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EFFERENT INFLUENCES ON THE AFFERENT ACTIVITY FROM THE OCTOPUS ANGULAR ACCELERATION RECEPTOR SYSTEM

By R. WILLIAMSON*
Zoological Institute, University of Regensburg, D-8400 Regensburg, Federal Republic of Germany

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SUMMARY

Electrophysiological recordings were made from afferent units of the octopus angular acceleration receptor system during the electrical stimulation of efferent axons to this system. Of the afferent units examined, 93% changed their activity in response to stimulation of the efferent axons.

During efferent stimulation 77% of the afferent units decreased their activity. The magnitude of the inhibition and the time to maximum response were frequency dependent, with most units showing an increase in inhibition with increase in efferent stimulation frequency. The post-stimulus recovery from inhibition was of two types: either a gradual increase in activity to the pre-stimulus resting level of activity (Fig. 3) or a rapid increase in activity to a level above the pre-stimulus level, i.e. a post-inhibitory rebound or facilitation, and then a gradual decline to the resting level of activity (Fig. 4). During long periods of efferent stimulation (> 40 s) the inhibition was not maintained.

During stimulation of the efferent axons 16% of the afferent units increased their activity. The post-stimulus response consisted of either a gradual decrease in activity to the pre-stimulus level of resting activity or a rapid increase in activity followed by a gradual decrease to the resting level of activity (Fig. 6). During long periods of efferent stimulation the excitation increased to a plateau level which was maintained for the duration of the stimulus period (Fig. 7).

Sinusoidal oscillations of the statocyst evoked bursts of afferent activity in time with the movement. The magnitude of these bursts could be decreased or increased by stimulation of the efferent axons (Fig. 8).

It is proposed that two populations of efferents are present in the octopus statocyst, one inhibitory and the other excitatory, and that both types of efferent affect single afferent units.

INTRODUCTION

The innervation of sense organs by efferent fibres occurs in both vertebrates (e.g. Klinke & Galley, 1974) and invertebrates (e.g. Kondo, 1978; Patterson & Silver, 1983). The functional significance of such efferent innervation is not yet satisfactorily

*Present address: Department of Physiology, University of Basel, Vesalgasse 1, CH-4041 Basel.

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understood although hypotheses proposing a tuning of the afferent system's responses (Russell & Lowe, 1983) or an exclusion of particular, predictable inputs (Piddington, 1971) are well supported. A major problem in the study of the influence of efferents in most preparations is that the number of efferent fibres present is known to be small: approximately 8% of the fibres in the monkey vestibular nerve (Goldberg & Fernandez, 1980) and 18% in the frog vestibular nerve (Gribenski & Caston, 1974) are efferents. In the octopus however, 70–80% of the fibres in the statocyst nerves are efferents (Budelmann & Thies, 1977; Colmers, 1977; B. U. Budelmann, M. Sachse & M. Staudigl, in preparation). This may therefore be a favourable preparation to observe the action of efferents upon a complex sense organ.

The octopus statocyst contains receptor systems for the detection of linear accelerations (the macula) as well as angular accelerations (the crista). Morphological studies of the octopus crista system have shown that it closely parallels the vertebrate semicircular canal system in that the receptor system covers three almost orthogonal planes, and that it has cupulae, with underlying secondary hair cells and first-order afferent neurones (Budelmann, 1977; B. U. Budelmann, M. Sachse & M. Staudigl, in preparation). Although there are also significant morphological differences present, it has been proposed that the statocyst crista/cupula system operates in a manner similar to the semicircular canal system (Govardovskii, 1971; Maddock & Young, 1984). This view has been to a large extent confirmed by an analysis of the response characteristics of the crista afferents (Williamson & Budelmann, 1985*a*).

Although the efferent innervation in some gastropod molluscs (Wolff, 1970) has been shown to have an inhibitory effect on the statocyst afferents, no information is available on the influence of efferents in the more complex cephalopod statocyst. The aim of this paper is to investigate the influence of the large efferent innervation of the octopus crista on both the resting activity and the dynamic responses of the afferents. The afferent units studied are those from crista section C2 (for numbering see Budelmann, 1977). This section has been chosen because access to it is relatively easy, the majority of its units are known to have a resting level of activity (Williamson & Budelmann, 1985*a*) and therefore an efferent influence is likely to be more overt. Furthermore, its innervation is advantageous in that it arises from two separate nerves (Williamson & Budelmann, 1985*a*; B. U. Budelmann, M. Sachse & M. Staudigl, in preparation).

MATERIALS AND METHODS

Twenty-five octopuses, *Octopus vulgaris*, within the size range 80–300 g, were used in these experiments. The animals were obtained from the Gulf of Naples and maintained in a closed seawater system in Regensburg until used for experiment.

