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THE FLOW AND INTEGRATION OF SENSORY INFORMATION IN
THE CRAYFISH OPTOMOTOR SYSTEM

by

Wendy B. Stern-Tomlinson

A THESIS SUBMITTED
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

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ABSTRACT

THE FLOW AND INTEGRATION OF SENSORY INFORMATION IN

THE CRAYFISH OPTOMOTOR SYSTEM

Wendy B. Stern-Tomlinson

Activity in crayfish optomotor neurons was recorded extracellularly by microelectrode penetration of the eyestalk musculature. Because optomotor units are under sensory control by the statocysts, excitation of a given unit is modified in response to body rotation about either the longitudinal or transverse body axis. Each unit is maximally excited at an angular body position (the preferred position) which is 90° distant from the normal horizontal orientation. The position corresponding to minimal excitation (the non-preferred position) lies 180° from the preferred position. The excitation of any unit increases continuously to a saturation level in response to rotation from the non-preferred to the preferred position. However, the excitatory threshold and the level of saturation excitation varies from unit to unit.

With body position held constant, increase or decrease of the ongoing motoneuron firing rate can be produced by directing pulsed light into the appropriate eye receptive field, or by presenting moving patterned stimuli. Therefore, optomotor neurons are under at least two types of sensory control: statocyst-mediated and visually-mediated. In some cases, the
response to pulsed light consists of an excitatory transient followed by a brief inhibition, and then a steady-state component of the response is initiated. It is suggested that the visual input to the optomotor neuron operates in a negative feedback system which continuously adjusts the rate at which the eye reflex progresses. In this context, the mixed excitatory/inhibitory type of response may represent the result of stimulation of a movement-perceptive component of the visual system by a stationary light pulse.

It was proposed, as an initial hypothesis, that the optomotor response is driven through a specific visual channel, the sustaining fiber visual interneurons. Therefore, a sustaining and an optomotor unit with overlapping excitatory receptive fields were stimulated with pulsed light and a simultaneous record of the responses was made. A correlation between the spike patterns of the two units was found, and possible interpretations of this finding are discussed.

The hypothesis was also advanced that the statocysts may have a modifying influence on the expression of visual input by optomotor neurons. For one type of motoneuron, this was found to be the case, since the size of the light-evoked excitation varies as a function of (1) absolute body position and (2) the presence or absence of a continuous rotatory stimulus.
Acknowledgements

I would like to thank my dissertation advisor, Dr. Raymon M. Glantz, for his guidance and support during the course of this work. Also much appreciated is the assistance which has been provided by Dr. Arnold Eskin, Dr. Harvey B. Nudelman, and the late Dr. Clark P. Read. I am grateful for the efforts in my behalf of Dr. Stephen Subtelny and Dr. Krystina Ansevin, during the early part of my graduate career. Special thanks also goes to Dr. Kenneth D. Roeder, of Tufts University, Medford, Massachusetts, whose encouragement was of great value to me.
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Introduction

1. Optomotor and other eyestalk reflexes.

   a. Behavior description.

   The crayfish shares with a number of other crustaceans the ability to reposition its eyestalks in response to changes in its body position about the transverse axis (pitch), or about the longitudinal axis (roll) (Wiersma and Oberjat, 1968). When it is not visually tracking an object, a quiet animal maintains its eyes directed approximately lateral to the long axis of its body. Under conditions of pitch, the eyestalks rotate backwards and move upwards, or rotate forwards and move downwards, depending upon whether the animal's rostrum is directed downward or upward. When a roll occurs, the eyestalk ipsilateral to the direction of the roll is pulled upwards, whereas the contralateral eyestalk is drawn downwards. Therefore, the optomotor reflex is compensatory to any such movements the animal might make, insuring a relatively constant visual field even though the animal changes its orientation in space. The reflex is adaptive because it improves visual capability. Readjustment of the eye position during rapid body motion probably improves visual acuity by partially compensating for the shift of retinal image (see Discussion, section 1).

   Optomotor behavior as described above is distinct from optokinetic behavior, following the classification of Wiersma
(Wiersma and Oberjat, 1968). The latter consists of slow horizontal eyestalk movements alternating with rapid flipbacks, in response to rotation of the animal about the dorso-ventral body axis. In a third type of behavior, the eyestalks are reflexly withdrawn under the rostrum when the mechanoreceptors of the head or thorax are stimulated.

b. The eyestalk musculature and its innervation.

In _Procambarus clarkii_, ten eyestalk muscles control the eyestalk reflexes. A given eyestalk movement is the result of the active and passive tensions in a number of muscles (Sugawara, *et al.*, 1971), although the muscles which are active during any given movement have not been determined in crayfish. Some portion of the musculature is innervated by fibers in the oculomotor nerve, which originates in the supraesophageal ganglion and includes a total of forty-seven motor axons (Hisada and Higuchi, 1973), all of which appear to be excitatory to the muscles (Wiersma and Oberjat, 1968). It is impossible to assess the total number of motoneurons controlling the eyestalk reflexes on the basis of the anatomical studies done by Hisada and Higuchi, since the oculomotor nerve carries mechanoreceptive fibers, and since there are additional eyestalk motor axons running in the optic nerve (Bullock and Horridge, 1965, p. 828). The distribution of motor axons to
the muscles has not been investigated either anatomically or
physiologically, in crayfish, although physiological studies
have been done in the crab (Burrows and Horridge, 1968a.,
1968b). There is no evidence that the eye reflexes in decapods
are controlled peripherally, by way of feedback from tension
or stretch receptors (Wiersma and Oberjat, 1968; Horridge,
1965).

c. The response of optomotor neurons to changes in the
angular position of the body.

The optomotor neurons respond to mechanical vibration of
the substrate and to changes in body position about the trans-
verse or the longitudinal body axis. The body position cor-
responding to the maximum discharge rate is called the "pre-
ferred" position, and occurs about 90 degrees from the normal
position. About 180 degrees from the preferred position, the
discharge rate is at a minimum. For any unit, a plot of the
discharge rate, as a function of angular body position, yields
a bell-shaped curve. The maximum and minimum points on this
curve define the preferred and the non-preferred positions,
respectively (Wiersma and Oberjat, 1968).

The presence of both phasic and tonic motoneurons has
been described in the crayfish and in the crab (Wiersma and
Oberjat, 1968; Wiersma and Fiore, 1971 a., b.; Horridge and
Burrows, 1968 a). In the crayfish, certain motor units are more excited, at a given position, by motion in the preferred direction than they are by motion through the identical angular positions in the non-preferred direction. The excitatory response to motion adapts, upon maintenance of a steady position. If motion in the preferred direction is prolonged, the discharge rate at a given position eventually decays to that characteristic for the particular position. In the crab, there are unidirectional neurons which fire only during rapid motion toward the preferred position. These motoneurons are extreme examples of the phasic type (Wiersma and Fiore, 1971b).

In contrast, purely tonic motoneurons are sensitive only to the angular position of the animal about its transverse or longitudinal body axis. Tonic units would of course be active during motion of the animal through a succession of angular positions, but they do not signal motion in a particular direction.

d. Reciprocity in neurons of opposite function.

Each optomotor neuron can be characterized by the particular maintained tilt of the body which maximizes the discharge of that neuron. The position of the animal about its transverse body axis affects the discharge rate in two functional groups of axons. When the animal's rostrum points above the
horizontal, such that the angle formed between the rostrum and the horizontal plane is about 90 degrees, the head-up neurons are firing maximally and the head-down neurons are firing at their minimal rate. The reverse is also true, since when the head is pitched 90 degrees below the horizontal, the head-down neurons are excited and the head-up neurons are slowed or silent. There is an equivalent reciprocal system for angular body positions relative to the longitudinal body axis. At about 90 degrees side-up, the ipsilateral side-up neurons fire strongly, while the ipsilateral side-down neurons are barely active. At this same position, the contralateral side-down units fire strongly, and the ipsilateral side-down units do not. In both cases, the behavioral effect is to maintain the eyestalks in a nearly normal position.

2. The sensory control of optomotor neurons.
   a. Differentiation among statocyst receptor elements.

One afferent input to the optomotor system is via the bilateral statocyst organs. Ablation of the statocysts destroys the response to maintained tilt or rotation of the body in darkness (Wiersma and Oberjat, 1968). The statocysts in the crayfish and lobster are fluid-filled, ovoid concavities located in the basal segment of the antennules (Fig. 1), and they contain the statolith and a variety of receptor hairs.
Figures.

Figure 1. Dorsal aspect of the crayfish, *Procambarus clarkii*, not drawn to scale. The eyestalks are extended laterally and slightly caudally, having been glued to the head carapace. The medial side of the eyestalk musculature is thus exposed, and can be penetrated with steel electrodes. Central to the eyestalks is seen a soft membrane, behind which lies the optic peduncle, containing the optic interneurons and some eye reflex motoneurons. Also seen are the antennae and the shorter antennules, which contain the statocyst organs, membrane-covered depressions which are surrounded by a rather flat, chitinous area at the antennule bases. The centrally-located soft membrane and the basal part of the antennules are normally covered by the overlying rostrum, which in this preparation has been cut away.
In the lobster *Homarus*, the sensory hairs consist of chitinous, hollow projections, into which extend the dendrites of the primary sense cells (Cohen, 1960). In *Astacus*, there are three sense cells associated with a single statolith hair (see below), and each may abstract a different feature or range fraction of the stimulus (Schöne and Steinbrecht, 1968).

In the statocyst of *Homarus*, there are two morphologically identifiable receptor types, the hairs whose tips are embedded in the statolith, and those which float freely in the statocyst fluid (thread hairs). Statolith-associated hairs are primarily sensitive to absolute position about the longitudinal or the transverse body axis, although they are also sensitive to aspects of angular body rotation (see below: Type I and Type II receptor elements). With respect to their position sensitivity, they behave as linear accelerometers in response to gravitational acceleration. Because the vector component of the statolith weight which is perpendicular to the hair shaft axis increases with tilt of the animal from its normal position (angle $A$), a given hair is caused to change its angle with the cyst floor, with a resultant change in the impulse rate along the receptor axon. The laterally-directed force (or shear force) changes proportional to the sine of $A$, and the discharge rate varies with sine $A$ as well. As in the
optomotor system, the discharge maximizes when $\theta=90$ degrees and minimizes when $\theta=270$ degrees (Introduction, section 1c). The thread hairs are sensitive to angular acceleration (a change in the magnitude or direction of rotational velocity), and to vibration. They are apparently not sensitive to linear acceleration, either gravitational or that produced by linear motion of the animal along a horizontal substrate (Cohen, 1960).

Using both natural and artificial stimulation (manipulation with a fine needle), and recording from individual afferent axons, Cohen found receptors of four physiologically distinct groups. All of these response groups have some qualitative counterpart among crayfish optomotor neurons responding to the same stimulus (see Discussion, section 4). The different groups are described in the following way:

1) Type I: The response reflects the absolute position of the body about the transverse body axis, and is practically non-adapting when motion ceases and an angular position is maintained. The units that have been found have a maximum static discharge in the head-up position. Over a range of angular positions, the discharge rate varies as a bell-shaped curve. The response magnitude, per given angular position, differs dependent upon the rotation direction, being greater for rotation toward the position of maximum static discharge.
Type I receptor elements are briefly excited by mechanical vibration of the substrate. Since their discharge rate, per given position, tends to be greater if the velocity of motion is greater, they are described as being slightly velocity-sensitive.

2) Type II: The response also reflects absolute body position, and those units which have been observed have a maximum static response in either the head-up, head-down, or side-down positions. The response is strongly influenced by the direction of motion, since the adapted rate, after cessation of rotation, and the non-adapted rate of discharge are markedly different. Motion toward the preferred position produces a gradual increase in the discharge, which adapts downward when the motion stops and a steady position is maintained. Motion which is directed away from the preferred position silences the discharge, which then increases when the animal is held in a static position. The adapted rate is not dependent upon the direction of previous body displacement, but only upon the particular maintained position.

All position-related responses are abolished with stato-cyst removal, and units sensitive to absolute position can also be stimulated by the manipulation of statolith-associated hairs.
3) Acceleration: These units are sensitive to changes in the rotational velocity of the body, and are not sensitive to maintained positional changes. An inertial flow of the stato-cyst fluid, produced by angular acceleration or deceleration of the body, deflects the hair, and the ensuing receptor discharge reflects the direction of the hair displacement. Onset of motion such that a hair is deflected by the fluid flow in the posterior or ventral direction produces a high-frequency burst, followed by a return to the background firing level. Onset such that the hair is deflected in either the dorsal or anterior direction produces a transient cessation of the ongoing discharge. A return to the background level of firing ensues after the preparation reaches a constant angular velocity, since the hairs are restored to their rest position by their own elasticity. The same unit responds to motion about the longitudinal, lateral, and dorso-ventral body axes. The response is associated with the presence of statolith fluid, and with the artificial stimulation of one type of thread hair.

4) Vibration: The response is associated with mechanical vibration of the substrate, and with the imposed movement toward the cyst wall of a second type of thread hair.

It is possible that the statocysts also receive water-borne vibrations in the form of audible clicks (Taylor, 1968).
b. Differences within the group of statolith-associated receptor elements.

After removing the statolith, Cohen (1960) manipulated the hairs that had been associated with it. At the same time, he recorded from the axons of the stimulated hair cells, located in the antennular nerve. Lifting any hair from the cyst floor toward the vertical was excitatory to the hair cell, with a peak response occurring about 55 degrees from the cyst floor. Further elevation of the hair produced a progressive depression of the response. At 90 degrees from the cyst floor, the response was at a minimum. When the direction of the stimulation was reversed, resulting in movement if the hair from the vertical toward the cyst floor, the unit was first excited, with a peak response again occurring at an angle of 55 degrees from the cyst floor. When the hair was further depressed, the response progressively diminished. Therefore, any movement of a hair toward the 55 degree position was an excitatory stimulus to that hair cell, irregardless of the direction from which the movement was initiated. Secondly, a plot of angular position versus discharge rate generated a bell-shaped curve. For any unit, the approximate peak amplitude of this curve lay at the 55 degree position.

By contrast, when the statolith was left intact, the
relative responses of different units to a small imposed movement of the statolith varied greatly. For example, during a multi-unit recording, the response of one unit was blocked almost immediately following the start of the statolith movement, whereas a second unit was sequentially excited and then silenced. Upon the return motion of the statolith, both units were excited. Evidently, the statolith determines the portion of the unit response range which is related to a given statolith perturbation, and, by implication, to a given degree of tilt. For each hair, the statolith sets the angle with the cyst floor which corresponds to a given angular body position. The result is that units of the same response type (i.e., units which are both excited by motion of the statolith, or of the animal, in one direction), differ in relative sensitivity. Put another way, units of the same response type differ in the magnitude of the response each gives to the same angular body position. Therefore, the composite output, at a given position, of receptor elements of the same response type may comprise many different discharge rates.

c. Statocyst organs: comparative in the lobster and the crab.

The statocyst organs in most crabs are in one way similar to those of the lobster, since in both there are statolith-associated hairs and hairs which move freely in the statocyst
fluid. However, the gross structure of the crab organ is more differentiated than that of the lobster or crayfish (Cohen and Dijkgraaf, 1961). The crab organ resembles the vertebrate membranous labyrinth, but has two perpendicular toroids, instead of the vertebrate three (Aidley, 1971). During rotatory motion about any of the three orthogonal axes, the resultant fluid motion through the toroids of both statocysts deflects the freely moving receptor hairs in each of three groups, according to the direction and the magnitude of the acceleration. For any given motion, the response spectrum across the freely moving hair groups is unique, and so specifies the code for that particular direction and axis of rotation (Sandeman and Okajima, 1972).

It may be argued that since the crab organ directs the main vector of inertial fluid flow through the narrow toroids and directly over the receptor hairs, that it is probably more efficient in detecting the direction and magnitude of an acceleration than is the lobster or crayfish organ, where no such channels exist. This structural difference in the statocysts may form one basis for error in the crayfish compensatory eye reflex systems (see Discussion, section 2b(3)).

3. Visual influences upon the optomotor neurons.

The crayfish optomotor system has a major afferent control
through the visual system. One class of optic nerve inter-neurons, the sustaining units (Wiersma and Yamaguchi, 1966; 1967) possibly carries at least some of the visual information (Wiersma and Oberjat, 1968). The effect of visual stimulation by pulsed light upon an optomotor neuron may be excitatory, inhibitory or both, depending on the receptive field being stimulated (Results, section 2b). In addition, the motoneuron discharge is affected by moving stripes, which mimic the apparent environmental motion which is produced by rotation of the animal. A more complete description of the properties of the response to moving stripes is given in the Discussion, sections 1 and 2b(2). Moving stripe patterns were not used as visual stimuli in the present work.

As described by Wiersma and Oberjat (1968), the receptive fields for pulsed light stimulation are located such that the light-evoked and the statocyst-mediated responses are synergistic when light comes from above the animal. The inference can be made that the natural stimulus is sky light. Therefore, with the animal's eyes directed laterally, the excitatory receptive fields for head-up motoneurons are located at the anterior part of both eyes, and the inhibitory receptive fields are at the posterior. For head-down motoneurons, the locations of the two receptive fields are reversed. For side-up motoneurons, the excitatory receptive field is the ipsilateral eye,
and the inhibitory field is the contralateral eye. For side-down motoneurons, again the locations are reversed. The effect of pulsed light stimulation has thus been described as producing an increased excitation in the set of neurons which is already being activated by a position-related stimulus. At the same time, motoneurons of antagonistic function are inhibited. In this way, the motoneuron response may be reinforced through two distinct sensory channels. The spatial organization of the system on the sensory side appears to be such that different types of information can be combined in an unambiguous way at a more central point, and thus peripheral processing may be functionally related to central integration. However, it is not clear whether optomotor neurons can be excited by moving visual stimuli being presented to the inhibitory receptive field to pulsed light, and in one instance this would seem to be the case. The data of Hisada and Higuchi (1973) appear to indicate that a head-down motoneuron may be excited by a light moving ventro-dorsally across the anterior portion of the eye (see Discussion, section 1, p. 104).

