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RESPONSES IN THE RAT THALAMUS TO WHISKER MOVEMENTS PRODUCED BY MOTOR NERVE STIMULATION

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SUMMARY

1. The effect of electrical stimulation of the motor nerve supplying the whiskers on the activity of single cells in the vibrissal region of the ventrobasal complex of the thalamus has been studied in rats under urethane anaesthesia.

2. The stimulation caused protraction of the ipsilateral whiskers. 60% of the cells which fired to mechanical movements of the whiskers were found to respond to this electrical stimulus with 1–2 impulses at short latency (average 7·7 msec), provided the stimulus was sufficient to move the whiskers.

3. When the moving whiskers hit a barrier, 92% of the cells responded to the stimulus. The most effective position of the barrier was in front of the whiskers, although other positions often produced a response as well. Static displacement of the whiskers, particularly in the forward direction, could abolish the response or increase its latency.

4. The following-frequencies for these cells were 5–10 stimuli/sec. Combinations of electrical stimuli with mechanical ramp movements of the whiskers showed that similar recovery times followed both types of stimuli.

5. These results are compared with those reported from studies in the afferent nerve fibres after electrical stimulation of the motor nerve and also with responses in the thalamus following mechanical movements of the whiskers. The possible importance of the latency of these sensory responses is considered.

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INTRODUCTION

The importance of whiskers in producing a sensory input for rats has been indicated in a number of studies using a variety of techniques (Vincent, 1912, 1913; Welker, 1964, 1968, 1971; Davidson, 1965; Nord, 1968; Zucker & Welker, 1969; Waite, 1973*a*). The types of responses recorded in the vibrissal region of the ventro-basal complex of the thalamus following mechanical movements of the whiskers have been described in a preceding paper (Waite, 1973*b*). Those responses were all the result of mechanical movements of different directions, amplitudes and velocities on individual whiskers. When exploring, a rat protracts and retracts all the whiskers in synchrony. In an attempt to approximate more closely to this natural movement, the motor nerve supplying the whiskers was stimulated electrically. Although this synchronous stimulation of all the motor nerve fibres on one side gives a far from natural movement, this study is of interest for two reasons. The first reason is to compare the types of responses found with electrical stimulation with those following mechanical movements and to look at the effects of barriers placed near to the moving whisker. The second is to compare the responses in the thalamus with those found by Zucker & Welker (1969) who used a similar type of stimulation in their study of cells in the trigeminal ganglion. While 50% of these afferent cells were excited only by the movement of the whiskers produced by the stimulus, 90% responded if the whiskers struck a barrier.

METHODS

The experiments were performed on twenty-four albino rats, of either sex, weighing between 200 and 250 g. They were all anaesthetized with urethane (1·4 g/kg, I.P.). The details of the preparation have been described previously (Waite, 1973*a*); the same whisker nomenclature is also used.

In addition to the craniotomy, a dissection was performed to expose about 1 cm of the buccal branch of the facial motor nerve on the right side. Care was taken to ensure that the incision made in the cheek did not extend into the vibrissal area. The nerve was ligatured and cut close to the animal's ear. When the rat had been set up in the head holder, a paraffin pool was formed with the skin of the cheek and the nerve mounted on silver stimulating electrodes. The nerve was stimulated by square-wave pulses (0·05 msec wide, 0–4 V amplitude) produced by an isolated stimulator (Devices, Ltd).

Recordings were made from single cells in the ventro-basal complex of the thalamus, as described by Waite (1973*b*). The effects of changes in the stimulus amplitude and repetition rate were studied. Also, the effect of a barrier, held close to the whisker whilst the motor nerve was stimulated, was investigated. The barrier consisted of a metal rod, mounted in a micromanipulator (Prior, Ltd) so that it could be positioned at any orientation perpendicular to the long axis of the whisker. In some cases, a whisker was also constrained by inserting it into a syringe needle attached to a mechanical vibrator (Waite, 1973*b*, stimulator C). In this way the

effect of static displacements of a whisker and combinations of mechanical movements and electrical stimulation of the motor nerve could be studied.