The recording arrangement was similar to that already described (Williamson & Budelmann, 1985*a*). Briefly, the animal was killed by decapitation and the cranial cartilage containing the statocysts was dissected out and mounted in the upright position in a wax-bottomed dish. The central nervous system was removed and a window through the cartilage was opened into the statocyst cavity to expose the statocyst sac in the area of crista section C2. A fine suction electrode (170 μm diameter) could then be placed on the axons of crista section C2 as they leave the crista section and single unit, or few unit, afferent recordings obtained.

The efferent axons to crista section C2 were activated by electrically stimulating the medial crista nerve. Since crista section C2 is innervated from both the middle and anterior crista nerves it is possible to stimulate the efferents in the former and record the afferents in the latter, thus avoiding the possible antidromic activation of the afferents recorded from. In fact this problem could be surmounted and recordings were also obtained from axons contributing to the middle crista nerve. The middle crista nerve was stimulated at a position within the cranial cavity, by drawing the cut end of the nerve or a part of it, into a second suction electrode. The nerve at this point first passes through 3–5 mm of cartilage before entering the statocyst cavity. The spread of stimulus and the recorded artefact were minimized by coating the electrode with gold in a sputterer, and using this shield as the second pole of the stimulating electrode. For stimulation, trains of pulses were normally employed; the pulses were of 0·01 ms duration and could be varied in amplitude from 0·1–10 μA. The frequency (10–200 Hz), duration (500 ms–120 s) and repetition rate of the pulse trains (one train every 10–300 s) could be independently varied.

The preparation, complete with recording and stimulating electrodes, was then mounted in the desired orientation, usually in the normal upright position (cf. Messenger, 1969), on a rotation device capable of oscillating the statocysts in the pitch plane (see Williamson & Budelmann, 1985*a*).

The afferent activity recorded from crista section C2, a signal indicating the orientation of the statocyst, the pulse sequence used for stimulating and a voice commentary were recorded on an FM tape recorder for subsequent analysis. For the construction of peri-stimulus time (PST) histograms, the afferent activity was, where necessary, passed through a window discriminator to ensure single unit analysis, and then to a Nicolet laboratory computer system.

The standard experimental procedure consisted of obtaining a single unit recording from a C2 afferent, usually showing a resting level of activity, and then electrically stimulating the medial crista nerve. If no response to the shock sequence was observed the position of the stimulating electrode on the medial crista nerve was altered, thus stimulating other fibres, and a further shock sequence applied. Where a response was obtained, the amplitude, frequency of shocks and the duration of the shock train were sequentially varied and the unit's responses observed. Finally, the preparation was sinusoidally oscillated in the pitch plane (0·24 Hz frequency, 8° amplitude) and a further shock sequence was applied.

RESULTS

Recordings were obtained from 81 afferent units in crista section C2 of the octopus statocyst. With the statocyst in the normal upright position the units showed resting levels of activity that varied from less than 1 impullse s^{-1} to 95 impulses s^{-1} (averaged over 80 s). All of these units showed an increase in activity during the head-up part of an applied sinusoidal oscillation of the statocyst in the pitch plane and could thus be identified as recordings from first order afferent neurones in contact with ventrally polarized, secondary hair cells (Budelmann, 1977; B. U. Budelmann, M. Sachse & M. Staudigl, in preparation; Williamson & Budelmann, 1985*a*).

Electrical stimulation of the middle crista nerve produced a change in the activity

patterns of 75 (93 %) of the units recorded from. In addition to these 81 units, other afferent units were found that responded in a one-to-one manner to the stimulus shock, with steady delays of between 0·8 and 2·2 ms, and reliably followed the stimulus up to a frequency of at least 200 Hz. Since this appeared to be a direct antidromic activation of the units they were not included in this analysis.

Inhibition

The commonest response of the crista afferent units to the electrical stimulation of the medial crista nerve was a decrease – here termed an inhibition – of the resting activity. This was observed as a partial or total inhibition of activity in 77 % of the afferents examined. Fig. 1. shows an example of total inhibition during the shock train, followed by a slow return to the original level. Such responses did not usually occur as all-or-nothing responses at a distinct stimulus threshold. Instead, a gradual increase in the amplitude of the shock produced at some point a small inhibition of the unit's activity; this became more pronounced with increasing stimulus amplitude, until a point was reached where a further increase in stimulus amplitude produced no further increase in the level of inhibition.

The magnitude of the inhibitory response was also dependent on the frequency of the pulse train stimulus. Whereas single shocks had no overt effect on the level of resting activity of an afferent unit, stimulus rates as low as 10 Hz could produce an inhibition. In most cases an increase in stimulus resulted in an increase in the level of inhibition, at least up to a frequency of 200 Hz – the highest frequency used in these experiments. However, in 16 % of the afferent units showing an inhibitory response, an increase in stimulus frequency at first led to an increase in inhibition up to a frequency of about 125 Hz, but thereafter any further increase in stimulus frequency produced either no increase, or a decrease in the magnitude of the response. An example of this latter type of response can be seen in Fig. 2, where PST histograms of the response at different stimulus frequencies are shown. Each histogram is the sum of four stimulus repetitions.

