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THE RESPONSES OF CELLS IN THE RAT THALAMUS TO MECHANICAL MOVEMENTS OF THE WHISKERS

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SUMMARY

1. The responses of single cells to mechanical movements of individual whiskers have been recorded from the ventro-basal complex of the thalamus, in rats under urethane or barbiturate anaesthesia.

2. With ramp-shaped displacements of a whisker above a critical velocity, the cells gave a short latency response of 1–5 impulses, while with sinusoidal movement (1–35 Hz) they usually responded with 1–2 impulses per cycle.

3. The cells did not respond to maintained deflexions of a whisker. Small static displacements did not modify the response to a superimposed movement; larger static displacements reduced or abolished the response.

4. Three-quarters of the cells were found to be particularly sensitive to movements in one quadrant (90° or less). For any one cell, there was no obvious relationship between the most sensitive direction and the position of the whisker on the face.

5. The ramp amplitude appeared to have little effect on the response. However, increases in ramp velocity decreased the response latency and, in some cells, increased the number of impulses per ramp.

6. Other studies have shown that most afferent nerve fibres from whiskers give slowly adapting responses and the possible modification of these thalamic responses, by anaesthesia, is discussed.

INTRODUCTION

The large number of afferent nerve fibres supplying a rat's whisker (Vincent, 1913) as well as the relatively large vibrissal representation in the trigeminal nucleus (Nord, 1968), thalamus (Davidson, 1965; Waite, 1969) and cortex (Welker, 1968, 1971) suggest that the whiskers provide an important sensory input in rats. Behavioural studies indicate their involvement in tactile exploration of the rat's surroundings and roughness discriminations (Vincent, 1912; Welker, 1964).

A single-unit in the trigeminal ganglion (Zucker & Welker, 1969) on cells which responded to whisker movements, concluded that these afferent neurones were capable of coding 'peripheral location, deflexion direction, onset, termination, amplitude, velocity, duration, repetition rate and temporal pattern' of a mechanical movement. Half of the cells gave slowly adapting responses to movements of a particular whisker in a certain, sensitive direction; the other cells showed no direction sensitivity and varying degrees of adaptation. At the trigeminal nucleus Nord (1968) reported that the responses from different cells varied greatly in receptive field size (one–eighteen whiskers), direction sensitivity and adaptation rates. However, at the cortical level, Welker (1971) found that cells were activated by relatively high velocity deflexions of single whiskers. The cells did not respond readily to slow movements, nor did they show the direction sensitivity reported in the afferent nerve fibres.

There have been several studies on whisker responses in cats and the results are, for the most part, similar to those in rats. However, the studies in cats have been limited to the afferent nerve fibres and trigeminal ganglion (Fitzgerald, 1940; Kerr & Lysak, 1964; Hahn, 1971) and the trigeminal nucleus (Gordon, Landgren & Seed, 1961; Kruger & Michel, 1962; Eisenman, Landgren & Novin, 1963; Darian-Smith, Rowe & Sessle, 1968).

This study describes the types of responses found in the ventro-basal complex (VB) of the rat's thalamus following mechanical movements of single whiskers. The majority of cells were studied with ramp-shaped displacements and the effects of changing the static position of the whisker and the direction, amplitude or velocity of the ramps is described. The results are compared with those reported at lower levels and in the cortex. A short report of this study has already appeared (Waite, 1972).

METHODS

The experiments were performed on fifty-one albino rats of either sex, anaesthetized with either urethane (ethyl carbamate) or pentobarbitone sodium. The details of the preparation have been described in a previous paper (Waite, 1973). In a few experiments the anaesthetic was changed from barbiturate to urethane by giving small doses of urethane as the barbiturate level became lighter. For referring to a whisker, the same nomenclature as given in the previous paper was used.

Recording. Recordings were made with glass micro-electrodes filled with an 18% solution of NaCl (2 μm tip, 1–4 MΩ impedance). The micro-electrode was located in the vibrissal region of VB as described in the previous paper. Recordings were made from single units, as judged by the usual criteria of spike amplitude and shape (Mountcastle, Davies & Berman, 1957). The extracellulary recorded potentials were fed into an F.E.T. high impedance input stage and then amplified and displayed by conventional techniques.