A rod barrier was initially placed in position just touching the front surface of the whisker, 1 cm from the whisker base, with the whisker at rest. It was then moved forwards in steps of 0·5 mm until it was 2–3 mm in front of the whisker, and then backwards in similar steps until it was pushing the whisker back by 3 mm. This procedure was repeated with the rod behind, above and below the whisker. In the alternative barrier situation, the whisker was inserted into the end of the syringe needle and was thus constrained on all surfaces. The needle tip was then adjusted so that it was at the whisker's rest position and 1 cm from the whisker base. It could then be moved forwards, backwards, upwards and downwards in similar steps as were used with the rod. At the end of each series of experiments on a particular cell, the whisker was plucked from its socket to see whether the receptor still responded to subsequent motor nerve stimulation.

RESULTS

General response characteristics

Either single or repetitive shocks to the motor nerve supplying the whiskers (at sufficient stimulus strength) caused protraction of all of the whiskers on the ipsilateral side; retraction was never produced. Although it was not possible to monitor the whisker displacement during a single twitch, the maximum displacement of the whiskers at different frequencies of stimulation was measured in some preliminary experiments. The displacement was measured under the microscope with a pointer mounted on a micromanipulator. A single stimulus caused a maximum whisker displacement of about 2 mm, measured at 1 cm from the whisker base. With repetitive stimulation, summation of the mechanical response occurred at frequencies between 20 and 40 Hz and a maximum displacement of 10–12 mm could be produced at about 200 Hz. All tetani were of 1·0 sec duration and the displacement was similar for all the large whiskers. A typical result is shown in Fig. 1.

Recordings were made from thirty-eight thalamic cells which responded to mechanical movement of a particular whisker. 60 % of the cells (twenty-three cells) were found to respond to a single electrical stimulus to the motor nerve provided it produced whisker movement. (No cells responded to an electrical stimulus to the motor nerve which was below threshold for movement of whiskers as seen under a microscope.)

The usual response to a single motor nerve stimulus was one impulse, the minimum latency for all the cells ranging from 5·2 to 13·4 msec (average 7·7 msec). The effect of increasing the stimulus voltage above the threshold for movement was to reduce the latency of this single impulse; only very occasionally were additional impulses produced at higher stimulus amplitudes. Fig. 2*a* is an example of a typical response of a cell at two different stimulus voltages while Fig. 2*b* shows a graph of the

average latency of response against stimulus voltage for the same cell. The responses from other cells gave similar curves. For all the cells, the change between the latency at threshold and the minimum latency ranged from 0·7 to 4·2 msec (mean 2·0 msec).

The remaining 40% of the cells (fifteen cells) could not be made to respond to either single or repetitive stimulation of the motor nerve however large the stimulus voltage. However, the majority of these (twelve

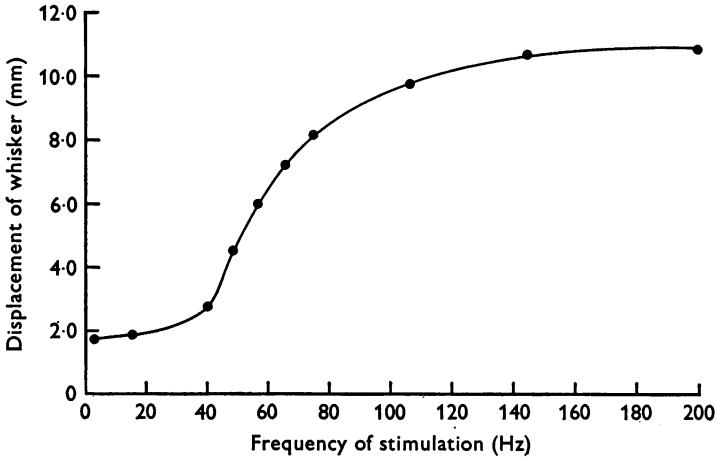

Fig. 1. Graph of the displacement of whisker B_1 measured at 1 cm from the whisker base (ordinate) against the frequency of electrical stimulation of the motor nerve to the whiskers (abscissa).

cells) did respond when a barrier was held near to one of the moving whiskers. The response in this case was similar to that described above, but will be considered in more detail in the section describing the effects of barriers.