4. Experimental rationale.

Certain earlier authors (Wiersma and Oberjat, 1968; Higuchi and Hisada, 1973) have suggested that visual and gravitational information flow independently to the motoneuron synapse, where
they are simply summed to generate the response. However, the data published by Wiersma and Oberjat (their Figure 4) show that, for a head-up motoneuron, there is a small amplification of the light-driven component of the response when the animal is moved into the preferred position. Similarly, the data of Higuchi and Hisada (their Figure 6) show that at every angular position except the non-preferred position, the discharge rate of a side-down unit during illumination of the excitatory receptive field exceeds that occurring during illumination of the inhibitory receptive field. At the non-preferred position, the motoneuron is silenced, even during illumination of the excitatory receptive field. In addition, Hisada and Higuchi (1973) report that when small moving lights and moving stripe patterns were presented as stimuli to optomotor neurons, with the animal in the normal body position, those head-up units which lacked an ongoing background discharge were also inexcitable visually. Therefore, although the above-mentioned authors did not make the inference, their data suggest that information in the statocyst-mediated channel to the motoneuron influences the expression of the visually-driven portion of the optomotor response. The specific proposal is that the visually-driven component of the response is greater at the preferred position than at more non-preferred
positions. Since, at non-preferred positions, visual excitation of the motoneuron would tend to contradict positional information, this proposal is a logically tenable one. The experimental work to follow does show that modification of the response to pulsed light according to positional and other statocyst-related information appears to exist in the crayfish optomotor system.

Candidate mechanisms which might underlie such a cross-modal integration are plentiful, and one of the foci of the discussion of the results is an analysis of the merits and drawbacks of a number of them. Part of this discussion is based upon some preliminary results which I have obtained, which suggest a likely area for further research. A part of the results is also devoted to a description of the optomotor response characteristics to statocyst-mediated and visual stimuli, and these results are discussed in terms of their known or possible sensory inputs within each modality, and in terms of the function of the visual input to the optomotor system. Another aspect of the results is based upon a direct attempt to test the hypothesis that the sustaining units represent one visual channel to the optomotor neurons. Although the findings may be interpreted as supportive, such an interpretation is open to criticism.
Methods

Crayfish of the type *Procambarus clarkii* were mounted above the substrate by means of a clamp extending about the dorsal carapace. The legs were lightly bound with tissue paper wrapped around the animal, and the claws were bound with elastic bands. The system of bars and clamps holding the preparation enabled motion through an arc of 180 degrees, the midpoint being the normal body position. Motion was possible in either of two orthogonal planes, the extremes corresponding to the ± 90 degree head-up/head-down or side-up/side-down positions. The apparatus holding the animal was coupled to a kymograph motor, enabling continuous rotatory motion of the animal. The rate of rotation was about 2 degrees per second. A voltage divider, mounted on one end of the motor-driven bar carrying the preparation, made it possible to visualize the angular body position being traversed via a calibrated DC offset displayed on an oscilloscope.

A photic stimulator was built, and contained two projector bulbs mounted separately behind electromagnetic shutters (Vincent Associates, Rochester, N.Y.). One end of a length of 6 mm. diameter fiber optic light guide was mounted close to the shutter diaphragm; the other end was either mounted in a micromanipulator or in the rotation apparatus. The latter
arrangement enabled stimulation in the same visual receptive field throughout rotatory motion of the animal, since the light guide and the animal were rotated together. In many cases, the fiber optic end diameter was reduced by fitting it with a hypodermic needle, cut off at the tip, of 1 mm. diameter. Square-pulsed light stimulation was applied at, or very close to the corneal surface. The light intensity could be varied at the source by use of a neutral density wedge calibrated over six log units.

Direct current to the shutter was controlled through a mercury-wetted, magnetic reed relay. The signal source to the relay was the gate output of a waveform generator (Tektronix type 161). The waveform generator was triggered either manually or by a clock motor running at 2 cycles per minute. The delay of the light pulse onset from the signal source trigger was 8 ms., and the gate duration was adjustable in the range 0.1 ms. to 10 seconds. When larger stimulus delays from the trigger were required, a pulse generator having a delay mechanism (Tektronix type 162) and another waveform generator were added in series. In all cases, a brief pulse marking the signal source trigger, and thus the subsequent occurrence of a light stimulus at some known interval, was part of the experimental record.

In preparation of an animal for an experiment, the eye-
stalks were glued to the lateral carapace, and the rostrum was cut back. Motoneuron spikes were then recorded extracellularly by electrode penetration of the eyestalk musculature on the medial side. Insulated steel electrodes of about 5 micron tip diameter were used. Optic nerve units, and very occasionally motor units, were found in the area just behind the soft membrane central to the eyestalks (Figure 1). Motoneuron spikes had a shorter waveform duration than muscle potentials and a constant amplitude to excitatory stimuli. Therefore, motoneuron spikes and muscle potentials were readily distinguishable on a lead.

The recording lead was connected to the differential input of a low-level preamplifier (Tektronix type RM 122), and then single-endedly to a second, similar preamplifier, for a total gain of $10^4$. The amplified signal was put through a 60 Hz. notch filter, and then was led to one input of a commercial stereo tape deck (Tandberg model 64). A parallel input went to a small audio monitor system. Two recording channels of the type just described were available for simultaneous use.

The taped data was continuously monitored during the course of an experiment, by playing back the tape into a dual beam oscilloscope. The oscilloscope screen was always shielded from the animal's vision. Experiments, except where specified in the text, were done in nearly complete darkness. The moto-
neurons were therefore maximally sensitive to light, and in addition they could not be confused with sustaining fiber interneurons. (In darkness, sustaining units are nearly silent, and they remain so at all body positions.)

When required, the statocysts were destroyed bilaterally by penetration of the sac membrane with a red hot needle.

Some experiments were quantitatively analyzed directly off the tape played into a storage oscilloscope. Statistical analyses, such as poststimulus time histograms, were done automatically through use of a time histogram analyzer (Ortec, model 4620 and 4621), often in parallel with a digital counter. In one experiment, the data was entered on computer tape, and was analyzed using a DEC model PDP 12 computer.

Results

1. Properties of the optomotor response to a change in the angular position of the body.

a. The change in discharge rate.

Optomotor neurons modify their discharge rates in response to changes in the angular orientation of the animal's body. The motoneurons are categorized according to the body position at which they are maximally excited (the preferred position). Four types of motor unit have been thus described: head-up, head-down, side-up, and side-down.
In the work to follow, the motoneuron responses are quantified by the discharge rate (Hz), and they are specifically related to body position, measured as angular position in degrees. Unit responses are recorded at intervals within a stimulus range of +90 and -90 degrees, where the sign designates the orientation of the ipsilateral side or the rostrum with respect to the horizontal. (Using the head-up/head-down system as an example, +90 degrees indicates that the animal's rostrum points 90 degrees above the horizontal; 0 degrees, that it has the normal orientation; -90 degrees, that it points 90 degrees below the horizontal.) For any neuron, when angular position is plotted against discharge rate, the resultant curve is approximately sigmoid-shaped, and usually indicates the full dynamic range of the neuron.

Measurements of the unit discharge rate have been made under one of two stimulus conditions: either the animal was rotated continuously, or it was placed in a series of maintained positions (steady-state stimulation). In a number of recorded cases, it was found that, for any given angular position within the excitatory range, the mean discharge rate was greater for continuous rotation through a position than for the equivalent stationary stimulus. In each of these cases, the rotation direction was from the non-preferred to the preferred position.
(see Figs. 2a, curves SDI and MDI; 9a(2); 9b(2); Higuchi and Hisada, 1973, their figure 1). The difference may indicate the presence of a phasic component of the response, evoked by movement in the preferred direction, or it may result from the addition of vibratory stimuli transmitted to the preparation from the rotation motor. That the neurons tested were phasic neurons is an assumption which could only have been tested by noting the response, per given position, of a given neuron during rotation toward and away from the preferred position.

The motoneurons of a given response type (e.g., head-up) behave in qualitatively the same way in response to a change of angular body position. However, the units of a given type may differ greatly in their maximum discharge rates and in their thresholds. Figure 3a(1) shows the response of two side-up motoneurons obtained on a single recording lead. The animal was placed in a series of maintained positions, and each trace corresponds to a different angular position. The small amplitude unit begins firing at -30 degrees, and has a maximum discharge rate of 57 Hz., whereas the large unit begins firing at a higher threshold position, 0 degrees, and has a lower maximum discharge rate (19 Hz.). Figure 3a(2) shows the results of a similar experiment done with two head-up units. The threshold for the small unit is 0 degrees, and the maximum discharge rate is 10.4 Hz. For the large unit, the
Figure 2a. Side-down motoneuron. The mean discharge rate, per given angular position, is plotted as a function of angular position. The standard errors corresponding to each mean are entered in brackets. MDI: The animal was continuously moving through the set of angular positions; there was no light stimulation; the statocysts were intact. The number of measurements used to construct each mean (n) was six. The direction of the rotation was from side-up to side-down (from the non-preferred to the preferred position). SDI: The animal was placed in a series of maintained angular positions; there was no light stimulus; the statocysts were intact; n=3.

MDO: Same as MDI, but the statocysts were ablated. n=6.

SDO: Same as SDI, but the statocysts were ablated. n=3.

For any position within the range of excitation, the mean response during motion exceeds the mean response during steady-state stimulation. After statocyst ablation, the motoneuron is no longer responsive to rotational stimuli, or to maintained tilt of the body. The response, per given position, during continuous motion of the animal is very similar to the response under steady-state conditions.

Figure 2b. Side-down motoneuron, not the same preparation as used for Fig. 2a. The mean discharge rate, per given
angular position, is plotted as a function of angular position. The standard errors corresponding to each mean are entered in brackets. SDI: The animal was placed in a series of maintained angular positions; there was no light stimulation; the statocysts were intact. The number of measurements used to construct the mean for each position varied between 6 and 11 (n=6-11).

SDO: Same as SDI, but the statocysts were ablated. n=6-11.

The mean responses to steady-state stimulation are absent after statocyst ablation.
Figure 3a(1). Two side-up motoneurons of different amplitudes were recorded on the same lead, and the responses of the units at each of a number of steady-state angular positions are shown. Each trace represents the responses at a single angular position. The discharge rates, per given position, were determined by counting the number of impulses during the one second duration sweep, and these rates are tabulated below. At all positions other than -60 degrees, at which the neurons are silent, the discharge rate of the smaller unit exceeds the discharge rate of the larger unit. The small unit begins firing at -30 degrees and the large one begins firing at 0 degrees, thus indicating that the units have different threshold positions.

<table>
<thead>
<tr>
<th>Position, degrees</th>
<th>Discharge rate, Hz.</th>
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<tbody>
<tr>
<td></td>
<td>Large unit</td>
</tr>
<tr>
<td>0</td>
<td>7</td>
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<tr>
<td>+30</td>
<td>17</td>
</tr>
<tr>
<td>+60</td>
<td>19</td>
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<td>+90</td>
<td>17</td>
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<td>-30</td>
<td>0</td>
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<td>-60</td>
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Figure 3a(2). Two head-up units of different amplitudes were recorded on the same lead. The responses of the units at a
series of steady-state positions were recorded. In the figure, each trace represents the responses to a single steady-state position. The discharge rates corresponding to each position are tabulated below, and were calculated by counting the number of spike occurrences during the five second duration sweep, and dividing by five. At all positions other than -30 degrees and -60 degrees, the discharge rate of the smaller unit exceeds that of the larger unit. The small unit begins firing at 0 degrees, and the large unit begins firing at +60 degrees, thus indicating that these units have different threshold positions.

<table>
<thead>
<tr>
<th>Position, degrees</th>
<th>Discharge rate, Hz.</th>
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<tr>
<td></td>
<td>Large unit</td>
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<tr>
<td>0</td>
<td>0</td>
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<tr>
<td>+30</td>
<td>0</td>
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<tr>
<td>+60</td>
<td>0.4</td>
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<td>+90</td>
<td>2.4</td>
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Figure 3b(1). Two head-up motoneurons (HU-1 and HU-2) were recorded in different preparations. For each unit, the mean response, per given steady-state position, is plotted as a function of angular position. For each mean, the standard
error is entered in brackets. The number of measurements on unit HU-1 used to construct each mean was four (n=4). For unit HU-2, n=4.

At each steady-state position above 0 degrees, the mean discharge rate for HU-1 exceeds that for HU-2. The threshold position for unit HU-1 is +30 degrees and that for HU-2 is +60 degrees.

Figure 3b(2). Two side-up units (SU-1 and SU-2) were recorded in different preparations. For each unit, the mean response, per given steady-state position, is plotted as a function of angular position. For each mean, the standard error is entered in brackets. The number of measurements on unit SU-1 used to construct each mean was three (n=3). For unit SU-2, n=2. Unit SU-1 was also used to construct part of Fig. 2a.

For all steady-state positions, the mean discharge rate for SU-1 exceeds that for SU-2. The threshold position for unit SU-1 is less than -90 degrees. The threshold position for unit SU-2 is -30 degrees.

Figure 3b(3). Two side-down units (SD-1 and SD-2) were recorded in different preparations. For each unit, the mean response, per given steady-state position, is plotted as a function of angular position. For each mean, the standard error is
entered in brackets. The number of measurements on SD-1 used to construct each mean was three (n=3). For unit SD-2, n=2
For unit SD-1, the threshold position is less than or equal to +90 degrees. For unit SD-2, the threshold position is at 0 degrees.
FIG. 3b(1)

FIG. 3b(2)
FIG. 3b(3).
threshold is at +60 degrees and the peak discharge rate is 2.4 Hz. (The presence of head-up units of low peak discharge rate and high threshold has also been reported by Hisada and Higuchi (1973)).

It appears from the data just given that different motoneurons of the same response type can vary in responsiveness to the same stimulus; that is, the motoneurons differ in sensitivity. However, in the two experiments cited, there was but a single stimulus trial at each angular position. One might argue that the validity of the conclusions depends on the amount of variability in the motoneuron response rate per given position. In Fig. 3b(1) are shown the mean responses of two head-up motoneurons to changes in the animal's steady-state position. The mean responses, and their standard errors, are plotted as a function of angular position. (In contrast to the data of Figs. 3a(1) and 3a(2), the unit responses being compared were not recorded from the same preparation.) Figure 3b(2) and Fig. 3b(3) are derived from similar experiments, but the units responding to the steady-state stimuli are side-up and side-down units, respectively. Note that in Figs. 3b(1), (2), or (3), for any position at which at least one neuron is excited, the mean responses of the two motoneurons are different. These results indicate that variability
in the data cannot account for the sensitivity differences observed between units of the same response type.

The general conclusion that can be made is that, for a given angular position, the active array of motoneurons discharge at many different rates. Each unit, although being of one response type or another, may be unique in its capacity to produce postsynaptic effects, whether by recruitment of muscle fibers of different electromechanical properties, or by summation in parallel on the same muscle fiber with other motoneurons. The variation in threshold imposes a temporal sequence of postsynaptic activation which may provide fine control of the muscle, and in addition may extend the muscular response range beyond that which could be produced by any one motor unit.

b. The effect of destruction of the statocysts.

Bilateral ablation of the statocysts eliminates all moto-neuron responses to gravitational stimuli (Wiersma and Oberjat, 1968; Higuchi, 1973). The present work confirms that observation. After the destruction of the statocysts, the moto-neurons assume a discharge rate which is independent of the angular position of the body (Fig. 2a, curve SDO; Fig. 2b, curve SDO). In addition, the discharge rate does not appear to depend upon whether the stimulus is static or dynamic,
although, as has been mentioned, this effect might be wholly
due to the elimination of the statocyst vibration receptor
elements. In Fig. 2a, comparison of the curve labelled MDI
(statocysts intact; dynamic stimulus) and the curve labelled
SDI (statocysts intact; steady-state stimulus) shows that,
for any given angular position within the excitatory range,
the motoneuron discharge rate for a dynamic stimulus exceeds
that for a steady-state stimulus. On the other hand, the
curves labelled MDO (no statocysts; dynamic stimulus) and
SDO (no statocysts; steady-state stimulus) are virtually
identical.²

2. Properties of the response to pulsed light in some eye
reflex motoneurons.

a. The excitatory response pattern in optomotor neurons.

Pulsed illumination of the appropriate visual receptive
field excites optomotor neurons. Figure 4a shows the response
of a head-up motoneuron to a one second duration square pulse
of light. The onset of the pulse is 108 ms. from the beginning
of the one second sweep. The stimulus intensity was well
above the threshold intensity. The stimulus was positioned
at the corneal surface, and was directed, via a 1 mm. diameter
light guide, into the approximate center of the excitatory
receptive field in the ipsilateral eye. (The approximate
Figure 4a. Head-up motoneuron. The unit was excited by a one second duration pulse of light, with onset 108 ms. from the beginning of the sweep, which also has a duration of one second. The 1 mm. diameter stimulus was directed into the approximate center of the excitatory receptive field, in the ipsilateral eye. The body was maintained at a pitch angle of +90 degrees. Note the presence of the transient excitation occurring about 60 ms. following the stimulus onset. This brief, high-level excitation is followed by the tonic component of the response.