Stimulation. Three types of mechanical stimulators were used. The first two (*a*

and *b*) were used in the initial experiments of thirty-five cells (twelve with *a*, twenty-three with *b*) for the effects of static displacements of a whisker and changes in direction of movement. The third (*c*) was used in the later experiments on direction sensitivity and the effects of changing the amplitude and velocity of movement (thirty cells).

(*a*) This stimulator (Stephen, 1969) consisted of a d.c. motor connected to a cam which moved a lever to give a sinusoidal variation in the displacement of its tip (peak to peak amplitude, 3 mm; range, 0·5–40 Hz). The whisker was held in a clamp at the tip of the lever. The stimulator could be rotated through 150° so that the whisker could be moved in different directions. The movement was monitored by a capacity gauge (Cambridge & Haines, 1959) and a trigger pulse was produced every cycle by a photocell and a shutter on the cam.

(*b*) This was similar to *a* except that the cam was modified to produce ramp-shaped displacements of the lever (amplitude at lever tip, 5 mm; range 0·001–0·5 m/sec). One cycle consisted of a ramp displacement followed by a sustained deflexion lasting 2·5 × the ramp duration, and then a similar return ramp and sustained deflexion. The whisker was held by inserting it into a no. 18 hypodermic syringe needle, mounted on the end of the lever. This prevented the pulling of the skin at the base of the whisker which had occurred with the clamp on the first stimulator. The stimulator could be rotated through 180° and had a capacity gauge transducer and trigger pulse arrangement similar to stimulator *a*.

Both these stimulators produced a repetitive movement; they were also of fixed amplitude. A further disadvantage was that the motor speed was too variable for them to be useful in a study of the effects of different velocities.

(*c*) The third stimulator consisted of a Ling–Altec vibration generator (V 47; 30 Ω model) which moved a lever, again carrying a syringe needle. Movements were monitored by a photocell and a piece of graded density film rigidly fixed to the lever. The transducer was linear for movements up to 3 mm and the calibration was checked regularly. The lever was moved with ramp-shaped displacements. Tip amplitudes of more than 2 mm were seldom used and, for the movements used, the rise time (10–90 % total amplitude) for step-voltage inputs was proportional to the amplitude. For 2 mm 'steps' the rise time lasted 10 msec; this gave an upper velocity limit of 0·2 m/sec. The lowest velocity used was 1×10^{-3} m/sec (using a signal generator; Feedback, Ltd.). The vibrator could be rotated so that movements could be given at any angle to the horizontal. It was mounted on three lathe slides at right angles so that the lever could be lined up with the whisker.

For all stimulators, when a cell had been isolated, the whisker driving it was identified and its rest position marked with a pointer. The tip of the syringe needle (or clamp) holding the whisker was adjusted to be 1 cm from the whisker base (i.e. the skin surface) and all amplitudes and velocities given refer to movements at this point. The lever tip was also adjusted to be at the whisker's rest position and the long axis of the lever was set perpendicular to the rat's sagittal plane.

Analysis. Photographic records were always taken as a check on the single unit and in some cases analysis was done by direct measurement from the photographs. In the experiments with stimulators *a* and *b*, spike distributions over 100 cycles were averaged on a C.A.T. 400 B (T.M.C.) computer and later analysed on a Linc-8 computer (Digital Equipment Corp.). With the third stimulator, averages of 10 or 100 responses were done on a Biomac 1000 (Data Laboratories Ltd.) and again analysed on a Linc-8.

RESULTS

General characteristics of the responses

Under urethane or deep barbiturate anaesthesia, the cells in the vibrissal region of VB were usually silent unless the whiskers were moved. With lighter levels of barbiturate there was often some spontaneous activity, usually in the form of short bursts of 3–9 impulses lasting 20–30 msec and with an inter-burst interval of approximately 200 msec. A typical example of this spontaneous activity from a group of cells is shown in Fig. 1*a*.