Repetitive stimulation

The response to the second of a pair of motor nerve stimuli, or to later stimuli in a train, was identical to the first response (i.e. that described above) provided that the interstimulus intervals were greater than 150 msec (range 100–200 msec). At intervals between 50–150 msec, the cells did not respond to every stimulus and, at intervals below 50 msec, the cells only responded to the first stimulus in the pair or train. Thus the following-frequency for these cells was 5–10/sec. It should be noted that at this frequency, each stimulus to the motor nerve appeared to produce a separate twitch response of the whisker musculature (Fig. 1). Second or subsequent stimuli never evoked more impulses than did the first stimulus, nor were previously unresponding cells recruited.

Combined electrical and mechanical stimulation

All thirty-eight cells responded to mechanical movements of a particular whisker (this was the means of identification). To compare the response to mechanical movement with that produced by electrical stimulation of the motor nerve, forward ramp movements of 2 mm amplitude (at 1 cm from the whisker base) were used, with the fastest velocity available (0·2 m/sec). The response was similar to that described before (Waite, 1973*b*) and typically consisted of 1–3 impulses at a mean latency of 5–6 msec.

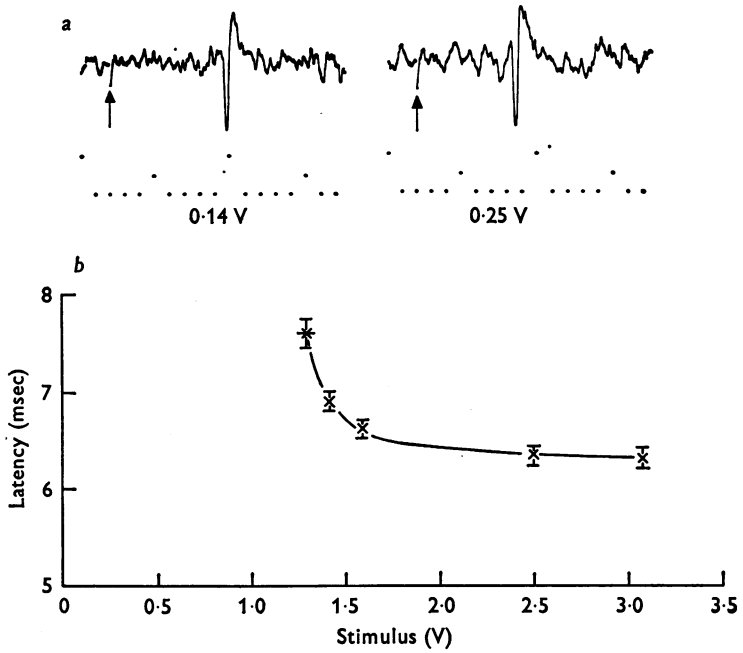

Fig. 2*a*. Photographs of the response of a cell to stimulation of the motor nerve at two different voltages (given below). In each case the arrow marks the time of stimulation and the lower trace gives the time scale in msec. The cell also responded to mechanical movements of whisker E_3.

b, graph of the mean latency of the response (ordinate) against the stimulus voltage (abscissa) for the same cell as in *a*. The bars indicate ± S.E. The asterisk marks the voltage producing a threshold response from the cell.

When the responses to both the mechanical movement and the electrical motor nerve stimulus had been recorded separately, the effect of giving both stimuli at various intervals was studied. The electrical motor nerve stimuli were given at different intervals ranging from 150 msec before to 150 msec after the start of the ramp movement. Typical examples are shown in Figs. 3 and 4. Fig. 3 shows photographs of the response of a cell

which fired to both the electrical motor nerve stimulus and the ramp movement, while Fig. 4 is a graph plotted from the results of a cell which only fired in response to the ramp movement.