Figure 4b. Head-up motoneuron, not the same unit as in Figure 4a. A PST histogram was constructed, at a time base resolution of 20 ms. per bin. Each division on the y axis represents 5.4 spikes. The vertical marks crossing the x axis indicate time bins within which no impulses occurred. The first bin never contains spikes, a characteristic of the time histogram analyzer. The stimulus was a one second duration pulse of light, directed into the approximate excitatory center of the ipsilateral eye. The steady-state angular position of the body was +90 degrees. The stimulus onset occurs at 90 ms. from time zero on the x axis of the histogram, and the largest entry, in the approximate center of the histogram, marks the end of the pulse. The number of individual responses entered as data was fifteen.
light on

FIG. 4a
5.4 spikes

256 ms

FIG. 4b
location of the center, or the dorsal anterior eye rim, was previously determined as shown in the Results, section 3a.) For this particular neuron, the magnitude of the light-evoked excitatory response was dependent upon the angular position of the animal's body (see Results, section 3b). The body position was held at +90 degrees, thus maximizing the response to light.

The response pattern is described as follows. After a 50 ms. response latency, there is a burst of four spikes, which fire at an average rate of 100 Hz. Following this burst is a silent period, lasting 100 ms. The discharge which then ensues has an average rate of 23 Hz., exceeding the background firing rate by 10 Hz. (The background discharge of 13 Hz. is not shown in the figure. It was determined by counting the number of spikes occurring within a 5 second period, beginning 4.9 seconds after the stimulus onset. The mean background rate in Hz. could then be calculated.) Therefore, the excitatory response pattern of this neuron, and of all optomotor neurons observed in this study, consists of a relatively high frequency transient, followed by a tonic component of lower discharge rate. The silent period following the initial excitation is not a general feature of the response (e.g., see Fig. 10a(1)).

The averaged response pattern of a neuron to a stimulus
presented a number of times can be represented by a post-stimulus time histogram (PST histogram). In Fig. 4b, is presented the PST histogram for a head-up motoneuron, being stimulated with pulsed light presented at 30 second intervals. The time resolution along the x axis is equal to 20 ms./bin, starting with the second bin. The number of individual responses used to construct the histogram is equal to 15. Each large division along the y axis represents 5.4 impulses. The conditions for stimulation are similar to those specified for Fig. 4a, except that the stimulus onset in this case occurs 90 ms. after time zero on the x axis. The data of Figs. 4a and 4b were taken from different preparations.

According to Fig. 4b, the latency of the response onset from the stimulus onset is about 50 ms., on the average. The transient portion of the response is followed by the tonic component. The mean peak discharge rate in the transient is 50 Hz., and the tonic rate is about one-third this value, or 17 hz. The average background rate is 6 Hz. (as determined from data not included in the PST histogram).³

b. The response pattern of some optomotor neurons to stimulation in the inhibitory receptive field.

Records of the response of side-down motoneurons to pulsed illumination of the ipsilateral eye show that the neuron may
either be briefly inhibited, or may be inhibited following a brief excitation. (The latter response pattern has also been noted occasionally, when the excitatory field of a motoneuron is stimulated (Fig. 4a).) It is not clear what circumstances contribute to the evocation of one type of response or the other. Figure 5a is a PST histogram, based on a series of 18 responses to a one second duration light pulse, which was directed into the whole ipsilateral eye. There are 13.5 spikes per large division on the y axis, and the time resolution is 10 ms. per bin. The onset of the stimulus occurs about 90 ms. from time zero on the x axis. The excitatory receptive field, or the contralateral eye, was shielded from any extraneous light with a black, opaque cloth draped over it. In Fig. 5a, a cessation of the ongoing firing rate (18 Hz.) is seen to have an average latency of 40 ms., and a duration of 50 ms. There is a small rebound excitation following the silent period. In order to elicit an inhibition which was discernible in a PST histogram, it was necessary that the stimulus illuminate the entire eye, rather than the central pole only.

On another occasion, and under nearly similar stimulus conditions (the contralateral eye was not shielded), another type of response was evoked. Figure 5b(1) is a single trace from this series. The stimulus onset occurs about 90 ms. from
the beginning of the sweep, and the sweep duration is one second. The most notable part of the response consists of a 400 ms. period in which no impulses occur, and this period is preceded and followed by a group of two spikes, separated by a 40-45 ms. interval. Inspection of individual records similar to that presented in Fig. 5b(1) shows that the inhibitory periods have variable latencies and durations, with the result that the PST histogram (Fig. 5b(2)), based on the series of 14 stimulus trials, did not exhibit a clear-cut period in which the rather irregular ongoing discharge was silenced. (Figure 5b(2) was constructed at a time resolution of 20 ms. per bin. The offset of the light pulse is marked by a prominent artifactual transient. Therefore, the median level of ongoing discharge, both before and after the stimulus offset, is estimated at 15 Hz.) There is nevertheless some indication of a 40 ms duration inhibitory period, beginning 190 ms. after the stimulus onset. The brief excitation seen in Fig. 5b(1) is clearly evident in Fig. 5b(2), having an average latency of 50 ms., with a peak discharge of 43 Hz.

In Fig. 5b, the contralateral eye might have received extraneous light, with the result that the response pattern might have been due to the excitation and inhibition produced by the illumination of both receptive fields. However, in a
Figure 5a. Side-down motoneuron. PST histogram, constructed at a time resolution of 10 ms. per bin on the x axis, and with 13.5 spikes represented per division, on the y axis. In this and in the following histograms, the vertical marks crossing the x axis indicate time bins within which no impulses occurred. The first bin never contains spikes, a characteristic of the time histogram analyzer. The histogram includes 18 individual responses to a one second duration light pulse, directed into the entire ipsilateral eye. The contralateral eye was shielded from any extraneous light. The stimulus onset occurred about 90 ms. from time zero on the x axis. There is a 50 ms. period, occurring 40 ms. from the stimulus onset, which contains no impulses. It is followed by what appears to be a small rebound excitation.

Figure 5b(1). Side-down motoneuron. Individual record, taken from a series of responses to one second duration pulses of light, presented to the ipsilateral eye. The stimulus onset occurs about 90 ms. from the beginning of the one second duration sweep. The contralateral eye was not shielded from extraneous light. In this figure, a period in which no spikes occur is preceded and followed by spike doublets.

Figure 5b(2). Side-down motoneuron: PST histogram, based
upon the responses to 14 stimuli, one of which is presented in Figure 5b(1). The histogram is constructed at 20 ms. per bin. On the whole, the discharge both before and following the stimulus offset is rather irregular. There is a prominent, brief excitation following the stimulus onset.

Figure 5c(1). Side-down motoneuron. Stimulation was as in Figure 5a. Each horizontal row of dots represents the response to a single stimulus trial, and the sweep duration is one second. An arrow marks the time of stimulus onset. A period of inhibition of variable latency and duration is preceded by a brief excitation.

Figure 5c(2). Side-down motoneuron: PST histogram based upon the 11 responses in Figure 5c(1), and constructed at a resolution of 20 ms. per bin, with 5.4 spikes represented per division on the y axis. The prominent post-stimulus excitation is clearly seen.

Figure 5c(3). Side-down motoneuron. The analysis conditions and the stimulus conditions were as in Figure 5c(1), except that the stimulus diameter was reduced to about 1 mm., presented at the central pole of the ipsilateral eye. An arrow marks the time of stimulus onset. The period containing no impulses is no longer apparent.
Figure 5c(4). Side-down motoneuron: PST histogram based upon the responses to the 10 stimulus trials presented in Figure 5c(3). The time resolution was 20 ms. per bin, and there were 5.4 spikes per division presented on the y axis. There is a very brief excitation following the stimulus onset.
13.5 spikes
128 ms

FIG. 5a

light on

0.1 mv
0.1 sec

FIG. 5b(1)
light on

0.1 sec

FIG. 5c(1)

5.4 spikes

256 ms

FIG. 5c(2)
light on

0.1 sec

FIG. 5c(3)

5.4 spikes

256 ms

FIG. 5c(4)
subsequent experiment, a response of the same type was still elicited, even when the contralateral eye was shielded. Figure 5c(1) shows the results of one such stimulus sequence. The stimulus onset occurs at about 90 ms., and the sweep duration is one second. Each row of dots represents the spike train associated with a single stimulus trial. As before, the latency and duration of the inhibitory period are both unstable, the maximum duration being about 200 ms. The inhibitory period is preceded by an excitation consisting of two or three spikes. A PST histogram (Fig. 5c(2)) constructed from the same data indicates that the peak discharge during the 40 ms. duration excitatory period is 64 Hz., and that it occurs with a latency from the stimulus of 50 ms. (Figure 5c(2) was constructed with the same time resolution as Fig. 5b(2), and y axis division represents 5.4 spikes.) A small diameter central stimulus did not evoke a clearly defined period in which the discharge was silenced (Fig. 5c(3)). However, there is a very brief excitatory discharge occurring 70 ms. from the stimulus onset (Fig. 5c(4)). From these, and from the results in Fig. 5a, it appears that (a) the strength of the inhibitory response, in terms of its existence and perhaps in terms of its regularity from trial to trial, is dependent upon illumination of the whole eye field, and (b) that the inhibition is frequently preceded by an excitatory discharge.
c. The effect of pulsed light on a horizontal optokinetic unit.

Motoneurons responsive to unidirectional rotation about the dorso-ventral body axis have been described in crayfish (Wiersma and Oberjat, 1968), crab (Burrows and Horridge, 1968a; Horridge and Burrows, 1968b), and lobster (York, Wiersma, and Yanigisawa, 1972). In the crab, the sensory input to the motoneurons comes both from the statocysts and from the visual system, but in the crayfish, the sensory input is purely visual. Therefore, in crayfish, a given unit increases its discharge rate when the animal is rotated in the preferred direction in light, but not in the dark. The same unit is inhibited when the animal is rotated in the non-preferred direction, but again, this occurs only in lighted surroundings. An optokinetic unit can also be stimulated by rotating a vertically-striped drum about the stationary animal, and, in fact, this is the usual method of stimulation found in the literature.

Figures 6a(1) and 6a(2) show the responses of an optokinetic unit during clockwise (1) and anticlockwise (2) rotation of the animal under ambient light conditions. Clockwise rotation was directed toward the ipsilateral eye, and anticlockwise rotation was toward the contralateral eye. The rotation was hand-controlled and traversed a 90 degree arc in
Figure 6a(1). Horizontal optokinetic unit. The animal was rotated about the dorso-ventral body axis in the clockwise direction (toward the ipsilateral eye), under ambient light. The unit was excited by rotation in this direction.

Figure 6a(2). The same unit as in Fig. 6a(1). The animal was rotated about the dorso-ventral body axis in the anti-clockwise direction (toward the contralateral eye), under ambient light. The unit was inhibited by rotation in this direction.

Figure 6b(1). The same unit as in Figs. 6a(1) and 6a(2). The neuron was stimulated with a series of light pulses, directed into the central anterior rim of the ipsilateral eye. A PST histogram was constructed, at time base resolution equal to 20 ms. per bin, and with each large division on the y axis representing about 13.5 impulses. The onset of the light pulse corresponds to the second time bin. The duration of the light pulse was 1080 ms., and its end is marked by the prominent artifactual transient. The number of responses used to construct the histogram was eighteen (n=18). This unit is excited by pulsed light.

Figure 6b(2). The same unit as in the above figures. All conditions were as in Fig. 6b(1), except that the stimulus
was directed into the central anterior rim of the opposite, or contralateral eye. n=21. Excitation of the unit occurs, as before.
either direction. One can see that the unit is excited by clockwise rotation, and inhibited by anticlockwise rotation. These results were not seen when rotation was done in the dark. In addition, the unit did not respond to rotation about the transverse or longitudinal body axes.

The unit was stimulated at 30 second intervals by a 1080 ms. duration pulse of light. The 1 mm. diameter stimulus was directed into the center anterior rim of the ipsilateral or the contralateral eye. Figures 6b(1) and 6b(2) contain the PST histograms, at a time resolution of 20 ms./bin, corresponding to ipsilateral and contralateral eye stimulation, respectively. The beginning of the stimulus corresponds to the second time bin in the histograms. Notice that in each case, the PST histogram shows definite excitation, with a latency to onset equal to 60-80 ms. following the stimulus onset. After the initial excitatory period, the response adapts fairly rapidly. During the stimulation of the contralateral eye, the response shows a tonic component which slightly exceeds the background rate. During ipsilateral eye stimulation, the firing rate following the excitatory transient is indistinguishable from the background rate. Clearly, both optokinetic units and optomotor units can show similarly patterned responses to pulsed light. The similarity in response to the same type
of visual stimulus suggests the possibility that the two types of motoneurons may be driven by the same visual channel.

d. A possible channel for bringing visual information to optomotor neurons.

It has been suggested (Wiersma and Yamaguchi, 1967) that sustaining fiber visual interneurons carry sensory information to the optomotor neurons. Both sustaining units and moto-neurons are excited by a square-pulsed light stimulus, and their response patterns to this stimulus are very alike. To illustrate this point, Figs. 7a and 4a should be compared. Figure 7a shows the response of a sustaining unit (038) to a one second duration light pulse directed into the ipsilateral eye. The delay of the stimulus onset from the beginning of the one second duration sweep was 108 ms. Figure 4a is a record of the response of a head-up motoneuron to a pulse of light. (The two units were not recorded in the same preparation). In Fig. 4a, the duration of the stimulus was one second, and the stimulus delay from the beginning of the one second duration sweep was also 108 ms.

The similarity between the two responses is striking. Both neurons fire most strongly to the onset of the light pulse. The transient discharge of the sustaining unit is, however, much greater than that of the motoneuron. When the stimulus is maintained, the response of both units decays to a tonic,
Figure 7a. Sustaining visual interneuron 038. The unit was excited with a one second duration pulse of light, directed into the ipsilateral eye, with onset 108 ms. from the beginning of the sweep, which also has a duration of one second. The response pattern consists of a very high frequency transient, followed by a tonic discharge. The unit was silent when light stimulation was not present.

Figure 7b(1). Sustaining unit 019.

Figure 7b(2). Side-up motoneuron.

PST histograms were constructed for 019 and a side-up unit recorded simultaneously in the same preparation, using two separate recording leads. The two units were excited with pulsed light directed into the 019 excitatory center. The delay of the stimulus onset from the second bin in the histogram is 90 ms., and the duration of the stimulus was 1030 ms. The time base resolution in Fig. 7b(1) is 10 ms. per bin, with one division on the y axis representing about 27 spikes. The number of responses used to construct the histogram was 30. For Fig. 7b(2), the time base resolution was 50 ms. per bin, and one division on the y axis represents about 13.5 spikes. For this figure, n=29. The vertical marks crossing the x axis in both figures indicate time bins within which no impulses occurred.
lower frequency discharge.

In order to investigate possible quantitative relationships between sustaining fiber and motoneuron spike trains, attempts were made to obtain separate and simultaneous leads on a sustaining unit and a motor unit having overlapping excitatory receptive fields. Establishment of quantitative relationships could constitute a circumstantial argument for the sustaining fiber as one sensory channel to the motoneuron. Because this was a very difficult procedure, only one case was observed. In this experiment, the responses of sustaining fiber 019 and an ipsilateral side-up motoneuron were recorded during pulses of light directed into the 019 excitatory center. Since this point was near the central pole of the eye, it must be assumed that up to six other sustaining units were also stimulated near their centers (Glantz, 1973; Wiersma and Yamaguchi, 1966). The diameter of the stimulus was 1 mm., the duration was 1030 ms., and the intensity was around saturation for the sustaining unit.

The PST histograms for both units are shown in Figs. 7b(1) and 7b(2). Note that the calibrations along both the x and the y axes are different for the two histograms. The motoneuron response was rather weak (18 Hz. at the peak), and its background rate was moderate (about 5 Hz.). Although one would expect the stimulus to coincide reasonably well with the
motoneuron excitatory center (Wiersma and Oberjat, 1968), the
motoneuron was rather weak (18 Hz at the peak). The background
rate was moderate (about 5 Hz). The sustaining fiber, nearly
silent during the prestimulus period (90 ms.), fires at its
peak rate (235 Hz.) between 31 and 40 ms. after the stimulus
onset. When the time of occurrence of the first post stimulus
spike was averaged over 29 stimulus runs, the figure for the
mean was 32 ms., with a standard error equal to ± 0.5 ms. Since
the variation in this data was small, the figure of 32 ms. is
a good indication of the true latency.

It was not possible to get as fine an estimate of the
motoneuron latency from the stimulus onset, since the precise
time of the response onset was difficult to determine. From
the PST histogram shown in Fig. 7b(2), the peak response would
seem to lie between 61 and 110 ms. poststimulus. When the
analysis was done using a PST histogram at a finer time resolu-
tion (not shown), the latency to the peak response was found
to like between 71 and 90 ms. The mean response latency, as
calculated for the first motoneuron spike poststimulus, is 60
ms., with the standard error equal to ± 5 ms. The upper and
lower 95% confidence limits for this sample mean are c-1 =
70 ms. and c-2 = 50 ms. That is, one can be 95% confident
that the mean of the population from which the sample was
drawn falls within these limits. Taking into account the
small variation in the sustaining unit data, the conclusion
is that the average motoneuron response occurs at least 17 ms. later than the sustaining unit response. This order of response is a necessary condition for the postulated pattern of connectivity to hold.

On the hypothesis that the motoneuron sums presynaptic inputs to gain its spike threshold, and that the likelihood of a motoneuron spike depends on the recent history of synaptic inputs, one might then count the cumulative number of sustaining unit spikes preceding a given motoneuron spike (1st, 2nd, ..., Nth after the sustaining unit response onset). Therefore, the term N, as used here, designates the order of a given motoneuron impulse within the sequence of impulses contained in a spike train. One might then anticipate that the cumulative number of sustaining unit spikes might vary as a definable function of N.