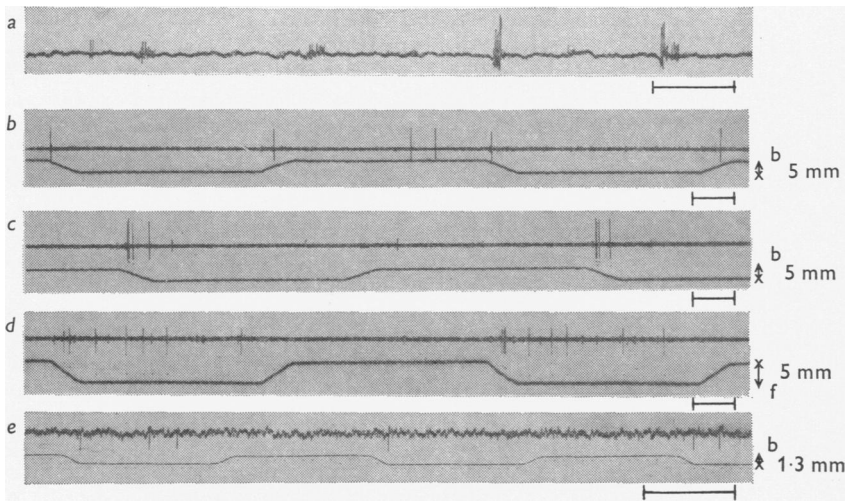

Fig. 1. Examples of the types of activity recorded from cells in VB responding to whisker movement (retouched).

a, Spontaneous activity from a group of cells in a rat under barbiturate anaesthesia.

b, *c*, *d*, *e*, The top trace in each pair shows the response of a cell to movement of a single whisker. The movement wave form is shown on the lower trace. In each case the whisker which was moved is shown at the side together with the direction and amplitude of the movement. x, whisker's rest position; *b*, backwards; *f*, forwards. *b*, *c*, *d* were recorded from animals under urethane and *e* under barbiturate. Time scale: bar = 100 msec.

Examples of the responses of four cells to movements of the whiskers are shown in Fig. 1*b–e*. The responses under either urethane (*b–d*) or barbiturate (*e*) were very similar. It can be seen that the responses are usually very rapidly adapting. For sinusoidal movements, each cell usually fired at only one part of the cycle, with 1 or 2 impulses. For ramp movements, a cell usually responded with 1–3 impulses per ramp in rats under urethane and 1–5 impulses per ramp with light barbiturate anaesthesia. Occasionally

less phasic responses, continuing after the ramp movement was over, could occur, but cells firing in this way were thought to be injured since they seldom responded consistently and their responses could seldom be recorded for long periods.

Under urethane, the receptive field of a cell was always localized to one whisker; movement of adjacent whiskers or the down hairs around the whisker did not fire the cell, unless the associated whisker was also moved. However, under light barbiturate anaesthesia, a cell which was giving spontaneous bursts of impulses could usually be made to respond to the

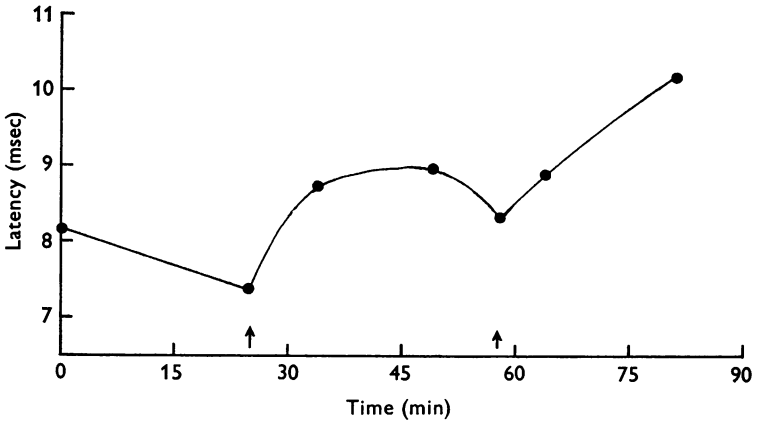

Fig. 2. Graph of the latency of the response (ordinate, msec) of a cell to ramp movement of a whisker against time (abscissa, min). The rat was initially under Nembutal anaesthesia. At each of the times marked by an arrow, the animal was withdrawing to a strong pinch to the hind limb and 0·4 ml. of 25% urethane were given I.P. The withdrawal responses disappeared about 5 min after the injections.

individual movement of up to six whiskers and sometimes also to movements of the down hairs between them. Deepening the anaesthetic level always localized the response to one or two whiskers.

Responses to the fastest movements available had minimum latencies between 4–8 msec (average 5·4 msec); these were measured from the start of the ramp to the first impulse in the response. The value of the minimum latency was not correlated with the whisker size nor with any particular direction of movement (provided they were measured for the most sensitive direction for a particular cell). Latencies were longer with slower velocity ramps (see later). They were also increased by increasing the depth of anaesthesia. An example of this for one cell is shown in Fig. 2. An additional dose of urethane (0·4 ml. of 25%, i.e. 0·5 g/kg) usually caused an increase in latency of about 1·5 msec.