For all cells, when the electrical motor nerve stimulus preceded the ramp by an interval less than 25–30 msec, the ramp response was abolished. When the separation between the two stimuli was increased above 30 msec,

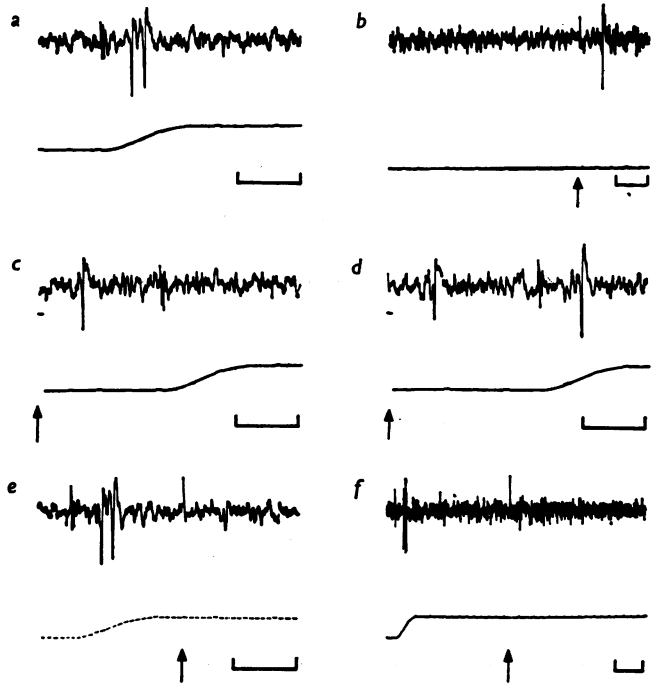

Fig. 3. Photographs of the response of a cell, driven by whisker E_3, to both ramp movement (amplitude 2 mm) of the whisker and electrical stimulation of the motor nerve. The ramp movement is shown on the lower trace and the arrows mark the times of electrical stimulation.

a, Ramp movement alone; *b*, electrical stimulation alone; *c*, electrical stimulation 23 msec before ramp movement; *d*, electrical stimulation 28 msec before ramp movement; *e*, ramp movement 25 msec before electrical stimulation; *f*, ramp movement 80 msec before electrical stimulation. Time scale: bar = 10 msec.

the ramp response appeared, but at a longer latency and lower probability of firing. Recovery was complete with intervals of 120–150 msec. This interaction occurred even for cells which did not fire an impulse in response to the electrical stimulus of the motor nerve alone. When the ramp preceded the electrical motor nerve stimulus, the inhibitory effect lasted even longer; the response to electrical motor nerve stimulation was usually

abolished for 80 msec after the ramp and did not show complete recovery even at 150 msec. For some cells, at very short intervals between stimuli (e.g. Fig. 4), a decrease in latency of the ramp response occurred, although no other sign of facilitation was seen.

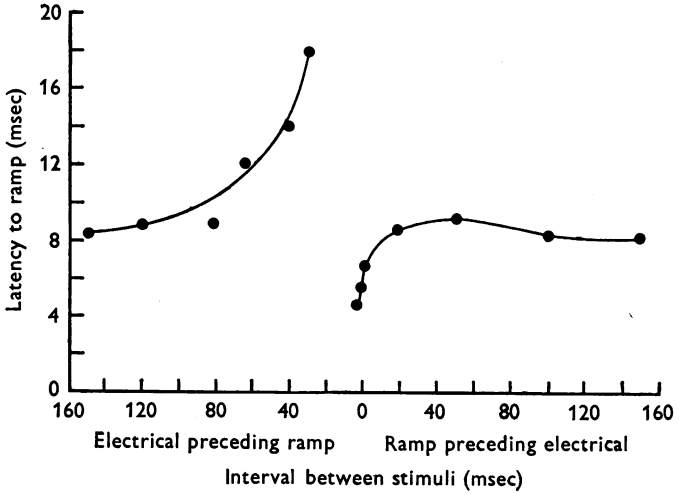

Fig. 4. Graph showing the effect of electrical stimulation of the motor nerve and ramp movement of whisker D_1 at different interstimulus intervals (abscissa) on the latency of the response of a cell to the ramp movement (ordinate). The ramp response is abolished when the ramp movement is preceded by electrical stimulation at intervals of 3–30 msec, even though this cell did not fire in response to the electrical stimulation.

