds and an absence of the corrective oscillations, because no visual feedback to the blind eye is possible. No experiments have been done with this preparation.

Some measure of the visual acuity can be gained from the least movement necessary to elicit the optokinetic response but these methods, although useful in determining the threshold of the entire response, cannot be successfully applied to the analysis of only the visual apparatus. This has been demonstrated by Burtt and Catton (1959) who showed in electrophysiological studies of the optic systems of various

insects that the threshold for movement perception by the eye itself was well below what previous behavioural workers had suggested. Burtt and Catton showed that previous measures of visual acuity were in fact measures of the threshold of the optomotor response and not of the actual visual acuity of the eye.

The upper limit of the optokinetic response is closely linked with the onset of the fast phase and the two must therefore be considered together. At drum speeds well below the flicker fusion frequency of the crabs' eyes, the optokinetic movement of the eye no longer maintains its linear relation to the stimulus throughout the slow phase; there is a marked increase in the lag between the eye and the drum during the last portion of the slow phase, and a consequent delay of the fast phase (figure 31). It has been suggested that the fast phase is centrally initiated by a mechanism which is triggered by a critical frequency of nerve impulses in the oculomotor nerve. At different speeds of the eye movement, the fast phase always occurs at the same angular deflection of the eyecup. However, in other known slow muscle systems of Crustacea the relative speed of muscular contraction is governed by the frequency of the impulses in the motor axons. The critical frequency of nervous discharge in the oculomotor nerve of Carcinus at which the fast phase occurs must therefore be different for different speeds of eye movement, otherwise the angular deflection of the eye could not be the same. This alteration of the frequency threshold could be performed by the visual feedback mechanism. Reduction of the stimulus by raising the drum speed or blinding one eye, raises the threshold of the onset of the fast phase and delays it. A position will be reached where the slow phase is still

carried out, but the necessary frequency to trigger the fast phase is set so high by the visual input that it is never attained. The upper limit of the response is therefore governed in part by the onset of the fast phase because at very high drum speeds which are above flicker fusion there will be no response at all.

Section IV

Perception of a stationary visual field

The ability of the eyes of arthropods to respond to stationary objects in their visual field has not been satisfactorily demonstrated by previous workers. In Carcinus, an eye which is presented with a moving visual field does not move if the other eye is presented with a stationary visual field. Many experiments show, however, that the stationary environment is dominant only when the eye presented with it makes the incipient movement caused by the visual input to the other eye. Prevention of this small movement, by clamping the eye to the carapace, effectively blinds the eye and the stationary environment no longer dominates the moving one. Spontaneous movements of the eye of the same amplitude, speed, and general form, are therefore adquate to allow vision of a stationary visual field. That tremor movements of the eye are visually significant is shown by the partial suppression of these movements when the eye is surrounded by a contrasting visual field.

Eye tremor is not unkown in Arthropods and has been reported to occur in Daphnia, Triops and Artemia (Waterman 1961). It has been suggested that eye tremor in these above animals may improve form-vision or increase the persistence of visual images as in human eyes (Waterman 1961), ~~It has been suggested~~ although it should be pointed out that the comparisons between compound eyes and vertebrate eyes are not always useful because they relyr on different optical and control systems. Scanning movements in locust hoppers, brought about by the animals swaying from side to side on their legs, have been found to be visually significant, but this peering movement does not elicit optomotor effects.

The insect therefore either cancels out the optokinetic stimulus caused by its own movements or disregards it (Wallace 1959). Although work on the optokinetic responses of the locust is being done (Thorsen unpublished) the possiblity of tremor movements of insect heads and their importance to vision has been overlooked by Reichardt and others in their work on the optomotor responses of insects. In all their experiments the insects' heads were immovably fixed to the thorax, before optomotor tests were made.

Nerve units which respond to stationary objects in the visual field, have been recorded in the optic lobe of decapods (Waterman and Wiersma 1963). These units, called sustaining units, normally fire in response to an increase of intensity of photic stimulation. They will also respond if a white card is placed in front of the eyes after they have been looking at a black environment. It would be of interest to know whether this type of unit would cease to respond to stationary objects if the stalked eye of the animal was fastened to the carapace and unable to carry out any small movements. There is also the possiblity that this unit was responding to the increase in reflected light from the white card.

Section V

Movable compound eyes and the function of the optokinetic response.

The compound eyes of most arthropods are movable with relation to the body segment which bears the locomotory appendages. In insects the whole head is movable and in the crustacea where the head is fused to the thorax the eyes are themselves movable with relation to the rest of the body. *Limulus* forms a notable exception to this generalization, but the optomotor responses of the Chelicerates does not seem to have been investigated. Optokinetic nystagmus is a characteristic response in all the arthropods in which the eyes, or head and eyes, can move relative to the body, even though the complete response with slow and fast phases is never normally elicited. Slow and fast eye movements do ~~not~~ occur in actively turning decapods but not in insects.