In the present case, the data for 28 stimulus trials was digitized on magnetic tape, using a PDP 12 computer. The time of occurrence of each nerve impulse was then printed out, using the appropriate program. The analysis to be described was done manually from these print-outs.

In Fig. 7c(1), the mean cumulative number of sustaining unit spikes to the Nth motoneuron spike is plotted as a function of N. The standard errors for each mean are entered via
Figure 7c(1). Sustaining unit 019 and a side-up unit, as in Figs. 7b(1) and 7b(2). The following analysis was done for the period during and slightly following the light stimulus period. The mean cumulative number of sustaining unit spikes to the Nth order motoneuron spike was determined, and is plotted as a function of N. Standard errors of the mean are entered via brackets. For N=1 to N=7, the function appears to be linear. For N=8 to N=11, the function becomes non-linear.

Figure 7c(2). Sustaining unit 019 and a side-up unit, stimulated and simultaneously recorded, as in Figs. 7b(1) and 7b(2). The following analysis was done for the period during and slightly following the stimulus period. The mean sustaining unit discharge rate was computed over the interval bounded by the Nth and the N-1th order motoneuron spikes. (The first mean discharge rate was computed over the interval bounded by the first motoneuron spike and the onset of the sustaining unit spike train). The mean sustaining unit discharge rates, with standard errors, are plotted as a function of time. N corresponding to each mean discharge rate is entered above the points in the graph.

Figure 7c(3). Sustaining unit 019 and a side-up unit, simultaneously recorded as in Figs. 7b(1) and 7b(2). The two units were excited by pulsed light, as described in the legends.
to Figs. 7b(1) and 7b(2), and computations were then done for the period during and slightly after the stimulus period. The mean intervals bounded by the Nth and the N-1th motoneuron spike, with standard errors, are plotted as a function of N. (The first mean interval was taken as the one bounded by the first motoneuron spike and the sustaining unit spike train onset.) The mean interval during no light stimulation is plotted as a line parallel to the x axis.
FIG. 7c(2)
brackets. It may be seen that the plot is distinctly linear for $N = 1$ through $N = 7$, even though the average discharge rate of the presumptive input under observation shows a progressive decline. (The slope of the initial part of the function in Fig. 7c(1) indicates that approximately 13 sustaining unit spikes occur during each of the first six motoneuron interspike intervals.)

The average sustaining unit discharge rate associated with the $N$th motoneuron spike is given in Fig. 7c(2). In this figure, the mean sustaining unit discharge rate, computed over the interval bounded by the $N$th and the $N$-1th motoneuron spike is plotted as a function of time. $N$ for each mean discharge rate is entered directly above each point. Since for $N = 1$ to $N = 7$, the range of sustaining unit decrement was $238 \pm 9$ Hz. to $95 \pm 3$ Hz., it appears that, for relatively high rates of sustaining unit discharge, firing rate is not a factor in determining the incremental number of sustaining fiber spikes preceding each motoneuron spike.

In Fig. 7c(3), the mean motoneuron interspike interval, bounded by motoneuron spikes $N$ and $N$-1, is plotted as a function of $N$. Considering the portion of the graph corresponding to $N = 1$ through $N = 7$, the results are consistent with the previous discussion. For the data through the third motoneuron spike, the incremental number of sustaining unit
spikes to each succeeding motoneuron spike is constant, (Fig. 7c(1)), and since the sustaining unit discharge shows a 70 Hz. decrement, (Fig. 7c(2)), the interval between successive motoneuron spikes increases, as expected, as N increases. The case is similar for N = 4 through N = 7, which is still in the linear portion of the curve in Fig. 7c(1). The average sustaining unit discharge rate changes more slowly for N = 4 through N = 7 (Fig. 7c(2)), and the motoneuron similarly reveals a more gradual decline in discharge rate as N increases.

For N = 8 through N = 11, the curve in Fig. 7c(1) becomes nonlinear. In effect, there are fewer incremental sustaining unit spikes preceding a given motoneuron spike. Sustaining unit discharge rate for the range N = 8 through N = 11 decreases from 78 ± 6 Hz. to 60 ± 8 Hz. A possible explanation is that the motoneuron is no longer being driven by the sustaining unit, and that it has returned to its background level of firing. That this is not the case can be seen from Fig. 7c(3). In this figure, the mean interspike intervals corresponding to N = 8 through N = 11 are smaller than the mean unstimulated interval. In fact, these intervals are certainly comparable in size to the intervals corresponding to N = 4 through N = 7. The data indicate that the mean size of a motoneuron interspike interval is not substantially changed, even though the
incremental number of sustaining unit spikes to each motoneuron spike decreases with increasing N. Provided that the sustaining unit does input to the motoneuron, an explanation for the maintained rate of motoneuron firing in the presence of diminished presynaptic spike rate might be the existence of a relatively long-term facilitatory process which increases the efficacy of the synapse (for further comment, see the Discussion, section 3a).


a. Determination of the approximate excitatory center for a head-up motoneuron.

In order to test the hypothesis that the response to a light stimulus is modified according to body orientation (Introduction, section 4), one would pulse light at the excitatory center of a motoneuron visual receptive field while the animal's body position was varied. Placing the light stimulus at the excitatory center would maximize the chances of observing a position-related change of responsiveness, should such a change exist. In order to determine the approximate excitatory center for a head-up neuron, ten light pulses, occurring once every 30 seconds were directed into each of nine different loci on the eye ipsilateral to the motoneuron. The duration
of the light pulse was one second, and the intensity was about 100 times the threshold intensity. The animal was held in the normal (0 degree) position throughout the experiment.

The data for each position was analyzed by computing the mean light-stimulated discharge rate exceeding the background rate. This defines what is meant by the term "mean light-driven response."\(^7\) Figure 8a is a map of the stimulated eye, in which are entered the mean light-driven responses of a head-up unit, corresponding to the nine loci which were tested. Each line in the map delineates adjacent loci whose mean light-driven responses were significantly different at the 95% confidence level, using the analysis of variance (Snedecor, 1967). The figure indicates that the largest excitatory response was produced by stimulation of the dorsal anterior rim of the eye. Therefore, this locus was taken as the approximate excitatory center, for pulsed light stimulation. In contrast to the results of Wiersma and Oberjat (1968), who limited the head-up excitatory field to the anterior rim of the eye, the central pole of the eye was also found to have considerable excitability. In support of their findings, the posterior third of the eye appears to be a zone of minimal excitability.
b. Dependence of the light-evoked excitatory response upon nearness to the preferred position, in head-up motoneurons.

The mean light-driven response of a head-up neuron was determined at seven different maintained positions of the animal's body. These positions ranged from −60 degrees (the least preferred position) to +90 degrees (the most preferred position). The stimulus was about 1mm. in diameter, and was directed into the excitatory center of the ipsilateral eye. The light pulse was 1020 ms. in duration, and was well above the threshold intensity. About 20 stimuli, arriving once every 30 seconds, were presented at each body position. A stimulus sequence at 0 degrees (the normal body position) was frequently included during the course of the experiment. This was done to control for spurious results due to drift of the preparation sensitivity.

Figure 8b is a sequence of PST histograms showing the results of the experiment described above. For each histogram, the stimulus onset occurs 108 ms. from the second time bin (the time resolution was 20 ms./bin). It can be readily seen that as the animal's position approaches the preferred position of the motoneuron, the response occurring during the light stimulus period is progressively increased. The response to light was blocked at positions below 0 degrees (not shown in the sequence of PST histograms, but determined
by inspection of the results of each stimulus trial on a
storage oscilloscope).

The quantitative data in Fig. 8c is derived from the data
in Fig. 8b. For each PST histogram, the mean light-driven
response and the mean background rate were computed as de-
scribed in Appendix note 3. In Fig. 8c, the mean light-driven
response rate (1) and the mean background rate (2) were then
plotted as a function of the animal's body position. The
means corresponding to the four stimulus sequences at 0 degrees
(see above) were plotted individually in curve (1).

In Fig. 8c, the steady-state background rate (curve (2))
has a very small dynamic range. This is characteristic of
one type of head-up neuron (see also Fig. 9b(2) for another
example of such a neuron). At -60 degrees and at -30 degrees,
there is no response to light, and no background discharge.
At 0 degrees, the background discharge is still absent, but
there is a small response to light, on the order of 2-4 Hz.
At +90 degrees, the background discharge is maximum, and the
mean light-driven response is modulated strongly in concert
with the statocyst-driven rate, showing a striking amplifica-
tion with an increase in the background rate. In later sec-
tions of this paper, a light-driven response of this type will
be referred to as a "modulated response." Additional recorded
cases can be seen in Figs. 9a(1) and 9b(1).
Figure 8a. Head-up motoneuron, map of the receptive field to light stimulation. The mean light-driven response exceeding the background rate was determined at nine different loci on the ipsilateral eye. The angular position of the animal was maintained at 0 degrees, the normal position. The mean light driven response, with its standard error, is entered in the figure at the approximate locus on the cornea at which the stimulation was done. Ten individual responses were used to generate each mean. Lines drawn between adjacent loci indicate that the means corresponding to the loci are significantly different at the 95% confidence level, according to an analysis of variance. The approximate excitatory center appears to be located at position 4, at the dorsal anterior rim of the eye.

Figure 8b. Head-up unit, a different preparation from that in Figure 8a. The unit was excited by pulsed light directed into the approximate center of the excitatory receptive field, as the animal's steady-state body position was varied. PST histograms were constructed from the responses to a number of stimulus trials \( (n) \), at the positions listed below:

(1) 0 degrees; \( (n=20) \).

(2) +15 degrees; \( (n=18) \).

(3) +30 degrees; \( (n=17) \).

(4) +60 degrees; \( (n=19) \).
(5) +90 degrees; (n=23).

The histograms were constructed at a time resolution of 20 ms. per bin, and one large division on the y axis represents about 5.4 spikes. The vertical marks crossing the x axis in the figures indicate time bins within which no impulses occurred. The stimulus onset occurred 108 ms. from the second time bin, and its duration was 1020 ms. Because the units did not exhibit a response during the light stimulus period at -30 and -60 degrees, PST histograms were not constructed from results of stimulation at these positions.

The magnitude of the response during the light stimulus period markedly increases with an approach to the preferred position.

Figure 8c. Head-up unit, as in Fig. 8b. The mean light-driven response exceeding the background rate (1) and the mean background rate (2) are plotted as a function of angular position. Four means for the light-driven response occurring at 0 degrees are plotted separately; these were computed from data taken at various times during the course of the experiment. As the mean background rate increases, the mean light-driven response increases greatly.

Figure 8d. Side-up motoneuron. The mean light-driven response
during steady-state conditions was plotted as a function of angular position. The pulsed light stimulus was applied at the center of the ipsilateral eye. The number of individual responses used to compute each mean was three, and standard errors of the mean are entered via brackets.
FIG. 8a
FIG. 8b(1)

FIG. 8b(2)
FIG. 8b(3)

FIG. 8b(4)
5.4 spikes
256ms

FIG. 8b(5)
FIG. 8c
FIG. 8d
In all, six head-up units, two side-down units, and one side-up unit were tested in experiments similar to the one described above. Five out of the six head-up units showed modulation of the mean light-driven response. The sixth result was ambiguous. Of the two side-down units, one showed a highly variable mean response, per steady-state position, which could not be further interpreted. The mean light-driven response under conditions of continuous body rotation (see below, section 3c) is shown in Fig. 10b(2). For the other side-down unit, the light-driven response had a gradually sloping decrement as the preferred position was approached (Fig. 10b(1)). The side-up unit showed a response which was approximately constant over the range of angular positions, the response at any position being relatively small (Fig. 8d). This was so even though the intensity of the stimulus was comparable to that used in the experiments with the other motoneurons.

A summary of the results of this section can be stated as follows. Optomotor neurons have responses to light which can either vary or remain relatively constant with a change of angular body position. Some neurons show a striking amplification of the light-driven response as the level of motoneuron excitation coming through statocyst-driven channels is increased. This is so under conditions in which the light
stimulus parameters are kept constant. The direct relationship of the level of visually-driven excitation to the level of statocyst-driven excitation is interpreted to mean that the expression of the light-driven response in at least some moto-neurons is modified by statocyst-mediated information. This interpretation is based on the supposition that the statocysts are the primary position-detecting sensory system having input to the motoneurons, a supposition which is supported by the results in section 1b.

c. Dependence of the light-driven excitatory response on the method of repositioning the animal (continuously, or via a series of maintained positions).

For two head-up motoneurons, the mean light-driven response was determined at each of seven angular positions, under both dynamic and steady-state conditions (Figs. 9a(1) and 9b(1)). The feature which is common to these results is that, for a given angular position within the excitatory range, the mean light-driven response during motion is generally less than the response during steady-state stimulation. (In Fig. 9b there is an exception to this statement, since at +60 degrees the two mean responses are statistically different only at the 90% confidence level, using a one-tailed T-test. This means that at +60 degrees, the response under the steady-state con-
Figure 9a(1). Head-up motoneuron. The mean-light driven response per given angular position during steady-state (SL) and moving (ML) conditions was plotted as a function of angular position. The number of individual responses used to compute each mean was three. Stimulation was as in Fig. 8b.

For each angular position within the excitatory range, the mean light-driven response during steady-state conditions exceeds the mean light-driven response during moving conditions.

Figure 9a(2). Head-up unit, as in Fig. 9a(1). The unit is the same as one of those in Fig. 3b(1). The mean statocyst-driven response, per given position, during steady-state (SD) and moving (MD) conditions was plotted as a function of angular position. The direction of rotation was toward the preferred position. The number of individual responses used to compute SD means was 4, and the number used for MD means was 11. For any angular position within the excitatory range, the mean background response during motion exceeds the mean background rate during steady-state conditions.

Figure 9b(1). Head-up motoneuron, a different preparation from that in Figs. 9a(1) and 9a(2). The mean light driven response during steady-state (SL) and moving (ML) conditions
is plotted as a function of angular position. The number of individual responses used to compute each mean was 4. Light stimulation was done as in Fig. 8b.

For almost every angular position within the excitatory range, the mean light-driven response during steady-state conditions exceeds the mean light-driven response during moving conditions. At +60 degrees, the confidence level (one-tailed) in support of the claim that the SL mean exceeds the ML mean is only 90%.

Figure 9b(2). Head-up unit, as in Fig. 9b(1). The unit is the same as one of those in Fig. 3b(1). The mean statocyst-driven response, during steady-state (SD) and moving (MD) conditions, is plotted as a function of angular position. The direction of rotation was toward the preferred position. The number of individual responses used to construct the SD means is four, and the number used to construct the MD means is eight.

For any angular position within the excitatory range, the mean background response during motion exceeds the mean background response during steady-state stimulation.
FIG. 9b(1)

FIG. 9b(2)
ditions does not significantly exceed the response under moving conditions.) The observation that the visually-worked response magnitude appears to depend upon the rate of change of body position suggests, again, that the visually-worked response may be under statocyst control.

In Figs. 9a(2) and 9b(2), the mean statocyst-mediated discharge is plotted as a function of angular position, for each of the two head-up neurons. The data are consistent with that in section 1a of the Results: for a given angular position, the statocyst-mediated response is greater during rotational motion of the animal than it is under steady-state conditions. Thus, for any given angular position, an increase in the background rate is related to a decrease in the light-driven response. This qualitative correlation forms the basis for several hypothetical control mechanisms (see Discussion, section 4c).

d. A preliminary inquiry into the mechanism for control of the light-driven response.

In the two preceding sections, it was reported that, for some motoneurons, the magnitude of the light-driven response to a given visual stimulus is (a) directly associated with the magnitude of the statocyst-mediated response over a range of angular positions, and (b) reciprocally associated with the magnitude of the statocyst-mediated response for a given
angular position. These results were interpreted to mean that
the visual response may be influenced by statocyst-mediated
information through some integrative mechanism. The work to
follow attempts to elucidate such a mechanism. In these
experiments, done on side-down motoneurons, the effect upon
the light-driven response of bilateral statocyst ablation was
investigated. The results may not be relevant in the way
intended, since the work was not done using head-up neurons,
but the experiments are cited because they are indicative of
an hypothesis which can be extensively explored.

Figures 10a(1) and 10a(2) are records of the light-driven
responses of a side-down neuron both before (1) and after (2)
bilateral statocyst ablation. Since the statocyst driven
response of the motoneuron was totally absent after the opera-
tion (Fig. 2b), the ablation was judged to be complete. Each
response pictured in Fig. 10a occurred during a single
presentation of the stimulus. The stimulus was a pulse of
light, 1080 ms. in duration, directed into the center of the
contralateral eye. There was an 8 ms. delay of the stimulus
onset from the beginning of each sweep. The animal's steady-
state body position was +90 degrees, in both the figures. At
this position, the background discharges before and after the
operation were 4.6 and 5.4 Hz., respectively. Given that the
Figure 10a(1). Side-down motoneuron. The unit was excited by pulsed light, of 1080 ms. duration, which was directed into the center of the ipsilateral eye. The sweep duration is 2 seconds, and the onset of the pulse begins 8 ms. following its beginning. The statocysts were intact.

Figure 10a(2). Side-down unit, the same as that used in Fig. 10a(1). The unit was excited by light, as described above, after the statocysts were ablated. The background rates in this and the above figure are about equal. Therefore, the light-driven response in this figure considerably exceeds that in Fig. 10a(1).

Figure 10b(1). Side-down motoneuron, the same as that used in Figures 10a(1) and 10a(2). The mean light-driven response, per steady-state position, with statocysts left intact (SLI), and with statocysts ablated (SLO) is plotted as a function of angular position. Each experimental point is the mean of 6 to 11 individual responses. Measurements at +90 degrees were done twice, as the first and the last sequences in the experiment. At every position, the mean light-driven response with the statocysts ablated exceeds the response with the statocysts intact.