The time taken for the maximum level of inhibition to be reached for a given stimulus was fairly constant for different units but varied with the frequency of the applied stimulus. As can also be seen in Fig. 2, at low stimulus frequencies there was a gradual decrease in activity. However, at higher stimulus frequencies, maximum

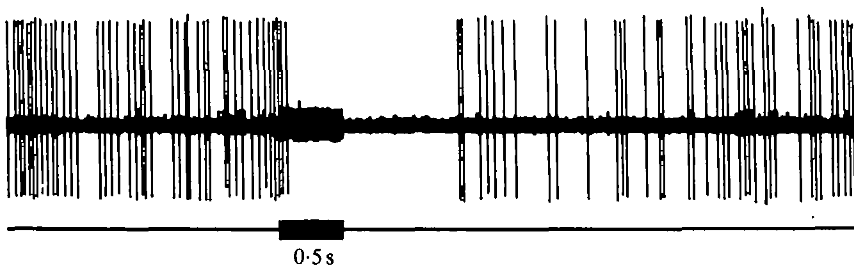

Fig. 1. Inhibition of the resting activity from a crista afferent unit of *Octopus vulgaris* by electrical stimulation of efferent axons. Resting activity = 17 impulses s^{-1}. Stimulation duration is indicated in the lower trace. The small units seen during the stimulus are stimulus artefacts. Stimulus 50-Hz pulses for 500 ms.

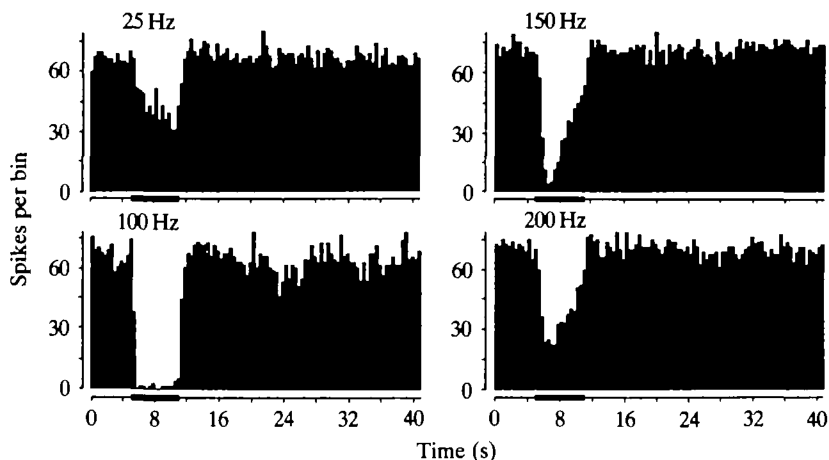

Fig. 2. Inhibition of crista afferents and the effect of efferent stimulation frequency. PST histograms showing the effect of different frequencies of efferent stimulation on a single unit's resting activity. The stimulus duration in each case is 6 s, as indicated on the time axis, with stimulus frequencies of 25, 100, 150 and 200 Hz. Each histogram is the sum of four repetitions. Bin width, 400 ms.

inhibition occurred much more quickly; the time taken for this to occur varied from 1·2 s at 50 Hz to 0·12 s at 200 Hz.

The time taken for a unit's activity to return to the pre-stimulus level of activity after a stimulus sequence varied considerably for different units. This can be seen from Fig. 3 where the response of four different units to a similar shock sequence are shown as PST histograms. It can be seen that although the activity of each unit was to a large extent inhibited within 1·2 s of the start of the stimulus, the recovery time could vary from 0·8 s to over 8 s.

Post-stimulus facilitation

The situation is further complicated in that 62 % of the afferent units showing an inhibitory response to stimulation of the efferents, displayed a pronounced post-stimulus increase in their activities to levels above the pre-stimulus levels. This post-stimulus rebound or facilitation could occur even in units with very low levels of resting activity. (Fig. 4). The magnitude of this response showed considerable variation between different units and although the time taken to reach the maximum level of activity was less than 1·2 s, the time taken to return to the pre-stimulus level was very variable, often more than 20 s (Fig. 4).

The ability of efferent stimulation to maintain inhibition over a long period was tested by applying a train of shocks of over 40 s duration. After an initial period of inhibition, varying from 4 to 33 s for different units, the level of activity during the applied stimulus gradually increased, often exceeding the pre-stimulus level. The length of the inhibitory period within the stimulus sequence could usually be increased by increasing the stimulus frequency or by increasing the amplitude of the stimulus. For example, in Fig. 5, although the initial stimulus amplitude of 1 μA (upper histogram) was sufficient to inhibit totally the activity of the unit, the duration of this period of inhibition was increased by increasing the stimulus amplitude to 4 μA (lower histogram). It can also be seen that the post-stimulus increase in activity was