The functional advantage of movable eye systems is not clear. It cannot be argued that they serve to extend the field of view because in many crustaceans with movable eyes the corneal surface is distributed around the eye so as to provide the animal with almost all round vision. In *Squilla mantis* the movable eyes are thought to enable the animal to gauge the distance of its prey before striking. The eyes of *Squilla* can be clearly seen to point directly towards the prey and appear to fixate on it. This immediately implies that the control of the eye movement employs a servo-mechanism instead of the feedback loop system of *Carcinus*. Accurate measurements of the eye movements of *Squilla* have not been made. Electrophysiological recordings from the eyes of *Squilla* (Schiff, 1963) have shown that they respond only to small movements in the visual field and not to stationary objects, but the tech-

niques employed by Schiff depended on the eye being held still. In the decapods, dramatic eye movements like those shown by Squilla have not been observed, and to decapods, the advantage of movable eyes may lie solely in the perception of still objects in the visual field.

Control and stabilization of a movable visual system is essential and the eyes own movements must be distinguished from the environmental movements. Standard proprioceptive monitoring systems are perhaps unsuitable for the flexible eyecup joints of the decapods, and experiments on Carcinus, and other Crustacea (Schöne 1952), suggest that the eye movements of the decapods are visually controlled by the optokinetic response which corrects spontaneous slow movements of the eyes. Visual control of the head and eye movements has not been demonstrated for insects and experiments suggest that self initiated movements of insects do not produce an optokinetic response. Thus a visual feedback mechanism of the sort envisaged for Carcinus could not function. Hair plates in the neck region of some insects (Mittelstaedt, 1957) monitor the head movements, and could also serve to control the eye movements, but the significance of optokinetic nystagmus with slow and fast phases still remains obscure. Experiments in which the head and eyes of insects are forced to one side or the other in front of a stationary visual field could prove to be interesting.

Other explanations for the function of the optokinetic response have suggested that they are useful for maintaining a straight course when an animal loses a leg and causes assymetry of appendages, (Hughes 1958), but this would be of little advantage to the animal in the dark.

Section VI

Eye movements during active turning and the reafference principle

Crabs first swivel their eyes around rapidly and then follow up slowly with their bodies while making a spontaneous turn (Dijkgraaf 1956). In doing so they obey conditions which agree with the main features of the optokinetic response. The initial voluntary eye movement is rapid and its movement relative to the environment may be too fast to stimulate visual receptors, although, as in the case of the interacting reflexes, there may be some central inhibition of the optokinetic response. During the subsequent body movement the optokinetic rules are obeyed, but blinded crabs move their eyecups in almost the same manner and behave as if they are not blind, (Dijkgraaf 1956). The slight impairment of the eye movements in the blind animals suggests that the eye movements are visually controlled, although not initiated by optokinetic stimuli. The fast phase and the slow phase are clearly centrally initiated in actively turning animals (Dijkgraaf 1956).

The central initiation of the eye movements in crabs during active turning was regarded by Dijkgraaf to exclude the possibility that these eye movements were caused by self induced optokinetic effects. However some crab eye movements, such as the extension of an eye after retraction, are initiated by the animal and apparently cause the optokinetic response. This contradicts the principals of the reafference theory and it is suggested that the eye movements of crabs during active turning may prevent self stimulation in the absence of a central neural mechanism, proposed by the reafference theory, which prevents self stimulation in

the insects. The head and eyes of insects do not show compensatory movements during active turning. Crabs which have been blinded for a long time still show eye movements during active turning, so that if the eye movements are initially learnt they are not "forgotten" by the removal of the normally reinforcing visual input. The neural mechanisms involved in the production of these movements cannot be understood until electrophysiological recordings are made from intact and unrestrained animals.

Crabs which move sideways and do not turn, generally keep their eyes stationary relative to the carapace, and if they do move them (Bethe 1897a), the movements do not include slow and fast phases which are characteristic of optokinetically produced eye movements. The absence of optokinetic movements in sideways walking crabs can be explained by the differentiation of the sensitivities of the various areas of the cornea to movement. Experiments have shown that the outside halves of the eyes must be stimulated by stripes moving in the same relative direction before optokinetic nystagmus will occur. The fact that a vertically striped sheet drawn straight across in front of a crab has no effect, also suggests that the effective angle of acceptance of the ommatidia is limited.

Section VII

Comparison with Mammals

The experimental evidence for the lack of proprioceptive control of eye movement in the crab is similar to that for vertebrates. In mammals, tendon organs (Tozer and Sherrington 1910) and muscle spindles (Cilimbaris 1910, Cooper and Daniel, 1949, Merrilees, Sunderland and Hayhow, 1950) have been reported. The presence of these proprioceptive mechanisms was at first denied because of the lack of experimental evidence. No complete explanation for the function of these proprioceptive organs has been supplied, and although similar muscle spindles are found to be associated with two neurone reflex arcs in the limbs of mammals, no stretch reflexes have yet been demonstrated in the mammalian eyes.