Figure 10b(2). Side-down motoneuron, a different preparation
from that in Fig. 10b(1). The mean light-driven response per given position during motion was plotted as a function of angular position. In one case, (MLI), the statocysts were intact, and in the other case (MLO), the statocysts were ablated. The light stimulation conditions were similar to those given in Fig. 10a(1).

Confidence levels, according to a one-tailed T-test, are listed below each angular position, indicating the probability that the MLO mean exceeds the MLI mean. At five out of eight positions, the MLO mean exceeds the MLI mean at a confidence level of 95% or greater.
FIG. 10b(1)
background discharges were about equal, it is apparent that the light-driven response in (2) considerably exceeds the light-driven response in (1). In fact, the response, after statocyst ablation was 25.6 Hz., as opposed to 16.4 Hz. before statocyst ablation.

In Fig. 10b(1), the mean light-driven response of the neuron in Fig. 10a was plotted for seven angular positions, both before (SLI) and after (SLO) statocyst ablation. The results show that, for every angular position, statocyst ablation is associated with response enhancement.

The experiment described above was repeated, using another side-down motoneuron. Visual stimulation took place with the animal at eight different angular positions, during continuous movement of the animal's body. After statocyst ablation, verified by the loss of the statocyst-mediated response (Fig. 1a), the stimulus paradigm was repeated. (The motoneuron was also stimulated with light under steady-state conditions, but the data was too variable to be informative.)

In Fig. 10b(2), the mean light-driven response both before statocyst ablation (MLI) and after statocyst ablation (MLO) is plotted as a function of the angular position of the animal. Below each angular position is listed a confidence level, indicating the probability that the population mean for MLO exceeds the population mean for MLI. At five out of eight
positions, the means are significantly different at the 95% confidence level. At no position does the mean for MLI exceed the mean for MLO. These results are consistent with the results of Fig. 10b(1) indicating that, for a given angular position, ablation of the statocysts can increase the magnitude of the light-driven response.10

Discussion

1. The behavioral role of the optomotor and optokinetic reflexes.

The adaptive significance of the horizontal and vertical eyestalk reflexes is probably based upon their role in improving the animal's visual capability during a period in which its body undergoes rotation. The reflexes serve to uncouple the visual field from body motion, making it less likely that the animal will lose sight of relevant environmental features. Secondly, rapid motion of external objects (real environmental motion), or rapid motion of the animal (apparent environmental motion) produces a shift of retinal image, which, if uncompensated by a following eye movement would produce blurring, a loss of acuity. Processing of a visual image takes a finite amount of time, necessitating a certain period of stabilization on a particular feature. By moving the eyes at a velocity somewhat less than that of the moving object, a given image can
be held and then, as the feature moves beyond the range in which the eyes will follow, another may be pursued. In the horizontal optokinetic system, a series of slow eye movements, alternating with rapid flipbacks can thus be generated (nystagmus). The single sweep angle travelled by the eyestalk is less than or about equal to the angle traversed by the visual stimulus. In the crab optokinetic system, the most accurate compensations are made in response to small amplitude, very slow stimuli, on the order of 0.01 degrees/second. It has been suggested that the slow behavior may be related to the tracking of celestial bodies, as a mechanism for determining compass direction (Horridge, 1965).

Among the decapods, horizontal nystagmus has been well documented in the crayfish, lobster, and crab. In the crab system, both visual and rotational stimuli drive all but the most phasic motoneurons. The responses summate when the stimulation occurs through both channels (Horridge and Burrows, 1968b.; Sandeman and Okajima, 1973a.; Wiersma and Fiore, 1971b.). In the lobster and crayfish horizontal systems, the source of stimulation is purely visual (Wiersma and Oberjat, 1968; York, Wiersma and Yanigisawa, 1972).

Considering the vertical eye reflexes, many optomotor neurons are responsive to moving visual as well as to rotational stimuli. Alteration of the discharge of optomotor neurons in
response to moving stripes or small moving lights has been confirmed in stationary crayfish. Crayfish side-down motoneurons sometimes fire in bursts suggestive of flipbacks, when they are driven by visual stimuli only, and perhaps one will be able to demonstrate nystagmus movements in the vertical plane (Wiersma and Oberjat, 1968; Higuchi, 1973). Crabs have been observed to track a small light moving vertically (Horridge, 1965).

For any type of optomotor neuron, the direction and configuration of moving stripes which excites corresponds to the apparent motion produced by a rotation toward the preferred position across a stationary field. Therefore, side-down motoneurons are excited by horizontal stripes moving ventro-dorsally across the ipsilateral eye and dorso-ventrally across the contralateral eye (Wiersma and Oberjat, 1968). For a moving light stimulus, the direction of the excitatory motion appears the same, and in addition it is claimed that the fiber is inhibited below the background discharge rate when the light is moved in the opposite direction (Hisada and Higuchi, 1973). For head-down neurons, a spoke-like arrangement of stripes, with the center positioned over the center of the eye, is excitatory when rotated posteriorly. When the pattern is rotated anteriorly, the motoneuron may be completely inhibited.
(Wiersma and Oberjat, 1968). The receptive field to a moving stimulus would thus seem to be near the anterior or the posterior eye rim (or both). The discharge to a small light moving dorso-ventrally across various sectors of the anterior eye half is 86 to 93% of that which occurs when the light moves ventro-dorsally. According to the data of Hisada and Higuchi (1973--their Table 1), the discharge rate does not differ greatly when the stimulus is moved across the posterior half of the eye in either direction. This suggests that the discharge of head-down neurons may be influenced by motion across the anterior portion of the eye only, even though the excitatory receptive field to pulsed light is found to be at the posterior. It may thus be that the responses to pulsed light and to moving stimuli may have separate physiological roles. The alternative explanation for the observation of Hisada and Higuchi cited above is that the neuron may be either excited or inhibited by motion across the posterior part of the eye, independent of the direction of the motion.

The suggestion has been made by Dr. R. M. Glantz (unpublished) that, while the eye is moving, the crayfish retina has a central zone of maximum sensitivity analogous to the mammalian fovea. (In mammals, compensatory eye reflexes serve to keep the retinal image positioned on the fovea). Of the three known classes of crayfish visual interneurons, the motion
detectors are not active during motion of the eye, leaving the sustaining and dimming units as the only possible seeing fibers (Wiersma and Yamaguchi, 1967). Among the sustaining units, the large field units predominate, and have their areas of maximum sensitivity near the central pole of the eye (Glantz, 1973). Therefore, the existence of a fovea-like zone is possible and is not contrary to the rationale for compensatory eye reflex behavior as previously stated. The presence of a fovea-like zone might demand a system of rather high tracking accuracy; that is, dependent upon the size and sensitivity contour of the foveal zone, the angle travelled by the eye and by the visual stimulus might have to be similar, at any point during the traverse. As stated earlier, when the crab optokinetic system is driven by moving stripes at very small velocities, the tracking accuracy is highest (90-95%), but it grows less with increase in the stimulus rate (Horridge, 1966b). Studies have not been done in crayfish in which the precise motion of the eyestalks is related to stimuli of various velocities and amplitudes.

If the eyestalk reflexes are seen to enhance visual performance, then one must explain why optokinetic and optomotor behavior can occur entirely in the dark, under the sole influence of the statocysts. The possible exception is the head-up reflex in crayfish, since some of the head-up neurons
appear to be much more sensitive to visual stimuli (Figs. 8c and 9b(1)) than to positional or rotational stimuli. On the one hand, it may be more economical for the animal to waste energy performing a useless behavior than it would be to evolve the neuronal circuitry necessary to negate the influence of the statocysts when the animal cannot see. Another possibility is that collaterals of the eye reflex motoneurons may have a coordinating influence upon circuits driving other related behavior. As an example, movement within a suspended animal's visual field which mimicks body rotation about the longitudinal axis produces both eye movements and characteristic leg movements. Were the animal in contact with the substrate and rolled to one side, the leg movements would accommodate the body to the forced movement, while simultaneously stimulating leg proprioceptors acting to restore the normal position. (The leg proprioceptors themselves influence eye position and therefore coordinate righting behavior and the angle of the eyestalks). (Bullock and Horridge, pp. 1129-1130). The hypothesis that leg movements and eye movements are coordinated by action of the optomotor neurons themselves rather than by interneurons or by the statocyst afferents is testable, since single motoneuron somata in the brain can be penetrated and so can be stimulated (Sandeman and Okajima,
1973b). Alternatively, it may be possible to stimulate moto-
nurons of a given functional type (e.g., head-down) anti-
dromically in the periphery, if it is first known that the
motor projections to a given eye muscle consist of one type
of motoneuron. In either case, stimulation of a motoneuron
or several of them should be correlated with the appropriate
leg behavior.

The question also arises whether visually-driven tracking
behavior in the vertical plane actually exists to any signi-
ficant extent, as it does in the horizontal plane. The extent
to which a visual stimulus alone can produce optomotor move-
ments can be most easily measured with the animal in the normal
position. At this position the composite input to the muscles
from antagonistic motoneurons is close to being balanced, and
there is little net influence from the statocysts tending to
draw the eyestalk in one direction or the other. The extent
of visually-induced tracking movements would depend in part
upon the maximum degree to which a given motoneuron could be
excited and its antagonists inhibited by the visual stimulus.
However, the visual input to the optomotor neurons may serve as
part of an error-correcting mechanism, as described in the
following sections.
2. The function of visual input to the optomotor neurons.
   a. Reinforcement of the statocyst-mediated response.

   The arrangement of the excitatory and inhibitory fields to stationary light stimulation is such that sky light and body rotation will affect the optomotor neurons synergistically (Introduction, section 3). Because the eyestalk movement lags somewhat the onset of roll or pitch, there is probably an initial sharp increase of agonist excitatory area and antagonist inhibitory area which faces the sky. Depending on the magnitude of the motoneuron response to this transient visual stimulation, and upon the synaptic efficacy at the neuromuscular junction, the effects of the visual stimulus could constitute a phasic input to the muscles, thereby overcoming their inertia. The effects of sky light would also tend to offset any upward drift of the eyestalks, in the absence of body rotation.

   Although the above proposal may operate in certain circumstances, there are drawbacks to considering it a sufficient explanation for the visually-evoked response:

   1. The response would depend upon the light gradient across the sky and the animal's orientation with respect to the gradient. Partial cloud cover, sunrise, or sunset could potentially affect the response.

   2. The proposal does not explain the responsiveness of
the optomotor system to moving visual stimuli.

3. The existence of a correlated phasic response in a motoneuron and an eyestalk muscle to turning toward an overhead light has not been experimentally demonstrated in statocystectomized animals.

b. Visually-controlled feedback as a fine control of compensatory eye reflex behavior.

1) The crab optokinetic system as a model.

When the crab visually tracks a horizontally moving object, the eyes' final position after one slow phase has elapsed is determined by an inference made by a directionally-sensitive component of the visual system about the velocity of the moving feature (Horridge, 1965). The information abstracted by the visual system is thought to comprise a series of estimates of the visual angle traversed by the stimulus and the time taken to make the traverse. Optokinetic "memory" experiments, in which the eye tracks a stimulus that has moved, without observing the movement in progress, indicate that this visual information can be stored for up to ten minutes (Horridge, 1966). The velocity information is then amplified and converted to a signal to the optokinetic motoneurons, resulting in an eyestalk movement which follows the stimulus at a rate which is somewhat less than the actual stimulus rate. The final position
of the eye after cessation of the stimulus motion is the integral of the eyestalk velocity over time. Since the inferred stimulus rate (slip speed) is the difference between the actual stimulus rate and the eyestalk rate, the latter will vary within a narrow tolerance, this tolerance depending upon the forward gain (or sensitivity) of the system. Any change of the eyestalk velocity without a change in the stimulus velocity will generate a slip speed and a signal to the moto-neurons which will oppose the eye velocity change. Therefore, the tracking performance of the eye is controlled by visually-mediated negative feedback.

When the visual input is interrupted (open-loop), by blinding the eye which moves while preventing the seeing eye from moving, the response to a small environmental movement is a much larger total amplitude eyestalk movement with a velocity which can be ten to twenty times the stimulus velocity. After cessation of the stimulus, nystagmus movements can continue for as long as a minute, in the absence of an inferred stimulus movement in the opposite direction (Horridge and Burrows, 1968b). The eventual cessation of the nystagnus is probably not due to a time-dependent loss of visual information, since optokinetic "memory" of an old and a new position can persist for ten minutes (Horridge, 1966). In the open-loop situation, the slip speed is equivalent to the actual stimulus
velocity, and the amplitude of the forward gain is observed directly.

Since the pattern of the motoneuron discharge for a given amount of angular movement is the same under closed and open loop conditions it appears that the lack of physical movement in the seeing eyestalk does not affect the efferent program. If both eyes are fixed in their sockets, or if the eye musculature is destroyed, the pattern of the motoneuron discharge to a given stimulus is similar to that obtained in open loop conditions. Therefore, it is thought that eyestalk joint receptors or intrafusal receptors monitoring parameters of the ongoing response do not feed back to the motoneurons.

In summary, the essential characteristics of this model are that the efferent program is centrally determined and that visual stimuli both evoke the appearance of the program and control the rate of its unfolding. As indicated in Discussion, section 1, a blind animal may also exhibit the optokinetic reflex under control of the statocysts. Wilson, studying the flight system of locusts, similarly concluded that visual, proprioceptive, and mechanoreceptive information is used to correct fundamental or transient changes in the centrally determined efferent program (Kandel and Kupfferman, 1970).

2) The crayfish optomotor system as an analogy.

It is now clear that moving stripe patterns, the usual
experimental stimulus to the optokinetic system, are effective also in modulating the firing rate of optomotor neurons in the absence of changing input from the statocysts (see Discussion, section 1.). The data of Wiersma and Oberjat (1968) and of Hisada and Higuchi (1973) are consistent with regard to the observation that the motoneuron is excited by a pattern moving in the direction opposite to the statocyst-determined preferred direction. The existence of visually-evoked inhibition in response to stripe patterns moving oppositely to the excitatory direction has been claimed by Hisada and Higuchi (1973--their Table 2), and by Higuchi (1973--his Figure 2). Their published data is open to the interpretation that the inhibition is simply a lack of excitation, since they do not include control records of the motoneuron discharge when no moving patterns are being presented. However, complete inhibition of the discharge of head-up and head-down motoneurons in response to moving stripe patterns has been reported by Wiersma and Oberjat (1968).

Operating in conjunction with a changing statocyst input, visual input may function as a continuous control mechanism which corrects for those changes in the motoneuron discharge rate or in the balance of muscular tension which interfere with optimal compensation behavior. When rotation of the animal's body occurs, the changing balance of agonist and
antagonist excitation to the eyestalk muscles will partly
determine the direction and the rate of the eyestalk movement.
At any point during the rotation, the position of the eyestalks
is a function of the time integral of the velocity. The
hypothesis is that visual information generated as a result
of body motion modifies the level of excitation either received
by or expressed by a motoneuron, and that its instantaneous
firing rate is under fine control by the visually inferred
motion, or slip speed. The magnitude of the slip speed at
any moment determines the rate at which the excitation of the
agonist and antagonistic motoneurons change. Movement in one
direction has been shown to be excitatory to the agonists and
inhibitory to the antagonists. Therefore, graded excitation
and inhibition may be the method of control for agonists and
antagonists, respectively. For example, to adjust for a
reduction in the slip speed (an acceleration of the eyestalk
motion without a change in the actual stimulus velocity), the
acceleration of excitation to the agonists would have to be
decreased and the deceleration of excitation to the antagonists
would also have to be decreased. If the rotatory motion is
then stopped, any continued motion of the eyestalks produces
a reversal of the slip speed direction, thus sharply inhibit-
ing the agonist motoneurons and exciting the antagonistic moto-
neurons. This acts as a brake to the eyestalk motion. When
the body position is maintained, the eyestalks are held at an appropriate angle, which, if perturbed, might also be compensated for by negative visual feedback.

To begin testing the above hypothesis, the first approach might be to measure the optomotor behavior of one non-seeing eye, while the other eye is treated experimentally (Horridge, 1965, 1966; Horridge and Burrows, 1968b). Since the behavior reflects the composite effect of motor unit activity and muscle response, observations on behavior rather than on moto-neurons constitute the more valid measure of the system's performance. However, since this method fails to elucidate changes in the activity of individual motor units or inter-neurons, parallel neurophysiological studies are required (Burrows and Horridge, 1968 a,b; Horridge and Burrows, 1968a).

3) Possible sources of statocyst-related error.

The view taken in the preceding discussion is that visually-evoked responses may be part of an error-correcting mechanism, enhancing the ability of the eyestalks to follow apparent environmental motion. Although sources of error might occur anywhere in the system, at the level of the statocysts alone the possibilities are numerous. They include active or passive movement of the antennules, irregularities in the statolith after a molt, and vibrations transmitted through the substrate
or through water. In crayfish, one other type of error may be inherent in the statocysts. The comparative anatomy of the crayfish and the crab statocysts suggests that the crab organ is specialized for the detection of angular acceleration, whereas the crayfish organ is not. In the crab, the freely moving hair receptor elements are enclosed within a system of narrow, perpendicularly arranged toroids, and the main vector of fluid flow is directed over the receptor hairs, but the crayfish statocyst is simply an ovoid concavity (Introduction, sections 2a and 2c). The hypothesis that the crayfish statocyst loses information on body rotation via system noise has been proposed independently (Fraser, 1974, p. 625).