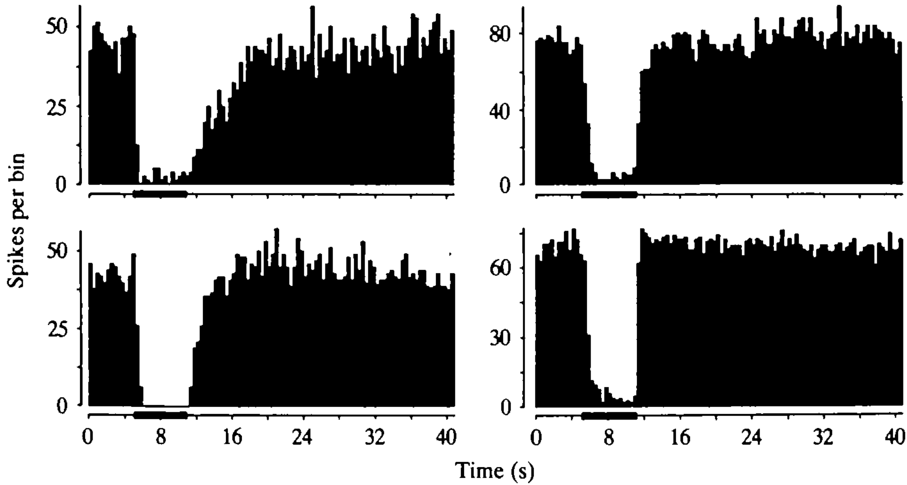

Fig. 3. Inhibition of crista afferent resting activity and post-stimulus recovery. PST histograms from four different units inhibited by efferent stimulation showing the variation in recovery times from the stimulus. Bin width, 400 ms; stimulus, 50-Hz pulses for 6 s.

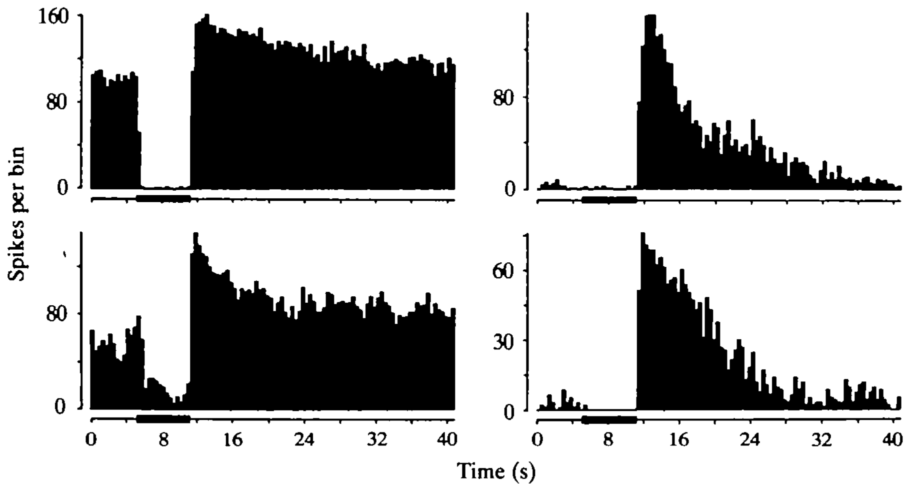

Fig. 4. Inhibition of crista afferent resting activity and post-stimulus facilitation. PST histograms from four different units showing post-stimulus facilitation and the variability in recovery time. Note that a strong post-stimulus facilitation can occur in units showing very little resting activity. Bin width, 400 ms; stimulus, 50-Hz pulses for 6 s.

increased by the increase in shock amplitude. A post-stimulus increase in activity was always seen when long duration (> 40 s) stimuli were applied.

Excitation

Although the majority of the crista afferent units recorded from showed an initial inhibitory response to stimulation of the medial crista nerve, 16 % of the afferents were found to show an initial increase in the level of activity; this will here be termed an excitation. In Fig. 6 it can be seen that the time from stimulus onset to peak response was often longer, and much more variable, than the equivalent time to peak