Static displacements

No cells were found which fired throughout maintained static displacements of a whisker. However, the response of a cell to movement of a whisker was modified by changes in the whisker's mean position. This was studied by statically displacing a whisker from its rest position, either horizontally or vertically, in steps of 1–2 mm, for up to 10 mm; at each displacement a similar sinusoidal or ramp movement was given. The results

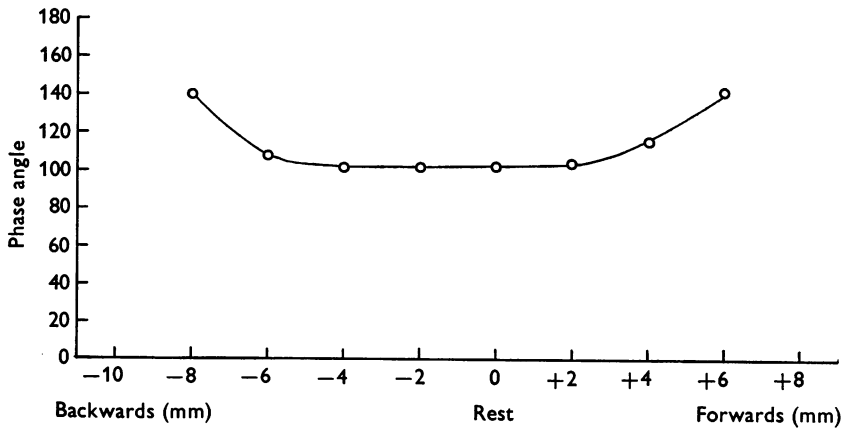

Fig. 3. Graph of the phase angle (ordinate, degrees after maximum velocity forwards) at which a cell responded to sinusoidal movement (6 Hz) of a whisker against the displacement of the mean position of the whisker (abscissa, mm forwards or backwards from the rest position). The sinusoidal movement was in the horizontal plane. The cell ceased responding when the sinusoidal movement was superimposed on a displacement of 10 mm backwards or 8 mm forwards.

of this for one cell, in which a sinusoidal movement was superimposed on horizontal displacements, are shown in Fig. 3. Small displacements (1–2 mm from rest in any direction) usually had little effect on the response to a superimposed movement. As the displacement from the rest position increased, there was a reduction in the number of impulses per cycle and an increase in the phase angle at which the responses occurred. Similarly, for ramp movements, there was a decrease in the number of impulses per ramp and an increase in the latency of the response. Most cells ceased firing to movements superimposed on displacements of 4–8 mm from the rest position.

Direction sensitivity

The effect of giving movements in different directions was studied on forty-six cells. For five of these, the sinusoidal motor stimulator was used

and the plane of movement was changed in 10° steps up to 150°. The number of impulses per cycle was averaged for 500 cycles in each plane. With ramp movements, the ramps were given in eight directions, namely back, forward, up, down and at 45° in each quadrant. For each direction, the movements were given both towards and away from the whisker's rest position (i.e. forward to rest or forward from rest). The number of impulses for 100 ramps were counted for each direction and polar plots were drawn of these total counts against the direction. To check the reliability of a cell, control ramps in the same direction were given at the

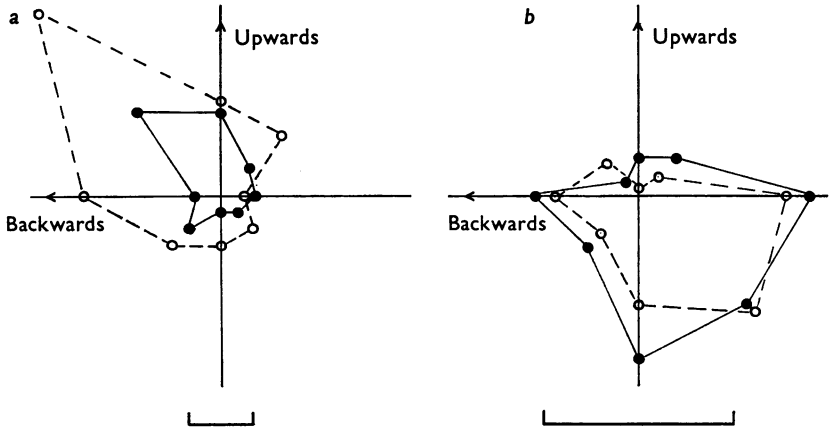

Fig. 4. Polar plots for two cells responding (*a*) to movement of whisker C_2 and (*b*) to movement of whisker B_1. The plots show the total number of impulses recorded for 100 ramps in a certain direction, against the direction. For each direction of movement, the responses were recorded both for ramps moving towards the whisker's rest position (--○--) and for ramps moving away from the rest position(—●—). The bar indicates 100 impulses.