That the anatomical differences referred to above represent a real source of error in the crayfish eye reflex systems is consistent with some physiological observations (see below: c), e)), but cannot be said to be consistent with a number of others: (a), b), d) and f)).

a) In the crab, the unidirectional, highly phasic optokinetic and optomotor neurons are under statocyst control solely (Wiersma and Fiore, 1971b). The motoneurons, as already described in the Introduction (section 1c), are excited by rapid motion in the preferred direction and are otherwise quiescent. The optomotor neurons must be controlled by the freely moving
hair group of statocyst receptor elements, and not by the
statolith-associated group, since they do not respond to main-
tained pitch or roll. Since in horizontal motion, there is
no change in the gravitational force imposed upon the stato-
lith, the primary and perhaps the only input to the optokinetic
neurons is probably the freely moving hairs. Therefore, crab
motoneurons which are probably innervated by the freely moving
hairs only can apparently maintain adequate function without
the addition of visual input. (However, the existence of
other sources of corrective influence—e.g., from the leg
proprioceptors—is possible).

b) Crab optomotor neurons having sensitivity to both motion
and to position are also said to lack visual input (Wiersma
and Fiore, 1971b). Therefore, it would appear that those moto-
nearons having positional sensitivity only form the group which
is under the dual sensory control (Burrows and Horridge,
1968b). One might speculate that the addition of freely moving
hair input confers an advantage upon the phasic neurons which
the purely tonic neurons do not have, thereby necessitating
the addition of visual control in the latter case. However,
it is not known whether or not the freely moving hairs actually
do input to the phasic neurons.

c) The crayfish optomotor neurons do not include purely phasic
fibers. All motoneurons are either responsive to movement and position, or to position only (Wiersma and Fiore, 1971b). Therefore, the possibility of motoneuron control by the freely moving hairs alone has been eliminated in this case, consistent with the idea that the freely moving hairs are an unreliable source of information.

d) The statocyst input to the crayfish optomotor neurons may include the free hairs, but there are other potential inputs (see the following Discussion, section 4). Secondly, there is no information on whether visual responsiveness is greater for phasic, rather than tonic motoneurons. Therefore, it is not possible to comment on the extent of visual influence on a motoneuron, as correlated with the degree to which it is influenced by the freely moving hairs.

e) Crayfish optokinetic neurons are not under statocyst control at all. Type I and Type II statocyst receptor groups do not include elements which are responsive to horizontal rotation, and therefore, assuming that the lobster and crayfish statocysts are similar, the freely moving hairs are the only potential source of statocyst input to these optokinetic neurons. Possibly due to the unreliability of their influence, the freely moving hair input has been bypassed entirely (Wiersma and Oberjat, 1968).
f) Some crab optokinetic neurons, which are probably under primary control of the freely moving hairs (see a)), are under both statocyst and visual control (Sandeman and Okajima, 1973b). According to Wiersma and Fiore (1971b), these neurons have maximum sensitivity to rather slower rates of movement than did those described in a). It may be that the reflex is driven visually when rotation at a constant velocity is so prolonged that the freely moving hairs have regained their rest position, or if rotation is so slow that the response of the hairs to acceleration is subliminal. These considerations might explain the existence of both visual and statocyst input to this type of optokinetic neuron, but the presence of both inputs is a fact which is not consistent with strong reliability in the crab acceleration receptor system.

(4) Optomotor responsiveness to pulsed light in the context of a feedback hypothesis.

It has been proposed that the rate at which some eye reflexes can proceed is under fine control by a movement-sensitive component of the visual system. Although the neuronal bases are not known, movement perception in arthropods has been modelled such that the excitation of nearby ommatidial groups is autocorrelated in time (Bullock and Horridge, 1965, p. 1094), thus enabling an estimate of the distance and direc-
tion travelled by the stimulus over a time span. Although the hypothesis on visual feedback control has been tested in the crab optokinetic system only, it has been observed that optokinetic and optomotor neurons are both driven by moving stripe patterns and lights, thus lending credence to the hypothesis that the control mechanisms for both are similar. The present study shows that crayfish optomotor and optokinetic neurons are excited by pulsed light, the strongest component of the response in each being a transient to the onset of the light (Results, sections 2a and 2c). It is not surprising that the same neuron can be driven by both stripes and pulsed light, for both types of stimuli fundamentally involve the transitory presentation of a bright field to an ommatidial group. However, a pulsed light stimulus cannot be inferred to have the dimensions of rate and direction, since it does not move from one retinal locus to another. Therefore, it is difficult to interpret the responses to pulsed light as responses which are functionally relevant to a control system based on moving visual stimuli.

This is not to say that pulsed light-evoked responses may not be mediated by components of such a control system or that they may not play some sort of physiological role. One can take several points of view. (a) The responses to pulsed
light are behaviorally irrelevant or even subliminal as far as the musculature is concerned, and are the result of an artificial stimulus having similarity to the physiological one. (b) On the other hand, a brief change in the ongoing firing rate in response to pulsed light may carry the message that there is movement in the visual field of as yet unknown velocity and direction. Perhaps pulsed light presented within wide retinal areas activates both excitatory and inhibitory processes feeding onto the motoneuron. If at certain retinal loci the excitatory inputs were preferentially activated, and at others the inhibitory inputs were preferentially activated, then the receptive field boundaries defined by Wiersma might be the result. It is of interest that pulsed light stimulation can at times elicit purely excitatory or inhibitory responses, and at times evokes mixed responses, consisting of a sequential facilitation and depression of the ongoing discharge (Results, sections 2a and 2b). Although it is not at all clear that this is the case, the mixed type of response may be seen as the non-specific result of a motion-sensitive system being driven by a stimulus in which the direction of motion is not given. Also, it may be (and this interpretation does not exclude the one just proposed) that the mixed type of response simply reflects the pattern of the sustaining fiber visual interneurons (see below, section 3, and Fig. 7a).
(c) A third alternative is that optomotor neurons respond to pulsed light and to moving stimuli, but that the two responses have unrelated physiological roles (see page 104 of this Discussion).

3. The sustaining fiber optic interneurons: considerations on their possible input to the crayfish optomotor system.

If it is assumed that one function of the visual system in the optomotor pathway is to correct eyestalk movements during rotational motion of the body, then the control must be exerted through a movement-sensitive visual mechanism. Even without this assumption, the finding that the discharge of optomotor fibers is influenced by the direction in which a stripe pattern moves implies the necessity for a visual network which can distinguish the direction of motion. Wiersma and Oberjat (1968) have observed a few cases of optic nerve fibers whose excitation is dependent upon the velocity and the direction of a horizontal motion. However, since the optic nerve also contains eye reflex motoneurons (Bullock and Horridge, 1965, p. 828), these units may not be sensory, but may be motor. No such candidate inputs to the crayfish optomotor system have yet been found, although they have been seen in the crab *Podophthalmus* and in the locust (Horridge, 1968b). The commonly encountered types of crayfish movement
detectors are not active when the eye is in motion (Wiersma and Yamaguchi, 1967). Therefore, of the known classes of visual interneurons, the sustaining fibers and the dimming fibers are left as possible inputs. These are tonic "on" and "off" fibers, respectively, which however have considerable sensitivity to contrasts.

In the present work, the hypothesis that the sustaining fibers input to the optomotor system has been considered to an extent. An a priori objection to this proposal is that the excitation of sustaining fibers has not been shown to be direction-dependent. Therefore, if the hypothesis is correct, then the network conferring directionality would probably have to be located central to the sustaining unit and might involve the outputs from several receptive fields. These intermediate channels might, for example, be connected by a unidirectional lateral inhibitory system, such as that found in the rabbit retina (Barlow and Levick, 1965), but there are other possible models (Horridge, 1968b, p. 272). However, it is entirely possible that the responses to pulsed light and to moving stimuli might be mediated by two separate visual channels, one or both of which remains as yet undiscovered. It is also possible that the sustaining units do input to the optomotor neurons, but do not confer the optomotor sensitivity to moving patterns.
The attempt has been made in the present work to compare and correlate the response properties of sustaining units and optomotor neurons, in order to develop points of evidence which appear either consistent with or inconsistent with the proposal regarding a sustaining unit and optomotor neuron relationship. The first consideration (Results, section 2d) was that the units have a similar response pattern to the same adequate stimulus. However, this similarity may be merely coincidental, since the pattern is common to many neurons (e.g., axons associated with statolith-related hairs—Sandeman and Okajima, 1972; eye withdrawal neurons—Burrows and Horridge, 1968c). Secondly, the average motoneuron response latency exceeds that for a sustaining unit with an overlapping receptive field, when the two units were simultaneously monitored. This piece of evidence is necessary, but not sufficient to establish the existence of the hypothetical relationship.

To develop a proving argument for the sustaining unit-optomotor neuron relationship would be a difficult task, ideally involving natural stimulation of a single visual interneuron, with simultaneous recording of the sustaining unit and the motoneuron responses. Limitation of the stimulus to one receptive field by using small diameter, low intensity stimuli is theoretically possible, but such a study would
demand that only the few sustaining units with well-isolated receptive fields be tested, and that there be no need for afferent spatial summation in order to elicit a motoneuron response. Extracellular electrical stimulation of a single sustaining unit would be impossible, due to the closely packed structure of the optic nerve. Possible approaches to the problem of exploring the likelihood of a sustaining unit-motoneuron relationship are discussed below in section 3d.

In addition to the possibility that stimulation of many sustaining units may prove unavoidable, there are other factors which would work against the finding of a tight correlation between sustaining unit and motoneuron response parameters. The optomotor neurons have sensory input from the statocysts, the leg proprioceptors, and possibly from the antennae and the antennules (York, Yanigisawa, and Wiersma, 1972). The effects of these additional inputs might be minimized by removing the various organs involved, but at the risk of superimposing non-specific effects due to the injury. Indeed, the suggestion has been made (Horridge, et al., 1965) that "in simple reflexes, such as the startle response and the optomotor response, the final behavioural output by the motoneurons represents the summation of a great deal of simultaneous, relatively simple excitation of interneurons in parallel." If the motoneurons have endogenous activity in the
absence of any sensory stimulation, this represents another complication. Lastly, the above discussion on motoneuron sensitivity to the direction of pattern movement suggests that, if the sustaining fibers are involved in the circuit to the motoneurons conferring movement sensitivity, the connection between the visual and motor units is not monosynaptic.

All the above considerations makes the finding of a sustaining unit and motoneuron response correlation all the more remarkable and all the more suspect (Results, section 2d). The motoneuron appears to linearly sum sustaining unit spikes over a wide range of sustaining fiber discharge rates; that is, the number of sustaining unit spikes to the Nth order motoneuron spike is a linear function of N, for N less or equal to 7.

a. Considerations on temporal summation as a possible mechanism underlying the observed correlation between a sustaining unit and a motoneuron response.

One explanation for the correlation observed is that the motoneuron temporally sums a certain number of successive EPSP's to threshold. Since the large-field sustaining units have receptive field centers near the center of the eye (Glantz, 1973), six units, including 019, were probably stimulated, although it is not known which combination of these, if
any, are included in the circuit presynaptic to the side-up motoneuron. The thirteen spikes in 019 which appear preceding the occurrence of each motoneuron spike might then represent a certain proportion of the total number of impulses impinging upon the motoneuron or upon premotor interneurons during this interval.

This proposal, however, requires that the unitary EPSP's have an atypically long time constant, since the first one of a summating series would have to last longer than the longest interspike interval, or about 140 ms. Unitary EPSP's of this type are rare synaptic phenomena, although a number of examples do exist. EPSP's with time courses on the order of 50 to 400 ms. are observed in gastropod mollusc neurons. In the larger cells, the soma and the remaining extrasynaptic area is thought to increase the capacity of the neuron, enabling it to store charge and extend the RC time constant. In smaller cells, the EPSP duration cannot be explained as a consequence of passive membrane properties, and is probably a result of prolonged transmitter action. In rabbit cervical ganglion cells, EPSP's may have a duration of 40 to 80 ms. (Tauc, 1967). Renshaw cells of the spinal cord exhibit 50 ms. EPSP's (Eccles, 1957, p. 84). It is conceivable that, even if the crayfish EPSP's were of normal duration, the effect of a barrage of presynaptic spikes would be a complex postsynaptic depolariza-
tion fluctuating near the spiking threshold. There are, however, no general arguments as to why threshold might be exceeded after a given number of spikes had occurred in one presynaptic cell.

Within the scope of the temporal summation argument, it is necessary to consider that the function in Fig. 7c(1) begins to deviate from linearity at the eighth motoneuron spike, and that the incremental number of sustaining fiber spikes is now less than for motoneuron spikes occurring earlier in the spike train. The motoneuron is thus presumably firing under conditions of less synaptic input, but the mean interval between motoneuron spikes remains approximately the same as that occurring somewhat earlier in the spike train (Fig. 7c(3)). This set of observations cannot be explained by saying that the motoneuron, once triggered to fire by a visual stimulus, does so at a constant instantaneous rate which occurs throughout its response. The mean intervals at the beginning of the motoneuron train are smaller than those occurring later on (Fig. 7c(1)). Alternatively, there is the likelihood that a number of sustaining units are being stimulated, so a small change in the discharge rate of one of them might have little effect upon the firing pattern of the motoneuron. Another possibility is that there is a facilitatory process of fairly long time constant, which would enable the motoneuron to spike
at the same rate under conditions of diminished presynaptic firing rate. After a period of continued light stimulation, there may be an increased probability of quantal discharge (Aidley, 1971), thus increasing the efficacy of the synapse between the sustaining fiber and its follower cell. On the other hand, the presynaptic terminal might defacilitate at high discharge rates, in which case its effect upon the postsynaptic membrane would be similar at higher and lower discharge rates. Lastly, the motoneuron may be partially blocked during the high level depolarization associated with high frequency input, and it may increase its probability of firing at lower input frequencies (Bullock and Horridge, pp. 203-204).

b. Time-dependent threshold change following motoneuron firing: a possible alternative to the temporal summation model.

The difficulties posed by the summation model are avoided if the motoneuron is driven to fire by only that small part of the excitatory presynaptic discharge which immediately precedes the motoneuron spike. That would be the case if the motoneuron excitability fluctuated as a function of time since the last firing; specifically, the threshold would be greatest following an impulse and would gradually decline to a minimum at some time exceeding the maximum interspike interval during light stimulation. At the highest presynaptic rates, EPSP's
would summate strongly, and could then produce a postsynaptic spike with the threshold remaining quite high. At lower rates, the maximum excitation produced by summed EPSP's is not so great, and the motoneuron could not fire until the threshold dropped sufficiently for the total depolarization to exceed it. Therefore, the time of motoneuron firing would be determined by the balance of the excitation received and its threshold level at any particular moment. Were the decay rate of effective excitation always to lead the decay rate of the threshold, the motoneuron would not fire at all to the light stimulus, but in fact this situation is rarely if ever observed. The finding that the motoneuron appears to count, on the average, a certain number of sustaining fiber spikes before it fires could be an incidental result of the primary interactions postulated above, if the level of input excitation and the threshold level change with about the same rate from stimulus trial to stimulus trial.

The origin and magnitude of the motoneuron threshold changes might be endogenous, or a function of the depolarization imposed by the light stimulus. That is, the motoneuron may behave as a pacemaker, exhibiting spontaneous changes of membrane potential which partially determine its rate of firing. Alternatively, the effect may be related to a high level of presynaptic activity, taking the form of a post-spike
hyperpolarization or slowed repolarization. Following a period of intense stimulation, crab motor axons show a hyperpolarization which has a time course of some seconds, and crayfish optomotor neurons should be investigated for similar effects. Also, normal stimulation of crayfish stretch receptors gives rise to a slow after-hyperpolarization whose amplitude is related to the size of the depolarization imposed by the stretch (Bullock and Horridge, 1965, pp. 147-148).

I have described the possibility that the timing of motoneuron firing during light stimulation is determined by fluctuations in excitability coupled with the level of depolarization produced by the synaptic bombardment. On the basis of this model, one would predict that when the light-driven onset of a sustaining fiber discharge occurs soon after the occurrence of a motoneuron spike, the probability of a subsequent motoneuron spike occurring would initially be low and then gradually increase. On the other hand, when the sustaining fiber onset occurs later, the likelihood of motoneuron spiking would be initially higher. Therefore one would expect that if the interval between sustaining fiber onset and the last motoneuron impulse preceding the onset of sustaining unit firing were small (Interval A), the interval between the sustaining unit onset and the first subsequent motoneuron spike would be large (Interval B), and vice versa. When Interval A is actually
plotted against Interval B (Figure 11), the points are generally scattered and the predicted relationship is not apparent. The short B intervals which are correlated with A intervals of 150 to 200 ms. would probably have occurred in the absence of light stimulation, since the motoneuron background rate is about 5 Hz. Therefore, one variation of the simple, deterministic recovery-cycle model is not supported by this analysis, but neither can the model be said to be ruled out. The influences contributing to the motoneuron output pattern are probably numerous and complex, so that the effects of an isolated mechanism may not be apparent unless experimental manipulations of the suspected variables can be deliberately applied.

c. The use of correlation techniques in investigating physiological relatedness.

My work on the simultaneous recording of sustaining unit and optomotor neuron responses represents a very limited attempt to model the optomotor system in terms of the real neuronal relationships which underlie it. In doing so, I found a clear-cut quantitative correlation between the spike trains, an apparent high probability of association between the two. Such a correlation is disturbing not only because the probable complexity of the system makes it implausible, but because the
Figure 11. Sustaining unit 019 and a side-up motoneuron were recorded simultaneously, while being stimulated by pulsed light. The interval bounded by the first post-stimulus sustaining unit impulse and the motoneuron impulse immediately preceding it was called interval A. The interval bounded by the first post-stimulus sustaining unit spike and the first subsequent motoneuron spike was called interval B. There is no apparent correlation between intervals A and B.
particular nature of the correlation cannot be interpreted with any certainty according to known neurophysiological principles. The possibility that the finding may be misleading, that it might not reflect any properties of the neuronal circuit under study, is certainly very real. Any correlation, no matter how high, does not rule out the possibility that the correlated variables are related coincidentally. The parameters selected for the analysis are chosen according to the experimenter's more or less limited mental constructs, and may really be irrelevant to the functioning of the systems in question. The possibility also exists that the particular experimental design permits only certain mechanisms within the nervous system to come into play, thus forcing the systems to behave partially or even non-physiologically.