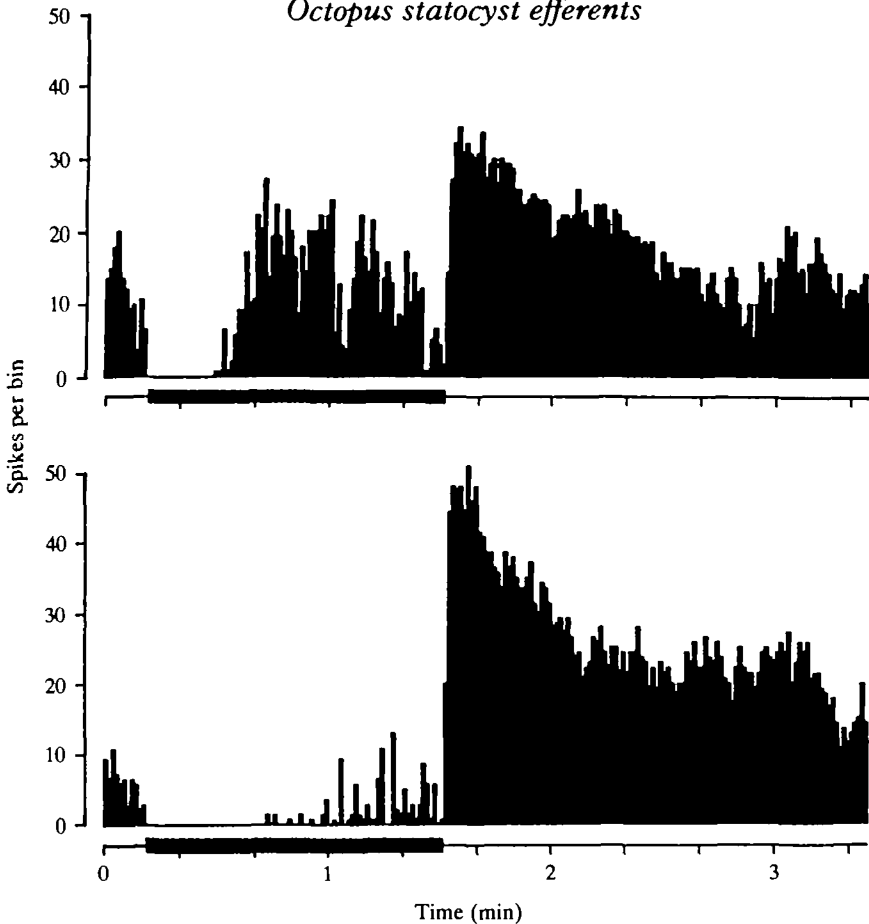

Fig. 5. Long duration efferent stimuli and the effect on crista afferent resting activity of stimulus magnitude. PST histograms from the same unit showing that inhibition is not maintained during long periods of efferent stimulation. Increasing the amplitude of the stimulus pulses from 1 μA (upper histogram) to 4 μA (lower histogram) increases the period of inhibition and also the size of the post-stimulus facilitation. Bin width, 1 s; stimulus, 50-Hz pulses for 80 s.

inhibition. This response time could be decreased by increasing the stimulus frequency. The time taken to return to pre-stimulus level of activity after the stimulus was very variable and in some cases (see right histograms) a post-stimulus facilitation could also occur in units showing an initial excitatory response.

As demonstrated in Fig. 7, stimulus trains of long duration (> 40 s) applied to this type of unit resulted in a steady increase in activity until a plateau level was reached; this was then maintained until the end of the stimulus train and was followed by a gradual decline in activity to the pre-stimulus level.

Oscillations

The increases or decreases in activity of the crista afferent units resulting from stimulation of the medial crista nerve were effective not only upon the resting levels of activity but also on the dynamic responses of the afferent units to an imposed sinusoidal oscillation of the preparation in the pitch plane.

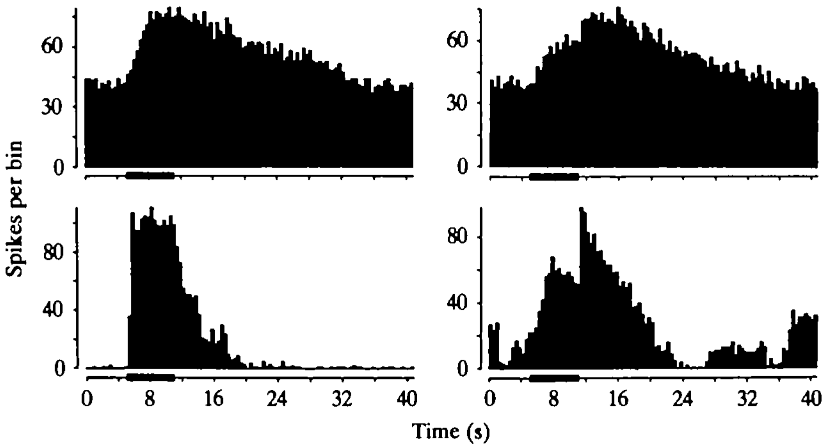

Fig. 6. Excitation of crista afferents and post-stimulus recovery. PST histograms from four different units showing an increase in their resting activity during efferent stimulation. Note that in the two histograms on the right a post-stimulus increase in activity is also present. Bin width, 400 ms; stimulus, 50-Hz pulses for 6 s.