Effects of barriers and constraints

The effect of a barrier placed close to, or just touching, a whisker during stimulation of the motor nerve was studied on thirty-one of the thirty-eight cells. Sixteen of these were cells which reponded to stimulation of the motor nerve alone, while the other fifteen gave no response. The effect of the barrier depended on whether or not the cell responded to the motor nerve stimulus alone.

Cells responding to motor nerve stimulation alone

The responses of the majority of the cells in this group (thirteen out of sixteen cells) were not modified by the barrier provided that it did not alter the whisker's rest position. For the three cells whose responses were affected by the presence of the barrier, the responses of two were abolished by certain barrier positions (one when the rod was behind, the other with the rod behind, above and below). The third cell showed a reduction in latency of its response when the barrier was held just off the front surface

of the whisker. This is shown in Fig. 5. An unusually large decrease in latency with increasing electrical stimulus amplitude occurred, but the barrier caused a further decrease. It should be noted that responses from other cells which showed as large a reduction in latency with increasing stimulus strength were not modified by a barrier.

Barriers which changed the rest position of a whisker altered the latency of the response of eleven of the sixteen cells; the responses of the remaining

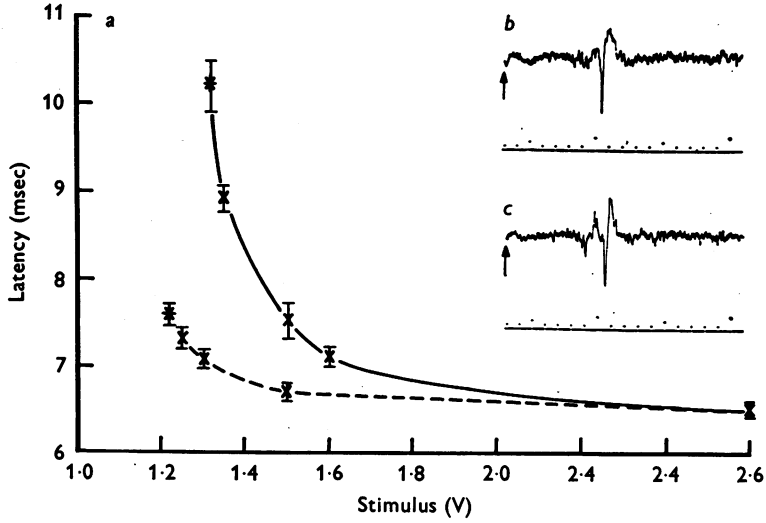

Fig. 5*a*. Graph showing the mean latency of the response of a cell to electrical stimulation of the motor nerve (ordinate) against the stimulus voltage (abscissa). Continuous line, latencies with the whiskers free; dashed line, latencies with a barrier in front of whisker D_1. Bars indicate ± S.E. and asterisks the threshold voltages in each case.

b and *c*, Photographs of the response of the cell from which graph *a* was constructed. In each case the time of stimulation is marked by an arrow and the lower trace indicates the time scale in msec.

b, Whiskers free, stimulus 1·5 V, latency 7·3 msec; *c*, barrier in front of whisker D_1, stimulus 1·25 V, latency 7·5 msec.

five cells were unaffected. For the eleven cells there was always a decrease in latency with backward displacement (mean decrease, 0·4 msec/mm) and an increase with forward displacements (mean increase, 0·4 msec/mm).

The response of half of the cells was abolished by large static displacements of more than 3 mm. Forward displacements were particularly effective in abolishing the response although some responses were abolished by displacements in other directions as well.