Similarly the investigations on Crustacean eyes suggest that there are no proprioceptive mechanisms involved, and nor have they been revealed by histological techniques. If they are discovered it will be equally difficult to explain their function satisfactorily.

The neural mechanisms involved in the slow and fast phases of optokinetic nystagmus appear to be exactly similar in both mammals and crustacea. The slow increase in the frequency of nerve impulses, during the slow phase of optokinetic nystagmus is followed by the onset of the fast phase in the cat (McIntyre 1939).

This parallel may be misleading in view of the basic difference between the inervation of vertebrate and invertebrate muscles. An increased rate of contraction of vertebrate muscle is brought about by the recruitment of muscle units by additional nerve fibres, and not by the increased frequency of nerve impulses in a few motor axons.

A system of raising the threshold of the frequency sensitive mechanism, and thus compensating for faster eye movement, does not have to be postulated for mammals. In both groups of animals it remains to be seen exactly what external or internal stimulus triggers the fast phase. In the crab it has not been possible to distinguish between the afferent supply to the central mechanism, and the efferent impulses, as likely stimuli for initiating the fast return phase. Antidromic stimulation of the motor fibres, if it were possible, would distinguish between these two theories. In the rabbit there is evidence that afferent trains of impulses to the brain are taken into account, because slow forward and fast return phases of optokinetic nystagmus are produced by stimulation of the optic tract. Moreover electrical stimulation, applied together with optokinetic stimuli, hastens ~~on~~ the onset of the fast phase regardless of the direction of the movement of the drum. It is probable that stimulation of either-way-movement receptor units in the optic tract is the effective stimulus. Alternatively, the threshold of the fast phase trigger may be lowered by increasing the visual input, as postulated for the crab. Similar stimulation of the optic tract in crabs leads to the retraction of the eye and a more delicate approach to the mechanism in the brain is necessary. The only marked similarity between the optokinetic responses of crabs and mammals, is the gradual increase of the frequency in the oculomotor nerve during the slow phase of optokinetic nystagmus. It would be interesting to show that the same neural mechanism was employed in both groups of animals for the production of the fast phase, especially as different types of control systems are used by the eyes in following moving visual fields.

Epilogue

The electrophysiological analysis of the movements of the crab's eye has proved to be an interesting and fruitful topic, but the preparation has not yet been fully exploited. Experiments which take into account the influence of the statocysts on postural alterations of the eye, the effect of stimulating either eye with the striped visual fields moving at different speeds, the effect of a slowly oscillating visual field, and many other aspects, may well throw light on the mechanism of central control.

SUMMARY.

1. The eyes of the crab Carcinus follow with constantly increasing lag the movement of a horizontally rotating (but not a linearly translated) visual field during the slow phase of optokinetic nystagmus. The difference between the eye speed and the drum speed is the effective stimulus for optokinetic nystagmus, and the response bears a constant relation to the stimulus over four orders of magnitude. The lower limit of the response is due to the breakdown of neuromuscular, and not visual mechanisms. At high drum speeds the fast phase is delayed, but the upper limit of the slow phase is caused by the failure of the visual mechanism.

2. An overall feedback mechanism exists in which the movement of the eye reduces the apparent movement of the drum. The control of the eye movement is by way of visual cues and proprioceptors play no part.

3. A seeing eye, provided with the appropriate visual stimulus, will drive the other eye if the latter sees no contrasting objects in its visual field or is blinded. Clamping an eye so that it cannot move relative to a stationary, contrasting visual field has the same effect as surrounding the animal with a blank field.

4. The rapid return phase of optokinetic nystagmus also takes no account of proprioceptors, but seems to be triggered when the efferent impulses to the eye muscles reach a definite frequency. Blinding one eye or increasing the drum speed cause a delay of the fast phase. Both eyes flick back simultaneously and the impulses in the oculomotor nerve which cause the slow phase are inhibited during the fast phase.

5. The fast protective retraction of the eye into its socket is a reflex which can be elicited by mechanical stimulation of a single sensory hair. The eyes can retract independently and if retraction occurs during the slow phase of optokinetic nystagmus, the efferent impulses in the oculomotor nerve of the retracting side are centrally suppressed. Peripheral inhibition of the optokinetic response occurs in the retracted eye when ~~i.e.~~ it is retained in its socket after retraction while the other eye continues with the slow phase of optokinetic nystagmus.

6. Movement of the eye relative to its environment seems to be essential for visual perception of a contrasting field of view. Small tremor movements of the eye when surrounded by a blank visual field are suppressed when the animal is surrounded by a contrasting visual field.

7. A comparison reveals similarities in the mechanism causing the onset of the fast phase of optokinetic nystagmus in the crab and in mammals.

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