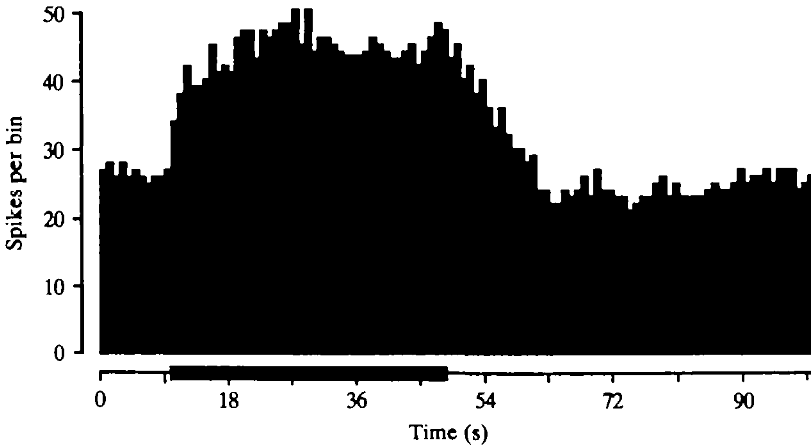

Fig. 7. Excitation of crista afferents during long efferent stimulation. PST histogram showing the effect of a long period of efferent stimulation upon a unit excited by efferent stimulation. Bin width, 1 s; stimulus, 50-Hz pulses for 40 s.

The upper PST histogram of Fig. 8, from a unit that showed an inhibition of its resting activity to electrical stimulation, shows that the repetitive activity pattern of the unit to the mechanical oscillation was inhibited during the period of electrical stimulation. This was followed by a small post-stimulus increase in the level of the response to the oscillation.

The lower PST histogram of Fig. 8, from a unit that increased its activity in response to stimulation, shows that the level of response to the oscillation was increased during the period of electrical stimulation and that this was here followed by an additional post-stimulus increase in activity which gradually declined to the original pre-stimulus level.

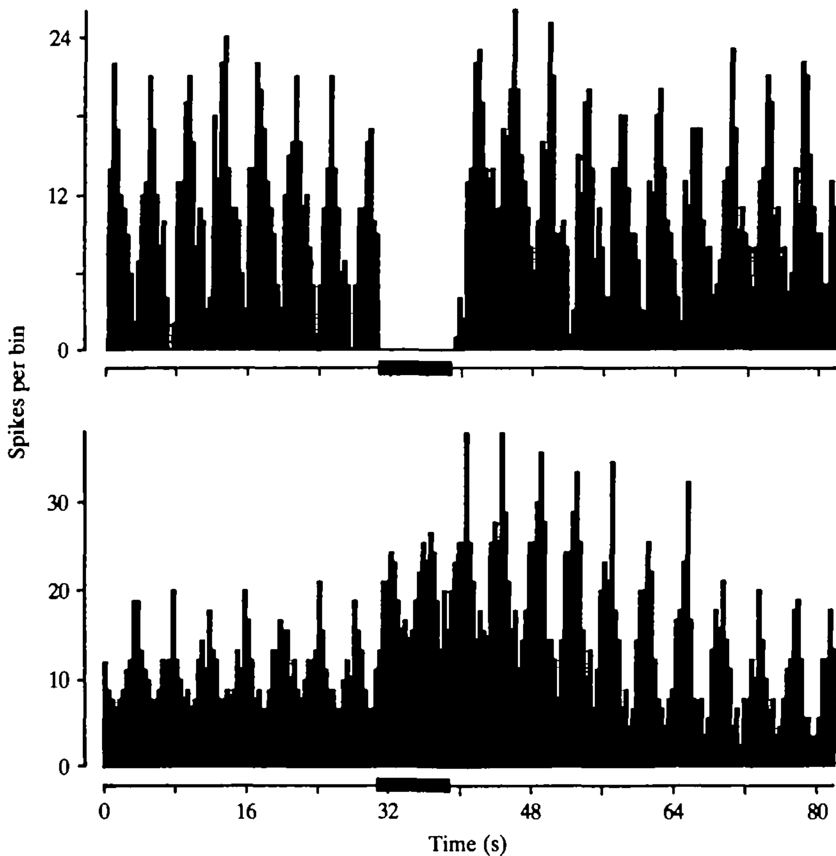

Fig. 8. Response of crista afferents to mechanical oscillations and efferent stimulation. PST histograms from two units, one inhibited (upper histogram) and the other excited (lower histogram) by efferent stimulation, showing their responses to imposed mechanical, sinusoidal oscillations of the statocyst in the pitch plane combined with a period of efferent stimulation. Bin width, 400 ms; efferent stimulus, 50-Hz pulses for 8·5 s; frequency of sinusoidal oscillation, 0·24 Hz, amplitude, 8°.

Multi-unit recordings

In some recordings, on the basis of differences in spike amplitude, the activities of two or three different units could be discerned and their individual responses to the same stimulus sequence observed. In such cases it was usually seen that the units differed in their response to the stimulus. Units in the same recording could differ in the amplitude of stimulus necessary to evoke a response, in the time taken to reach peak response, or in the time to recover from a stimulus, or even in the polarity of the response (i.e. one unit inhibited and another excited). In addition, during long duration stimuli, different units remained inhibited for different lengths of time.