But the fact remains that one of the major empirical tools which neurophysiologists have in testing neuronal models is the observation of some kind of correlation between recorded neuronal responses. It is rare that patterns of connectivity can actually be visualized, either histologically or by the simultaneous observation of presynaptic and postsynaptic activity. Since the use of less direct methods on complex systems appears unavoidable, the experimenter must rely on the internal consistency of his results under a variety of controlled conditions, in order to select the most likely of a
number of possible models. Since this is true, one must then be judicious in selecting experimental problems in terms of the information and the methods available, and must devise techniques so that the carrying out of the proper experimental design is a reasonably practical matter.

d. Avenues for exploring a possible sustaining unit-motoneuron relationship.

The following proposals are made with a view toward investigating the problems brought out in the preceding sections; namely, that the sustaining unit-motoneuron correlation may be spurious, and that a visual unit having unidirectional properties has not been found. Regarding the first point, it is certainly important that the simultaneous recording already done be repeated, although methods should be devised, if possible, to alleviate the difficulty involved in placing two highly unstable electrodes within a few millimeters of each other. One suggestion would be to make a dorsal or lateral hole in the head carapace, and then permanently implant the sustaining unit electrode before searching for a suitable motor unit. The hole should be large enough so that the location of the electrode in the optic peduncle can be directly visualized. Mounting one or both electrodes in micromanipulators is unsuitable, since this would prevent subsequent rotation
of the animal. By stimulating at its center a sustaining unit which is a candidate input to the motoneurons driving a certain response, and by lowering the intensity to the optomotor response threshold level, one may be able to stimulate that sustaining unit reasonably preferentially. Questions such as the following can then be asked:

1) Is the threshold of the sustaining unit less or equal to that for the response? The opposite finding would indicate that there are visual inputs in addition to or not including the unit being stimulated.

2) What is the effect on the sustaining unit response and the optomotor response of a moving stimulus which oscillates within the sustaining unit receptive field? Is the sustaining unit response or the optomotor response more excitatory to one direction of motion rather than to the opposite motion?

It may also be feasible to split the optic nerve, in order to enrich certain bundles in sustaining fibers. If so, it would be of interest to find out if electrical stimulation of such a bundle could produce an optomotor response.

Lastly, the search for units with unidirectional sensitivity to motion in the vertical plane should be continued both in the brain and in the optic nerve. The response characteristics of such units to visual stimuli, including pulsed light, should be determined.
4. The statocyst-mediated portion of the optomotor response: relationships of optomotor neuron response properties to the response properties of the statocyst receptor elements.

A number of crayfish motoneuron response properties appear to be close analogs of unit response properties recorded in the antennular nerve of the lobster (Cohen, 1955), suggesting the presence of rather direct connectivity between the statocyst afferents and the optomotor neurons. In the crab, Sandeman and Okajima (1973b--their Figure 7) have found that the ipsilateral central projections of one group of statocyst receptor elements (the thread hairs) overlap with those of the eye reflex motoneurons, indicating that few if any interneurons are interposed between the afferent and efferent units. Similar work has not been done in the lobster or the crayfish.

A review of sensory and motor response properties with an eye toward specific parallelisms yields the following points of comparison. The validity of the comparisons hinges upon the similarity of crayfish and lobster statocyst receptor properties, a point which has not been experimentally tested.

a) Type I and Type II statolith-associated receptor elements and all optomotor neurons alter their discharge rates in response to a shift of steady-state body position about the longitudinal or the transverse body axis. When angular position over a range of body positions is plotted versus discharge
rate, the resultant curve for either sensory or motor units is bell-shaped.

b) Type I statocyst receptor elements show histeresis dependent on the direction of the animal's motion, as do those crayfish optomotor units which have phasic response characteristics (Wiersma and Oberjat, 1968; Hisada and Higuchi, 1973). That is, when the animal is moving through a given angular position, the discharge rate is greater if the animal is moving toward the preferred position than if it is moving away from that position. However, phasic motoneurons also show adaptation of their discharge when motion ceases and a steady position is maintained. Since Type II receptor elements show a marked responsiveness to the direction of motion through a given angular position, and show adaptation in steady-state conditions, they also may drive the phasic motoneurons. Acceleration receptor elements may phasically affect the motoneuron discharge for some period following the onset or the stoppage of motion. Their influence on the motoneurons would eventually disappear if the velocity of the motion remained constant. Acceleration receptor elements would have to input to the phasic motoneurons in parallel with Type I or Type II receptors, which are the elements which confer position sensitivity.
c) The coding ambiguities inherent in the bell-shaped response curve of the statolith-associated receptor elements are resolvable because different units respond to the same positional stimulus with a different discharge rate (Introduction, section 2a). Therefore, the combined information from a range of receptors can specify a body position uniquely, whereas the information from a single receptor would have to be associated with two positions. Individual optomotor units of a given functional type also have unique position-related response curves (Results, section 1a; Hisada and Higuchi, 1973--for crayfish; York, Yanigisawa and Wiersma, 1972--for lobster). Therefore, in this aspect of its response, each member of a given motoneuron response type appears to reflect the input from a single statocyst receptor element, or from a group of statocyst receptor elements having similar sensitivities. Cohen (1955) estimates the number of position-sensitive receptor elements per lobster statocyst to be about 400, and the number of optomotor neurons innervating a set of eyestalk muscles is on the order of one-tenth this number (Sugawara, et. al., 1971, and see above, Introduction, section 1b). Thus, the conditions for input of many receptor elements to one motoneuron do exist.

5. Interaction of visually-mediated and statocyst-mediated systems.

According to the results in section 3b, the level to which the head-up motoneurons are excited by pulsed light appears to be directly related to the animal's proximity to the preferred angular position. As the statocyst-driven response grows in magnitude, over a range of angular positions, so does the superimposed visual response. This has been called the modulated response in head-up motoneurons. It was also found (Results, sections 1a, 3c), that the magnitude of the statocyst-driven portion of the response can be greater, per given position, for a moving stimulus than for a stationary stimulus. Correlated with this observation is the finding that the magnitude of the visually-driven portion of the response, per given position, is generally less than the magnitude of the statocyst-driven response (Results, section 3c). The set of observations can be taken to mean that the magnitude of the visually-driven portion of the optomotor response is dependent upon information ultimately contained in statocyst-mediated channels.

The results of a small number of experiments investigating the effects of statocyst ablation indicate that this operation can facilitate the light-evoked response (Results, section 3d). The finding suggests that the statocysts control
the magnitude of the light-evoked response by limiting its expression. However, the applicability of these results to the interpretation of the modulated response in head-up neurons is questionable on a number of grounds:

1) Because of the inaccessibility of head-up neurons during the summer months, it was necessary to use another optomotor type for this study. It might, but it does not necessarily follow that the results can be applied to head-up motoneurons as well.

2) The results were clear-cut in only one of the two experiments performed (Fig. 10b(1)), although the results of the experiments were not contradictory.

3) Controls were not done to eliminate the possibility that the findings were the result of gross injury. Such an effect might be likened to the hormonally-mediated response to threat or injury in mammals. During the course of the post-ablation part of the experiment however, which took about 1.5 hours, the level of optomotor neuron activity was quite low (Figure 2b), and I did not observe any prolonged, generalized activity of the appendages which might have accompanied an excited condition.

4) The destruction of the statocysts by cauterization is a highly effective procedure, which accomplishes statocyst ablation while minimizing the chances that the microelectrode
implanted in the eyestalk musculature will be displaced. However, the procedure undoubtedly damages the antennular nerve, a mixed sensorimotor nerve which carries not only axons from the statocyst hair cells, but also may carry olfactory and mechanosensory fibers from the joints of the antennules (Sandman and Okajima, 1973b; Bullock and Horridge, p. 828). Therefore, the effects of the operation may be associated with the destruction of a number of sensory afferent types. It is not known which of the afferents, besides those from the statocysts, might have a functional bearing on the optomotor response.

5) Because the statocysts were not ablated individually, no statement can be made regarding the relative influence of either statocyst on the light-driven response.

b. General considerations on the modulated response in head-down motoneurons.

One essential feature of the modulated type of response is that the firing rate during stimulation by pulsed light at or near the receptive field center is drastically limited, when the animal is at the non-preferred position. The finding suggests (but see below), that visual stimulation of the head-up neurons may be particularly effective in producing contraction of the head-up muscle group, and that the potentiality
for simultaneous activation of the opposing head-up and head-down muscle groups is circumvented by curtailment of the head-up motoneuron sensitivity to light. On the one hand, a relatively high tension level may result from minimal activation of the head-up motoneurons, and on the other, the effects of light on the head-up neurons, as opposed to other types, may be relatively large. To the latter point, two experiments (Fig. 8c and Fig. 9b(2)) have shown that the maximal effects of light stimulation are indeed relatively large, compared to the maximal effects of stimulation through statocyst mediated channels. However, it remains to be demonstrated that, compared to the other motoneuron types, the head-up units are preferentially sensitive to visual stimulation. Such a study would have to involve a large number of observations of the effect of light stimulation applied at the receptive field center. Quantitative comparison of the effects would only be meaningful if the intensities at which some standard response level occurs were measured. The fact that the visual responsiveness of head-up and perhaps other neurons is related to body position would have to be considered in the experimental design. There is also the problem that there are at least two kinds of visual stimulation (pulsed light and moving stripes) which are effective stimuli, and it is not known whether certain units are preferentially
stimulated by one type or the other. Indeed, the hypothesis which explains the modulated response in terms of the limitation of the motoneuron response at the non-preferred position is naive, in the absence of the knowledge that the response to moving stimuli is similarly limited.

Any interpretation of the functional role of the modulated response depends on knowledge of the neuron's position-related excitability, when a number of retinal loci are stimulated. Thus far, only the response at or near the receptive field center is known. One possibility is that the entire excitatory receptive field might lose sensitivity at the non-preferred position, and that the observed growth of the response with an approach to the preferred position would be paralleled in all parts of the excitatory receptive field. If this were true, then the proposal already made--to the effect that the visual response is limited to prevent simultaneous activation of antagonistic muscle systems--might be valid. However, another possibility is that the excitatory field and the non-responsive area reverse locations when the animal is head-down, thereby placing the excitatory field at the posterior of the eye. (This would be similar to the behavior of the space-constant sustaining fibers--see below, Section 5c.) Such a possibility has not been ruled out experimentally in this work. Dr. R. M. Glantz reports (unpublished) that the
motoneuron receptive fields appear not to shift with rotation of the animal.

c. Possible models for the interaction of the visually-mediated and the statocyst-mediated systems.

1) The model which most obviously follows from one interpretation of the statocyst ablation experiments is that the visually-evoked response is inhibited maximally at the non-preferred position and is then progressively disinhibited with nearness to the preferred position. Secondly, for any given body position, the statocyst-controlled inhibition is greater for a continuous rotation through a position than it is if the animal is maintained at that position. This scheme is based upon the conditions that the removal of the statocysts produces no non-specific facilitory effects, and that the results relate to statocyst organ removal only in head-up motoneurons. As stated above, these premises have not been directly demonstrated. However, the hypothesis remains a viable one because there are some experimental results in its favor, and because one group (Type I) of position-sensitive receptor elements of a given response type (e.g., head-down) makes a plausible source of control, since both the receptor discharge rate and the visually-driven motoneuron discharge rate change sigmoidally when the angular position of the animal changes. (The discharge
of Type I receptor elements changes sigmoidally, whether the rotation is continuous or via a series of maintained positions.) Assuming that a given change of body position will produce an increase in the excitation of some receptor elements and a decrease in the excitation of other elements, it is therefore reasonable that an increase of the visually-driven response with an approach to the preferred position may be produced by progressive disinhibition of some element in the visual input network. The inhibitor to the visual input network would be driven directly by the position-sensitive (Type I) statocyst element or elements—in this case, head-down—which are antagonistic to the position-sensitive statocyst element(s) driving the motoneuron (head-up). Therefore, the visual input to the motoneuron would be greatest (least inhibited) at the preferred position (head-up), and the smallest (most inhibited) at the non-preferred position (head-down). During motion of the animal in the preferred direction, excitation of the statocyst motion-sensitive receptor elements (Type I, II, and acceleration receptors) may add input to the inhibitor of the visual input network, while at the same time they add input to the motoneuron itself. (However, in the present work, it is not known to what extent the vibration transmitted to the statocysts from the motor driving the rotation had an effect upon the motoneuron response. That the head-up neurons tested
were phasic neurons is an assumption which was not tested, since their response to motion in the reverse direction was not explored).

Figure 12a diagrams a model in which the inhibitor to the optomotor visual input network is driven by the position-sensitive (Type I) receptor elements which are antagonistic to the direct motoneuron driver. Additional motion-sensitive input to the motoneuron both increases the statocyst-driven response and further decreases the visually-driven response.

2) Another model of this general type should be discussed. In this scheme, the inhibitor neuron is still driven by the Type I position-sensitive elements which are antagonistic to the direct motoneuron driver. However, the inhibition is imposed upon the motoneuron itself, instead of the visual input network (Fig. 12b). Progressive disinhibition of the motoneuron with the approach to the preferred position has the effect of imposing a unique saturation level, per given position, upon the motoneuron—a certain rate above which the motoneuron cannot fire. The value of the saturation rate is zero, or near zero Hz. at the non-preferred position. As the preferred position is approached, the value of the saturation rate increases (Fig. 12c). The magnitude, per given position, of the visually-driven and the statocyst-driven portions of the optomotor response would then be a function of the relative
Figure 12a. Model of a possible mechanism for control of the visually-driven motoneuron response by the statocysts. The head-up motoneuron is excited by light in the anterior part of the eye, by motion, by vibration, and by position near the preferred position. The antagonistic position-sensitive (Type I) statocyst receptor element, the motion-sensitive (Type II and acceleration) elements, and the vibration-sensitive elements drive the inhibitor neuron, which in turn feeds into the optomotor visual channel.

Figure 12b. Model of another possible mechanism for control of the visually-driven motoneuron response by the statocysts. The inhibitor neuron, still driven by the Type I statocyst receptor element which is antagonistic to the direct motoneuron driver, now feeds directly onto the motoneuron itself.

Figure 12c. Theoretical curves presented to illustrate a possible scheme by which the visually-driven optomotor response could be controlled.

(1) The saturation firing rate of the motoneuron, which increases with nearness to the preferred position.

(2) The statocyst-driven firing rate of the motoneuron, which also increases as the preferred position is approached.

(3) The visually-driven component of the motoneuron discharge
rate. It too, can increase with nearness to the preferred position, if curves (1) and (2) are in the relationship pictured.
EXCITATORY SYNAPSE

INHIBITORY SYNAPSE

statoecyst position receptor, head-down

head-down motoneuron

head-up motoneuron

statoecyst position receptor, head-up

statoecyst motion or vibration receptor

anterior, eye

FIG. 12a
FIG. 12b

- Excitatory Synapse
- Inhibitory Synapse

- Statozyst position receptor, head-down
- Statozyst position receptor, head-up
- Statozyst motion or vibration receptor
- Anterior, eye
- Head-down motoneuron
- Head-up motoneuron
FIG. 12c

MOTONEURON DISCHARGE RATE

ANGULAR POSITION, DEGREES
amount of input coming to the motoneuron through the visually-driven and the statocyst-driven channels. In Fig. 1lc, the curve relating statocyst-driven firing rate to angular position has a relatively slow rate of rise, compared to the curve relating saturation rate to angular position. It can be seen that under this condition, the visually-driven component of the response increases as the preferred position is approached. Excitation of the motion-sensitive statocyst receptor elements during a continuous rotation would increase the total amount of statocyst input to the motoneuron. Since the optomotor response magnitude is limited by an absolute saturation rate, and the relative magnitudes of the response components are determined by the relative amounts of statocyst-driven and visually-driven inputs to the motoneuron, there would be a proportional decrease of the visually-driven response rate during motion of the animal.

One property of either a direct or presynaptic inhibition model is that the efficacy of the inhibitory effects would likely decrease over a period of constant-level gravitational stimulation, due to accommodation. Presynaptic inhibition of transmitter release has been ascribed to increased Cl⁻ conductance (crustacean muscle), which raises the spike threshold by tending to hyperpolarize the membrane, and to increased Na⁺ permeability and Na⁺ inactivation. Postsynaptic or direct
inhibition is thought to occur via an increase in the K⁺ or Cl⁻ conductance, although in sympathetic ganglion cells the IPSP may be due to decreased Na⁺ conductance (Weight, 1974). Opening (or closing) of the ionic channels in any of these cases might be subject to inactivation, as the effect of a prolonged, unchanging stimulus. Therefore, it would be predicted that the threshold to visual stimulation would be initially high but would return to normal when the animal was maintained for a time at or near the non-preferred position. Although this observation was not made, the usual period for repetitive visual stimulation at one position was not more than five to ten minutes, and the period necessary for observable threshold changes to occur could have been longer.