start and end of the experiment and cells in which these differed by more than 20% were not considered. Fig. 4 shows polar plots constructed for two cells, both of which showed a direction sensitivity.

Although 76% (thirty-five out of forty-six cells) showed a direction sensitivity; it was usually limited to movements in 1 quadrant (1, 2 or 3 adjacent directions) although it extended to 4 adjacent directions in three cells and one cell was sensitive to movements at 180° (back-up and forward-down). Total counts for movements in the preferred directions were commonly 5–10 times greater than those in other directions. Fig. 4 also shows that the total counts for movements towards rest could differ from those from rest (i.e. movements in the same direction but from a different starting position). This is the effect of static displacement, mentioned

previously. For all the cells showing a direction sensitivity, about half were more sensitive for movements to rest, a quarter from rest, and a quarter showed an equal sensitivity for either. The static displacements were 2–3 mm and the difference in total counts for movements to and from rest was small (seldom more than a factor of 2) compared to the difference with movements of different directions.

Different cells from the same whisker could have different preferred directions. All directions tried were represented, approximately equally, although downwards sensitivity appeared to be slightly more common than upwards. This is shown in Fig. 5*a*, which is a plot of the preferred directions for all the cells; the whiskers which drove these cells are shown in the inset Figure. It should be noted that the sample of whiskers contained more lower than upper whiskers and none of the small rostral whiskers (numbers 5, 6 and 7) were represented. In an attempt to see whether there was any correlation between direction sensitivity and the whisker position, on the face, the most sensitive directions of the cells responding to the number 1, 3 and 4 whiskers were compared (Fig. 5*b*) and also the *A* and *B* whiskers, C_2 and *E* whiskers (Fig. 5*c*). Although the samples in each group were small (4–8 cells), it can be seen that the cells driven by the caudal (number 1) whiskers appeared to be preferentially sensitive to forward movements and that this sensitivity gradually shifts so that cells driven by the more rostral (number 4) whiskers were more commonly sensitive to backward movements. The situation was not so clear for vertical movements. Cells driven by *A* and *B* line whiskers seemed to be equally sensitive to movements up or down although cells from line *E* whiskers (the lowest line) were more sensitive to upward movements. The responses from all the cells driven by whisker C_2 (a middle line whisker) showed an overall preference for downward movement although all directions were represented.

Velocity and amplitude changes

As explained in the Methods, step-voltage inputs to the vibrator (stimulator *c*) produced movements whose velocity and amplitude were proportional. Changes in velocity, at constant amplitude, could be produced by using the signal generator to drive the vibrator. However, changes in amplitude at constant velocity could not be satisfactorily achieved. The effect of changing the amplitude and velocity was therefore studied on only 12 cells, in the hope that a fuller study could be made with more refined stimulating apparatus. However, the results from these cells were consistent and considered to be worth reporting. Three other cells were also studied in the preliminary experiments with the sinusoidal motor stimulator (*a*).