DISCUSSION

These experiments have demonstrated that it is possible to increase or decrease the activity levels of afferent units in the angular acceleration receptor system of the

octopus by stimulating efferent fibres. Although the investigation has been concerned only with afferents from crista section C2 of the statocyst, it is likely that the other crista sections have similar responses as they are similarly innervated by efferents (Budelmann & Young, 1984; B. U. Budelmann, M. Sachse & M. Staudigl, in preparation). However, there are small morphological and physiological differences between the crista sections, particularly between the odd and even numbered sections (Williamson & Budelmann, 1985*b*) and it is possible that the relative proportions of inhibitory and excitatory efferents differ between crista sections.

The fact that almost all (93 %) of the afferent units recorded from showed a response to stimulation of the medial crista nerve is not surprising, since the vast majority of the axons (75 %) in the nerve are believed to be efferents (B. U. Budelmann, M. Sachse & M. Staudigl, in preparation). In addition, the efferent fibres form a plexus that runs beneath the crista (Young, 1960; B. U. Budelmann, M. Sachse & M. Staudigl, in preparation) and so it is likely that a single efferent fibre makes contact with more than one afferent unit.

In the vertebrate vestibular system the percentage of efferent fibres is much smaller. Only 8 % of the fibres in the vestibular nerve are estimated to be efferent in the monkey (Goldberg & Fernandez, 1980) and a figure of 18 % has been suggested for the frog (Gribenski & Caston, 1974). The influence of these few fibres can be widespread, with 80 % of the vestibular afferent units in the frog being influenced by efferents (Rossi, Prigoni, Valli & Casella, 1980) and 77 % in the squirrel monkey (Goldberg & Fernandez, 1980), although only 8 % of the frog semicircular canal afferents are influenced by the activation of efferents (Dieringer, Blanks & Precht, 1977).

In octopus the commonest effect of the crista efferents was an inhibition of the activity of the afferent units (e.g. Fig. 1) and this has also been found to be the most widespread effect seen in the vertebrate semicircular canal system (Scala, 1965; Dieringer *et al.* 1977). However, recent work has shown that there can also be an excitatory efferent effect in the vertebrate system, of a type similar to that reported here (Hartman & Klinke, 1980; Rossi *et al.* 1980).

The method of stimulation used in the present experiments to activate the fibres of the medial crista nerve is likely to have stimulated a large number of efferent fibres. Since no distinct amplitude threshold was found for the onset of an efferent effect, it is probable that the increase in response, seen with increasing stimulus amplitude, was due to the recruitment of more efferent fibres. Thus, since the recordings were from single units, multiple efferents innervate a single afferent unit and this is in agreement with the morphological findings of B. U. Budelmann, M. Sachse & M. Staudigl (in preparation). Further, although increasing the stimulus amplitude was never seen to change the polarity of the response, i.e. inhibitory to excitatory or *vice versa,* it is possible that both inhibitory and excitatory influences impinged on the same afferent unit. This could explain the large post-stimulus increase in activity seen after both inhibitory and excitatory responses to stimulation (Figs 4, 6). If this post-stimulus increase had only occurred in units showing an inhibitory response then one could envisage this as a post-stimulus inhibitory rebound, perhaps due to the rebound of the suppressed generator potential. However, since it also occurred after an excitatory response (Fig. 6), it is likely that during the stimulus there was, in addition to the overt

excitatory response, a level of inhibition present and that at the end of the stimulus this was released and either the excitatory effect more obviously expressed or the inhibitory rebound summed with the excitation to produce an additional increase in activity.

The view that both inhibitory and excitatory efferents exert an influence over the afferent responses would also explain the large variation in response time constants observed, especially the post-stimulus recovery times. Here, each response would be a mixture of influences, with the final effect being determined by the relative number of inhibitory and excitatory efferents that were activated by the stimulating electrode, and the relative strengths of the synaptic contacts of the efferents upon the afferent unit. The fact that the inhibitory response was encountered more often than the excitatory one suggests that there are more inhibitory efferents present in the nerve, or that they were preferentially activated, or that they are more effective.

Further evidence to support this view of the afferents being dually innervated by inhibitory and excitatory efferents comes from the results of the long stimulus duration experiments. In responses where an initial inhibitory effect was seen, this inhibition was gradually replaced, within 4–33 s, by an excitation that could excite the unit's activity to above the pre-stimulus level. The overall response observed could therefore have been due to a weakening of the inhibition, perhaps due to synaptic fatigue, and/or to a steady increase in effectiveness of the excitation upon the same receptor unit. The latter would suggest that excitation and inhibition have different time constants; this would also contribute to the variability of response time constants seen. Since a plateau level was reached during long duration stimulation of units showing an excitatory response, it is clear that the effectiveness of this excitatory type of efferent does not diminish with time in the same way as the inhibitory influence.