Cells which did not respond to motor nerve stimulation alone

80 % of the cells in this group (twelve out of the fifteen cells) which did not respond to motor nerve stimulation alone, could be made to respond by placing a barrier in certain positions close to the whisker driving the cell. The most effective barrier position, which evoked a response in eleven of the cells, was in front of or just touching the front surface of the whisker. (The other cell had an unusual long latency response which will be described later.) It should be remembered that the electrical motor nerve

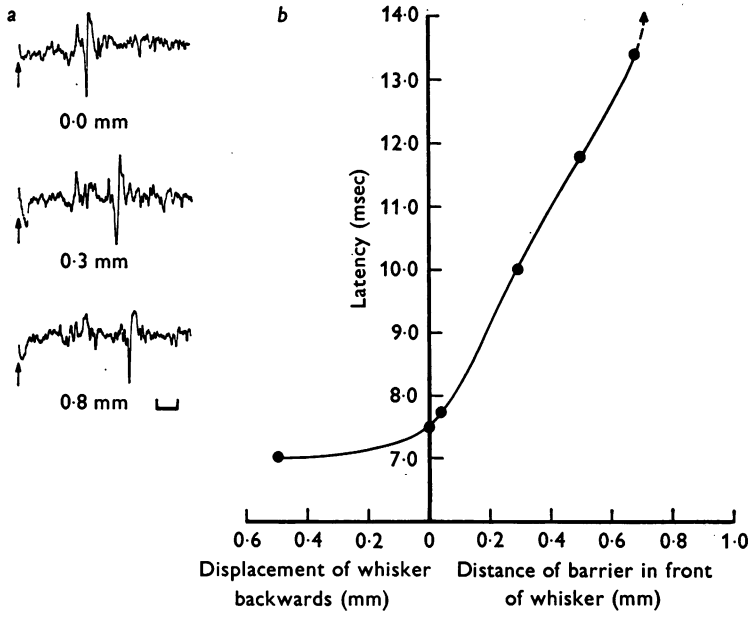

Fig. 6*a*. Photographs of the response of a cell to motor nerve stimulation at three positions of a barrier (shown below) in front of whisker D_4. In each case, the arrow marks the time of stimulation. Time scale, bar = 2 msec.

b, Graph of the mean latency of the response to motor nerve stimulation (ordinate) for the same cell as in *a* against the distance of the barrier from the whisker's rest position (abscissa).

stimulation caused a predominantly forward movement of the whiskers. However, about half of the cells also fired when the barrier was placed on other surfaces of the whisker, as well as in front of it.

The response in the presence of the barrier was similar to the responses described above for cells which fired to the motor nerve stimulation alone. It was usually a single impulse with mean minimum latency of 6·2–10·4 msec (average 7·6 msec). As in the group above, provided the barrier did not

alter the whisker's rest position, most cells showed no modification in the number of impulses, or latency of response with different barrier positions. However, there was one exception to this, shown in Fig. 6. This cell showed a change in latency with different positions of the barrier in front of the whisker. It can be seen that the latency is proportional to the distance of the barrier in front of the whisker between 0·1 and 0·7 mm in front. The inverse gradient from this graph is 0·109 m/sec, and in this particular case the barrier was 5 mm from the whisker base. This figure would approximate to the velocity of forward movement of the whisker if one assumes that the velocity forwards is constant (at least between 0·1–0·7 mm forwards) and that the latency change is due only to the different distance of whisker travel (i.e. that the effective stimulus is the same at each barrier position).

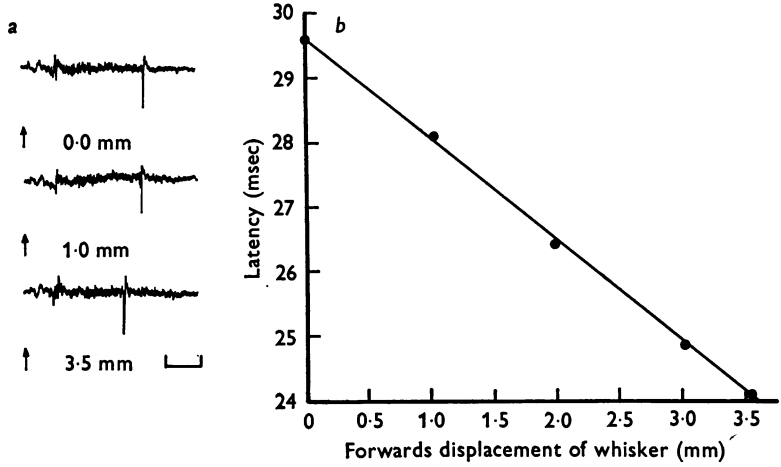

Fig. 7*a*. Photographs of the response of a cell to motor nerve stimulation at three displacements (given below) of whisker C_4 in front of its rest position. In each case the arrow marks the time of the stimulus. Time scale, bar = 10 msec.

b, Graph of the mean latency of the response to motor nerve stimulation (ordinate), for the cell shown in *a*, against the forward displacement of the whisker (abscissa).