3) There is also the possibility that the increase of the visually-evoked response with nearness to the preferred position is a result of input from the space-constant sustaining fibers. These units vary the size and shape of their receptive fields according to the body position of the animal, because they themselves are under control of the statocysts (Wiersma and Yamaguchi, 1966; 1967). Space-constant units, excitable by features moving in a single direction, have been found in the rock lobster (Wiersma, 1975), but have not as yet been demonstrated in crayfish. Of the two crayfish sustaining units, 073 and 023, the latter has the larger
receptive field; in other respects, the properties of the
two units are thought to be similar. When the animal is
normally positioned, 023 has an excitatory region covering
the dorsal half of the eye, but excluding the rims. With
rotation about the longitudinal body axis, the unit in the
upward moving eye increases the extent of its receptive field,
and when the same eye moves downward, the extent of the
receptive field decreases. At the eye-up position, the entire
central part of the eye is excitatory with respect to this
unit, and at the eye-down position, the entire part of the eye
is inexcitable. Upon rotation about the transverse axis, the
receptive field is always upward-looking. For example, in
the upside-down position, the excitatory portion would be
the ventral half of the eye, excluding the rims, and in the
head-up position, the excitatory portion would approximate
the anterior half of the eye. Therefore, no matter what the
position of the body, the 023 unit of at least one eye receives
input from the space above the animal, and only from that
space. There appears to be no information in the literature
on whether the degree of optomotor compensation has an effect
on the extent of the 023 receptive field, and this would be
an interesting detail to explore.

In comparing the receptive fields of a head-up unit
(Fig. 8a), and of 023 with the animal normally positioned, it
appears that at least a part of the head-up unit non-excitatory area (the dorsal posterior rim of the eye) may overlap the 023 excitatory area. However, because the head-up map is not precise with respect to loci of various sensitivities, it is also possible that the non-excitatory area of the head-up unit may be accounted for by the lack of 023 excitability at the eye rim. 073, which has a smaller excitatory field than 023, might also be a candidate input. Similarly, the head-up map is not sufficiently precise to say whether or not the excitatory field in the dorsal eye half covers the rim areas. Therefore, in considering only the dorsal half of the eye, it is possible that the head-up and the 023 (or 073) receptive fields are overlapping in position and in size. However, there remains a large excitatory region in the ventral half of the head-up field which cannot be accounted for by input from any known space-constant sustaining fiber.

4) An alternative explanation for the position-dependent modulation of the visually-evoked response is that the addition of statocyst-mediated input to visual input may be obligatory to reach spike threshold, for motoneuron synapses requiring considerable summation of input to attain threshold. However, there is no reason to limit the hypothesis to include the motoneuron synapse only. Activity in the statocyst-mediated channel may facilitate the effects of visual excita-
tion at any point presynaptic to the motoneuron, either by lowering a postsynaptic membrane potential toward threshold, or by increasing the presynaptic transmitter release (heterosynaptic facilitation). Any such facilitation may be graded according to the level of excitation in the statocyst-mediated channel, and thus the approach to the preferred position may increase the probability of motoneuron spiking by increasing the input from the statocysts. This possibility cannot be ruled out in light of the present evidence. However, it must also be recognized that this model cannot account for the reciprocal relationship of the statocyst-driven firing rate and the visually-driven firing rate—the observation that an increase in statocyst-driven firing rate (over the steady-state rate) due to motion of the animal is associated with a decrease in the visually-driven firing rate. Any model which involves facilitation of the motoneuron output which is solely dependent on the level of the statocyst-mediated excitation would predict that the greater is the statocyst-driven response, the greater should be the visually-driven response. The observation which inversely relates the visually and statocyst-driven response magnitudes were made on neurons which also increase the visually-driven response with an approach to the preferred position (Figs. 9a(1) and
9b(1)). Therefore, if the optomotor system amplifies the visually-driven response with heightened background rate, via a summation or facilitatory process, an additional mechanism must be postulated for opposing the amplification effect when the animal is being continuously rotated. Although this introduces another feature into the model, it cannot be on this basis ruled out (see below).

5) The counter-argument to that presented in 4) is that the threshold to firing may actually be raised as the summed input through the visual and statocyst-mediated channels becomes greater. Therefore, with an increase in the input to the motoneuron through statocyst-mediated channels, the excitatory effect of a superimposed visual stimulus would become reduced. It is known that excessive depolarization is associated with a loss of excitability through inactivation of the membrane (Bullock and Horridge, pp. 266, 270; Tauc, p. 564). Therefore, at low levels of ongoing depolarization, superposition of additional excitation may produce an augmentation of the firing rate, but at a higher level of ongoing depolarization, there may be a relative defacilitation of the firing rate. The reduction of the visually-evoked response when the animal is moved through rather than maintained at a succession of angular positions may be considered in this light, since the
average levels of ongoing depolarization, judged from the background rate firing, would be greater, per given position, for a moving stimulus than for a steady-state stimulus. One might then expect the visually-evoked response to grow less with the higher background rate, and this is in fact one of the observations which is made. However, continuous rotation of the animal toward the preferred position, which must also progressively increase the level of ongoing depolarization by adding position-dependent excitation results in an augmented visually-evoked response. The two observations can be reconciled by proposing a mechanism by which the effects of the visual input are facilitated to an extent with an approach to the preferred position, but that the degree of facilitation becomes less, per given position, when the animal is moving.

It can be seen that proposals 4) and 5) are rather complementary with regard to mechanism, and that both models depend upon an interplay of facilitatory and defacilitatory processes, based on the effect of depolarization on the firing probability of the neuron. The effects on the visually-evoked response of presetting the membrane potential at various levels might be measured by inserting a double-barreled electrode (Eccles, 1957, p. 41) into a motoneuron soma, in order to both apply current and record the resulting level of
depolarization. Attenuated spikes, resulting from a visual stimulus, might be recordable in the soma, therefore making it unnecessary to record with another electrode at the axon. However, since the degree to which the depolarization was passively conducted to the spike initiation zone could not be known, any interpretation of the results would carry a measure of uncertainty. Also, one could not weigh the results against the membrane potentials actually encountered under natural stimulation. Such information would be very difficult to acquire, since it would involve intracellular recording of motoneuron activity during rotational motion of the animal.

6) Throughout the previous discussion it was proposed that the visually-evoked response is superimposed on the ongoing statocyst-driven rate. This gave justification to the method by which the visually-evoked response magnitude was derived (Appendix note 3). No consideration has yet been given to the possibility that one effect of visual stimulation might be to suppress the ongoing discharge rate for the duration of the light pulse. The amplitude of the visually-evoked response would thus remain constant, rather than varying under the influence of the statocysts. However, total suppression of the background response is not consistent with the observation
that the average firing rate during a constant-level visual
stimulus does increase with an approach to the preferred posi-
tion. Therefore, some portion of the background response
would have to be expressed during visual stimulation. If the
amount of expression were about equal, per given position,
whether in moving or steady-state conditions, the visually-
evoked response would appear to decrease with a change from
steady-state to motion. There is one experimental detail
which cannot be easily accounted for according to the above
scheme, and that is the very low or absent response to visual
stimulation at the non-preferred position. According to the
above hypothesis, the visually-evoked response should be
observable irregardless of body position.

**Summary**

The present study represents an extension of the state
of knowledge with regard to the behavior of crayfish opto-
motor neurons, under stimulation through statocyst-mediated
or visually-mediated channels. In a number of ways, opto-
motor responses appear to reflect the properties of lobster
statocyst receptor elements rather closely. Both the receptor
elements and the motoneurons are sensitive to absolute angular
position, to rotatory motion and to the direction of motion,
and to vibration. Among individual Type I receptor elements
and within the group of motoneurons of the same response type, variations occur in the position corresponding to the excitation threshold. When the responses to maintained tilt of both Type I receptor elements and optomotor neurons are plotted as a function of angular position, the resultant functions are bell-shaped. Therefore, predicated on the assumption that the lobster and crayfish statocyst systems are similar, it appears that all the known receptor types have connectivity to an element in the optomotor system, and that at least some of these connections may be fairly direct.

The excitatory response to pulsed light in optomotor and optokinetic neurons may represent the result of stimulation of a movement perceptive visual network by rather artificial means. In the optokinetic system, and possibly in the optomotor system, this visual network would operate, under normal circumstances, within a feedback loop which continuously adjusts the rate at which the eye reflex progresses. The mixed excitatory and inhibitory pattern of some responses to stimulation of the excitatory or the inhibitory receptive field can be seen as the non-specific result of a movement perception system being driven by a non-moving stimulus, although this is by no means necessarily the case. On the other hand, the responses to pulsed light and to movement may
have unrelated physiological significance, and might also be mediated by different visual interneuron channels.

One such possible channel is the sustaining unit group of visual interneurons. Both sustaining units, optokinetic units, and optomotor units respond similarly to pulsed light stimuli. The results of an experiment in which the responses of a sustaining unit and an optomotor unit were simultaneously recorded, show that the motor unit appears to sum sustaining unit input to reach its threshold. The number of sustaining unit impulses preceding each motoneuron impulse is constant over a wide range of sustaining unit firing rate. However, interpretation of this finding according to known physiological principles is difficult.

In one type of optomotor neuron, the response to pulsed light is strongly facilitated by an approach to the preferred position, and therefore the response appears to be influenced by information contained in statocyst-mediated channels. Also, when the animal is continuously rotated through a set of angular positions, the light-driven response, per given position, is often smaller than the response under conditions of maintained tilt. A significant overall increase of the statocyst-mediated response, per given position, appears to be correlated with this decrease in the light-driven response. This represents another instance of the probable interaction
of statocyst-mediated and visually-mediated information. The neuronal mechanisms underlying the above relationships are not known, but a number of possibilities are discussed.

Appendix notes

1. For Fig. 2a, the motoneuron discharge rate, per steady-state position (SDI), was determined by first automatically counting the number of spikes occurring within a ten-second interval, beginning ten seconds after the onset of a one second duration light pulse. The discharge rate, in Hz., could then be calculated, by dividing the spike count by ten. This calculation was done over a number of trials, and the values were averaged to generate the mean steady-state discharge rate per given position.

To determine the motoneuron discharge rate during continuous motion (MDI), spike counts over a one second period were made at intervals, corresponding to different angular positions during a single traverse of the animal. The counts were made directly, by replaying the taped data into a storage oscilloscope. At the rotation rate used, one second was equivalent to about 2 degrees' rotation of the animal. The values of the spike counts per given position were averaged over a number of trials, to generate the mean discharge rate per given position during motion.
For Figs. 9a(2) and 9b(2), the mean steady-state discharge rate per position (SD) was determined as in Fig. 2a, except that the spike counts were made over a five second period, beginning about five seconds from the onset of the light stimulus. These counts were made directly, by replaying the taped data into a storage oscilloscope. The mean discharge rate per position during motion (MD) was determined exactly as in Fig. 2a.

2. For Fig. 2b, the motoneuron discharge rate, per steady-state position (SDI) was determined by first automatically counting the number of spikes occurring within a ten second interval, beginning ten seconds after the onset of a one second duration light pulse. The discharge rate, in Hz., could then be calculated. This calculation was done over a number of trials, and the values were averaged to generate the mean steady-state discharge rate per given position.

For Figs. 2a and 2b, the motoneuron discharge rate, per steady-state position, after statocyst ablation (SDO), was determined by first counting the number of spikes occurring within a five second interval, beginning five seconds after the onset of a one second duration light pulse. The counts were made directly, by replaying the data into a storage oscilloscope. The discharge rate, in Hz., per given position,
was calculated and the values over a number of trials were averaged to generate the mean steady-state discharge rate, per given position, after statocyst ablation.

For Fig. 2a, the motoneuron discharge rate per position during motion, but after statocyst ablation (MDO), was determined by counting spikes over a one second period, at intervals during a single traverse of the animal. The counts were made directly, by replaying the data into a storage oscilloscope. The values of the spike counts per given position were averaged over a number of trials, to generate the mean discharge rate, per given position, during motion and after statocyst ablation.

3. The mean background rate was determined by automatically counting the number of spikes occurring in the ten second interval following the trigger signal which slightly preceded the stimulus onset. For each stimulus, this number reflected the number of spikes occurring during a one second duration light stimulus plus the number of spikes occurring during a nine second period having no light stimulation. The number of spike occurrences within each ten second period was summed over all stimulus trials, and then the total number of spikes occurring within the stimulus period only was subtracted. This difference, divided by the number of stimulus trials x 9, was taken as the mean background response, in Hz.
To determine the mean light-driven discharge rate exceeding the background rate (the net response to light), the mean background rate was subtracted from the mean rate occurring during the stimulus period. In the case described above, the mean rate during the one second stimulus period (total number of spikes divided by the number of stimulus trials) was 17 Hz. Subtracting a 6 Hz. mean background rate, the mean light-driven response is 11 Hz.

4. The maximum transient discharge for a sustaining unit is about 250-300 Hz. (Glantz, 1971), and for a motoneuron is about 100 Hz. (see Fig. 4a). Therefore, should the neurons connect on a 1:1 basis, the minimum decline in discharge rate from sustaining unit to motoneuron would be about 60%.

5. One may ask why the analysis was done using the cumulative number of sustaining unit spikes to the Nth motoneuron spike. The alternative would be to count the number of sustaining unit spikes falling within the interval defined by the Nth and the N-1th motoneuron spike. The former procedure was used because it cannot be assumed that the Nth motoneuron spike is driven solely by sustaining unit spikes occurring within the immediately preceding interval. Suppose, for instance, that I wish to determine the number of sustaining unit spikes which, under the hypothesis, would excite the Nth motoneuron spike in
a given spike train. If the latter procedure were used, sustaining unit impulses which occurred on the order of 1 or 2 milliseconds prior to the N-1th motoneuron spike would not be counted. However, since there must be a certain conduction and synaptic delay time between the two recording sites, sustaining unit spikes occurring somewhat before the N-1th spike might actually excite the Nth motoneuron spike. Secondly, there is no a priori reason to believe that each motoneuron firing resets the motoneuron spike threshold to the resting level. Again, the probability of occurrence of the Nth motoneuron spike may be affected by excitatory influences occurring far earlier than the N-1th motoneuron impulse.

6. The first interval is computed by taking the time of the first motoneuron spike and subtracting the time of the sustaining unit spike train onset. Any influence predisposing the motoneuron to fire or not fire, occurring previous to the sustaining unit spike train onset, was not taken into account. However, since Fig. 7c(1) shows that the linear portion of the function includes the point at N=1, the neglect of influences other than the presumptive sustaining unit input may be justified.

7. For each stimulus trial presented at a given locus on the
cornea, the motoneuron discharge rate occurring during the stimulus period (one second) was determined by counting the number of spike occurrences during the stimulus period. The counts were made directly, by replaying the data into a storage oscilloscope. Also, for each stimulus trial, the number of spike occurrences were determined during the five second interval beginning about five seconds after the stimulus onset. This number, divided by five, yielded the background rate, in Hz., per given stimulus trial. Then the background rate was subtracted from the discharge rate during stimulation, yielding the net light-driven response for one stimulus trial. Summing the responses over a number of stimulus trials (n) and dividing by n yielded what is referred to as the mean light-driven response.

8. The mean light-driven response per given steady-state position was determined by subtracting the background discharge rate from the discharge rate occurring during the stimulus period, and then averaging the differences over a number of stimulus trials. The procedure was as is described in Appendix note 7. (For these experiments, the stimulus duration was a bit greater than one second. In one experiment, the duration was 1030 ms., and in the other, the duration was 1080 ms. The procedure in these cases was to count the number
of spikes occurring during the first second of the stimulus period only.)

To determine the response to light during continuous rotation of the animal, the light stimulus was applied for about one second (see above), equivalent to about 2 degrees rotation, at known angular positions during the 180 degree traverse. A similar traverse was made immediately following the one involving light stimulation, only this time the animal was kept in the dark. One second duration spike counts at each position could thus be made, under conditions of light stimulation and under conditions of no light stimulation. The net light-driven response, per given position, was determined by subtracting the spike count in darkness from the spike count during the light stimulation. This difference was averaged over a number of stimulus trials to yield the mean light-driven response during motion.

9. Head-up motoneurons were not used because they appeared to become inaccessible during the summer months. The experimental period for this phase of the work was limited to the period from mid-June to mid-July. During this period, many attempts were made to record a head-up motoneuron, but only one was seen. (Side-up and side-down units were frequently encountered.) An experiment was begun using this head-up
unit, but the lead was lost during the process of statocyst ablation. By contrast, during the period from May 15 to June 6, three head-up units were recorded.

There is a possible explanation for this. Wiersma and Fiore (1971a) have found in Carcinus that during the summer, the steady-state discharge of head-up neurons becomes very phasic; that is, after placement of the animal in a given steady-state position, the discharge decays rapidly to a low level. For any crayfish head-up unit, the steady-state discharge even at the preferred position is relatively low. If many crayfish head-up neurons behave as they do in the crab, the relatively low steady-state rate would decline after some minutes to an extremely low-level discharge, and such a neuron would be easily missed.

10. Although I believe that an increase in the light-evoked portion of the optomotor response after statocyst ablation constitutes a new finding, similar cases have been found in animals which orient to light only after removal of the equilibrium organs. Although many animals maintain their primary orientation via perception of sky light, certain animals seem to ignore the visual cues except when the gravity receptor organs are destroyed.

One example is the prawn Leander xiphias, which swims
normally with the dorsal side up. If a light is directed
toward the lateral side of the animal, it makes no attempt to
rotate its dorsal side toward the direction of the light. How-
ever, after statocyst ablation, if the animal is held in the
normal position, a laterally-directed light will cause it to
make pushing movements with the legs opposite to the direction
of the light. If it is held so the dorsal side faces the
light, this orienting behavior is absent (Fraenkel, 1961).

In the aquatic insect *Notonecta*, the gravity receptor
organ is a cavity associated with each antenna base. In the
cavity, an air bubble is trapped. Movement of the bubble
when the animal deviates from the primary orientation (ventral
side up) stimulates the gravity receptor elements. When the
antennae or the air bubbles are removed, the animal cannot
orient normally in the dark, but now uses overhead light to
attain the normal swimming position (Bullock and Horridge,
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