Although in mammals the vestibular efferents are believed to originate bilaterally from an area near the vestibular nucleus (Gacek & Lyon, 1974; Goldberg & Fernandez, 1980), in octopus the efferents stem from at least two different areas of the brain, the pedal lobe and the magnocellular lobe, with very little contralateral crossover (Young, 1971; Budelmann & Young, 1984). These two lobes have been assigned different functional properties, the former being a lower motor centre and the latter a complex relay centre involved in organizing escape reactions (cf. Wells, 1978), and it is tempting to consider that the two types of efferents, excitatory and inhibitory, might arise separately from these different areas in the brain.

It is not yet clear why, in some cases (Fig. 2), the applied stimulation was less effective at shock frequencies greater than 125 Hz. The antidromic firing seen in some units indicated that they could follow stimulation, one-to-one, up to at least 200 Hz, and although some small efferent fibres could have different characteristics, it seems unlikely that this effect is due to a limitation in spike conduction. It is more probable that the high frequency failure of some cells is due to differences in the properties of their synaptic connections or of the postsynaptic cells. It has been shown for both the statocyst macula (Colmers, 1977) and the crista (B. U. Budelmann, M. Sachse & M. Staudigl, in preparation) that the efferents make synaptic contacts with the hair cells and/or with the first order afferent neurones. This difference in target cell could be responsible for the difference in frequency response. In addition, there are three types of ventrally polarized hair cells in crista section C2, the 'large hair cells', the 'fairly

large hair cells' and the 'small ventral hair cells' (Young, 1960; Budelmann, 1977), and two types of first order afferent neurones (B. U. Budelmann, M. Sachse & M. Staudigl, in preparation); these could also have different properties and hence different responses to the efferent innervation.

There exists the possibility that the effects here described were not, or only partially, due to neuronal interactions within the crista epithelium. An alternative view is that the effects could have been due to the activation of muscle fibres in the wall of the statocyst sac if these were innervated from the crista nerves. Thus, a contraction of such fibres could deform the shape of the statocyst sac and hence produce a fluid movement relative to the crista that, depending on its direction, could excite or inhibit the crista hair cells. Young (1960) has reported the presence of thin muscle fibres in the statocyst wall. However, attempts to repeat this observation using a variety of light and electron microscopic techniques (R. Williamson & M. Schiwek, unpublished) have not indicated the presence of muscle fibres. Even if muscle fibres were to be present in the statocyst wall it seems unlikely that such an efferent system, acting through small displacements, would be effective, especially during fluid movements resulting from external circumstances, e.g. the animal's own movements.

Another possibility is that these efferent effects were due to the antidromic stimulation of the afferents. This is unlikely to be the case for a number of reasons. Firstly, all of the receptor units here examined were ventrally polarized and therefore first order afferent neurones and not the axons of hair cells whose membrane potential might be influenced by an antidromic spike. Secondly, none of the afferents included in the analysis were themselves antidromically activated during the recording sequence. Thirdly, afferents from crista section C2 which run in the anterior crista nerve (see Fig. 1, Williamson & Budelmann, 1985*a*), which was not electrically stimulated, showed similar changes in activity during the stimulation of the medial crista nerve. This last point supports the hypothesis (Young, 1960; B. U. Budelmann, M. Sachse & M. Staudigl, in preparation) that the efferents from the medial crista nerve cover the entire C2 crista section.

Although the functional significance of the statocyst efferent system is not yet known, its operation is likely to be similar to that of the vertebrate semicircular canal efferents where a variety of functional explanations have been put forward (reviewed by Klinke & Galley, 1974; Goldberg & Fernandez, 1975). In particular the feed-forward mechanism, proposed for both the lateral line (Russell, 1971) and the vestibular organ (Klinke & Schmidt, 1968), is of interest. The octopus employs two different forms of locomotion, slow crawling over the sea floor and fast, jet-propelled swimming. It has been shown that the angular acceleration receptor system is of dual sensitivity (Williamson & Budelmann, 1985*b*), presumably to cope with these two very different forms of locomotion. However, it is clear that an efferent system capable of suppressing the most sensitive inputs during a fast movement where they are likely to be swamped, and enhancing the gain of the least sensitive units during a slow movement, would be of great advantage. A similar type of dynamic adjustment of the afferent gain has been proposed for the monkey vestibular system (Goldberg & Fernandez, 1980) where the efferents are mainly excitatory.

The afferents of the octopus angular acceleration system are, in addition, sensitive to linear accelerations (Budelmann & Wolff, 1973; Williamson & Budelmann, 1985*a*)

and another function of the efferents could be to compensate for the changes in the afferent activity that occur when the animal changes its orientation with respect to gravity.

In conclusion, the octopus angular acceleration receptor system is innervated by efferent fibres which have inhibitory and/or excitatory effects upon the afferents. Thus this system continues to show strong parallels with the vertebrate semicircular canal system in both its afferent and efferent innervation and merits further investigation not only as an analogous receptor system displaying a high degree of evolutionary convergence but also for the light it may shed on the workings of the vertebrate receptor system.

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