Barriers which altered the rest position of a whisker caused a similar change in latency in this group of cells, as already described for the other group. Latencies were reduced by backward displacements and increased by forward displacements while large amplitude displacements, especially in the forward direction, abolished the response.

One cell in this group showed an unusual response, as can be seen in Fig. 7. This cell only fired when whisker C_4 was held at rest or displaced

forwards; the response was a single impulse at a latency between 24 and 29 msec (excluded from the previous calculation of mean minimum latency). This latency was proportional to the forward displacement of the whisker.

It was hoped that it would be possible to correlate any directional sensitivity exhibited by a cell in response to mechanical movement with the effects of barriers placed in different positions during electrical stimulation of the motor nerve. The cells here showed a similar range of directional sensitivities to that already described for thalamic cells (Waite, 1973*b*). However, no correlation between this sensitivity and the presence of a barrier just touching one surface of the whisker was apparent. Nor was there any obvious correlation between the mechanical direction sensitivity and the direction of static displacements which modified the latency of the response or abolished the firing.

Effect of plucking the whisker

Plucking the whisker out of its socket was tested on twelve of the cells which responded to the motor nerve stimulus alone. This was found to abolish the response in nine of these cells but did not modify the response of the remaining three. There was no other difference in the response characteristics of these cells. For the nine cells whose response was abolished, three could still be made to fire by a hard squeeze or prod to the socket area.

DISCUSSION

The responses found in the thalamus in this study are very similar to those reported by Zucker & Welker (1969) for the afferent nerve cells in the trigeminal ganglion. The latter workers found that about 50% of the afferent units responded to whisker protraction without any barrier present and a similar proportion, 60%, was found here. Our finding that 92% of the thalamic cells responded if the moving whiskers struck a barrier is also very similar to their figure of 90%. The slightly higher percentages in the thalamus may well be due to the small sample of cells in this study, or may reflect a slight convergence.

There is a good indication that some ventro-basal cells respond to 'natural' whisker movements from the increase in background activity observed under trilene anaesthesia (Waite, 1973*a*) and with the occasional spontaneous whisker movements which occur under barbiturate or urethane anaesthesia. However, it is not known whether only half the cells respond to natural movements (unless the whiskers strike an object) or whether this figure is due to the unnatural, synchronous nature of the stimulation used. In natural movements, as in those produced here, all

the whiskers appear to move together, the amplitude of natural movement is usually larger than that produced by a single electrical motor nerve stimulus. When a similar magnitude of movement to that occurring naturally was produced by tetanic stimulation, the cells responded in the same way as for a single stimulus and no previously unresponding cells were recruited. However, this may be an artifact of the anaesthetic. The recovery times found in this study (100–200 msec), although comparable to values reported by other workers for responses in the ventro-basal complex in anaesthetized animals, are likely to be much longer than in unanaesthetized animals (Poggio & Mountcastle, 1963; Angel, 1963). If this is the case, then the lack of responsiveness of certain cells, even during tetanic stimulation, may be due to the depressive effect of the anaesthetic. Nevertheless, the percentage of unresponding cells in the thalamus is so similar to that in afferent nerve cells, where any modification by anaesthetic is unlikely, that it may well represent the situation in the normal animal.