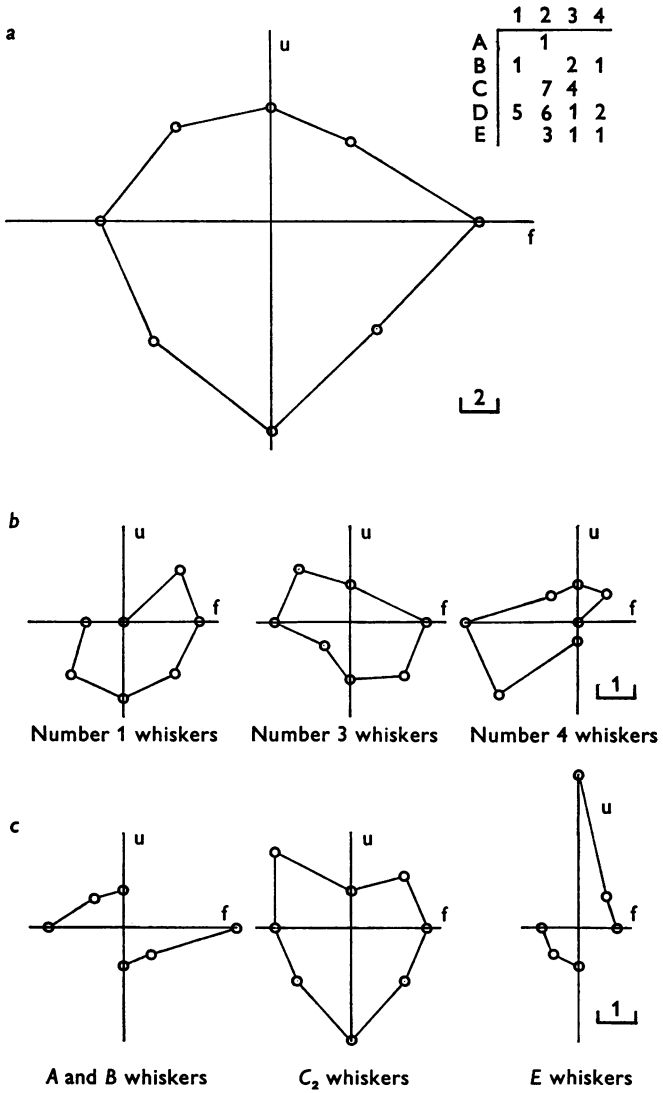

Fig. 5. *a*, Polar plot of the number of cells showing a preference for movements in a certain direction, against the direction. The plot was constructed from the results of all the cells (thirty-five) which showed a direction sensitivity and the whiskers which drove these cells are shown in the inset figure.

b, Polar plots constructed as in *a* but selected so as to include only those cells driven by no. 1, no. 3 or no. 4 whiskers. The total number of preferred directions is equal in each case.

c, Polar plots constructed as in *a* but selected so as to include only those cells driven by whiskers on lines *A* and *B*, whisker C_2 or line *E*. The total number of preferred directions is equal for the '*A* and *B*' group and the '*E*' group but the sensitivities of all the cells driven by whisker C_2 are included.

(u, upwards; f, forwards; scale shown by bar.)

The amplitude and velocity was varied in the most sensitive direction. Ten ramps at each velocity and amplitude were given and the average total number of impulses, latency and interspike intervals were calculated. Reliability was again checked by control ramps at the start and end of the experiment and the same criterion of not more than 20% variation in response was used.