Why some cells should respond to a single electrical stimulus alone (i.e. without a barrier) and others not, is uncertain. The ability to respond was not related to the size or position of the particular whisker driving the cell. It could perhaps be due to different kinds of receptors, or their different positions. Different sorts of endings certainly exist in hair follicles (Andres, 1966; Patrizi & Munger, 1966) and plucking the whisker out of its socket did not always abolish the responses. Another possibility is that the difference is related to the critical velocity needed to fire the receptor. The calculation of the velocity of movement forwards (109 mm/sec) for the one cell (Fig. 6) which only fired in the presence of a barrier and whose latency did vary with the barrier position in front of the whisker, is higher than the critical velocities found in the thalamus with mechanical movements (highest 20 mm/sec, Waite, 1973*b*). However, it is below the average velocity needed to excite the high velocity threshold units (mean 130 mm/-sec) in Zucker & Welker's study (1969). Perhaps the cells which did not respond to the motor nerve stimulation alone required high critical velocities which were not reached during a twitch. If this were the case, then the 30 % of the cells which only responded when a barrier was present would compare favourably with the 28 % of the afferent cells which had medium and high velocity thresholds (Zucker & Welker, 1969).

Zucker & Welker (1969) were able to produce retraction, as well as protraction, of the whiskers, but this was not found possible here. They write that 'comparison of the unit-activating positions of the barrier (in whisking vibrissae) and of the stimulating probe (in resting vibrissae) revealed that for 80 % of the units these positions were the same in the two conditions' (p. 149). However, no relation between effective barrier positions and

directional sensitivity to mechanical movements was found here. Barriers in front of the whisker were effective on all except one of the cells, irrespective of the mechanical direction sensitivity of the cell. Perhaps if retraction could also have been produced, some correlation would have been apparent.

The latency of the responses was usually unaffected by the exact position of the barrier. However, static displacements forwards increased the latency while backwards displacements decreased it and this presumably was related to the direction of the induced movement. For instance, the latency might be increased with forward displacements because the muscle had to contract further before starting to move the deflected whisker. Large amplitude static displacements (more than 3 mm), especially in the forward direction, often abolished the response; a similar effect occurred when mechanical movements were superimposed on large static displacement (Waite, 1973*b*).

The responses produced by electrical motor nerve stimuli and mechanical movements were also similar in a number of other respects. The response to motor nerve stimulation was typically only a single impulse while ramp movements of similar amplitudes could produce 1–3 impulses (under urethane anaesthesia). Although the main muscles which move the whisker follicles are striated (Vincent, 1913) no details of their twitch characteristics are known. Since no measurement of the velocity of forward movement could be made during a single twitch, no conclusions can be drawn about the relative efficacy of the two forms of stimulation. The experiment with combined ramp movements and electrical stimulation showed that similar recovery times follow both types of stimuli although recoveries after mechanical movements were somewhat longer. It is also interesting that the electrical stimulus could abolish the response to the ramp movement, without itself producing a response in the thalamic cell. The electrical stimulus may, in this case, produce some central inhibitory effect or it may be that the contraction of the whisker musculature modifies the receptor sensitivity.

The average minimum latency to electrical stimulation was 7·7 msec compared with 5·4 msec for ramp movements. This gives a time of 2·3 msec for conduction along the motor nerve fibres and excitation of the muscle, assuming that the receptors are excited by similar displacements of the whiskers in each case. Thus it is unlikely that the responses are the result of direct electrical excitation of the afferent endings. Further evidence in support of this is that thalamic responses never occurred below the threshold for movement. Increases in stimulus strength reduced the latency of responses but seldom increased the number of impulses per response. The lack of change in the number of impulses may be an artifact

of the anaesthetic and it is hoped that this point will be clarified in future studies. It is also possible that the latency *per se* provides the rat with useful information. For the auditory system, the latency in many central auditory neurones has been found to be highly correlated with certain stimulus parameters (Aitkin, Anderson & Brugge, 1970). For the somatosensory system, reductions in latency with increasing stimulus strength are well known (Rose & Mountcastle, 1954; Mountcastle, Davies & Berman, 1957; Mountcastle & Powell, 1959; Towe & Kennedy, 1961). With mechanical ramp movements of the whiskers, a reduction in latency occurred with increasing velocities of movement (Waite, 1973*b*). The latency shift found here with motor nerve stimulation is presumably mainly due to the recruitment of additional motor units which would increase both the amplitude and velocity of the whisker movement. If the normal rat is able to correlate motor activity producing whisker movements with sensory vibrissal activity, then the timing of the impulses in the ventro-basal complex may well carry information about the whisker position or velocity of movement.

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