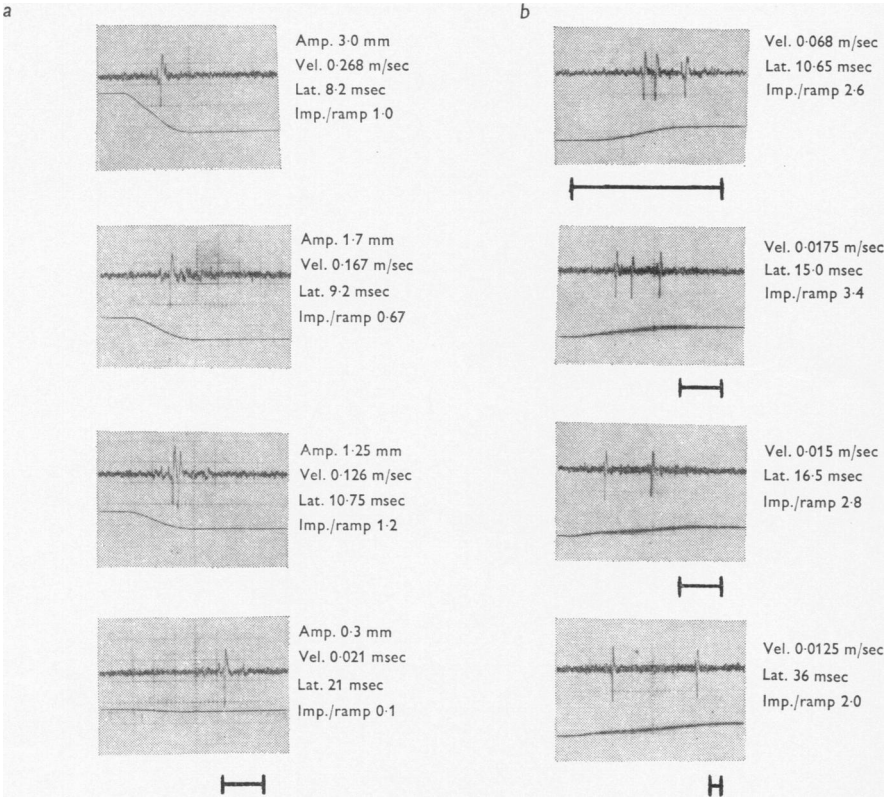

Fig. 6. *a*, Responses of a cell (upper traces) to ramp movements (lower traces) of whisker E_4. In each case the ramp amplitude and velocity are given at the side as well as the average latency of the response (from 10 ramps) and the average number of impulses per ramp.

b, Responses of a cell (upper traces) to ramp movements (lower traces) of whisker E_4. The ramps were of constant amplitude (0·8 mm) but varying velocity. In each case the ramp velocity, average latency of the response (from 10 ramps) and the average number of impulses per ramp are shown at the side.

Time scale: bar = 10 msec.

Fig. 6 shows the response of two cells; (*a*) for ramp movements in which both amplitude and velocity were varied simultaneously, and (*b*) for ramps of fixed amplitude but changing velocity. The phasic nature of these

responses is clear; for all twelve cells, the maximum number of impulses per ramp varied from 1 to 3 (mean 1·8). The cells had a critical velocity, below which no response was produced (with amplitudes of up to 2 mm). The critical velocity depended on the amplitude, being lower at higher amplitudes. At an amplitude of 0·8 mm, values for the different cells ranged from 0·001 to 0·04 m/sec. In two cases, critical velocities were determined for the least sensitive, as well as for the most sensitive, direction of movement. The critical velocities were found to be 4 to 5 times lower in the more sensitive direction.

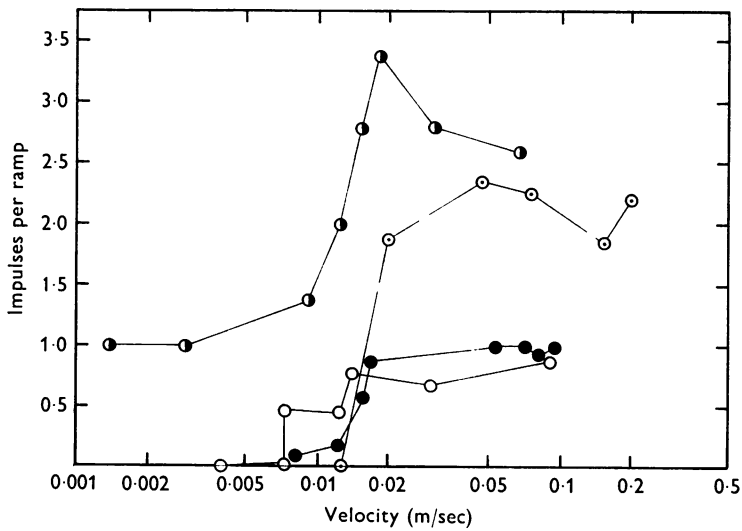

Fig. 7. Graph of the number of impulses per ramp (ordinate) against the ramp velocity (abscissa, log scale, m/sec) for four cells. For ◑, ●, and ○ the ramp amplitude was constant (0·8 mm) and the whiskers moved were E_4, D_1 and E_3 respectively. For ⊙ both the amplitude and velocity were varied and the whisker moved was B_2.

The effect of increasing the velocity above the critical value on the number of impulses per ramp is shown for four cells in Fig. 7. For three of these, the amplitude was kept constant at 0·8 mm, while for the other one it was increased in proportion to the velocity. For these four cells, the average number of impulses per ramp increased as the velocity was increased until a maximum response was reached at about 0·015–0·02 m/sec. However, the other cells showed no monotonic relationship between the number of impulses per ramp and the ramp velocity or amplitude. On all the cells, increases in velocity caused a reduction in the latency of the response, until a minimum value (4–8 msec) was reached. This is shown for two cells in Fig. 8*a*. This reduction in latency occurred whether the

amplitude was held constant or increased in proportion to the velocity. For six of the cells, log. latency was found to be proportional to log. velocity over most of the range studied. Two examples of these log. plots are shown in Fig. 8*b*, for the same cells as in Fig. 8*a*. Table 1 gives the

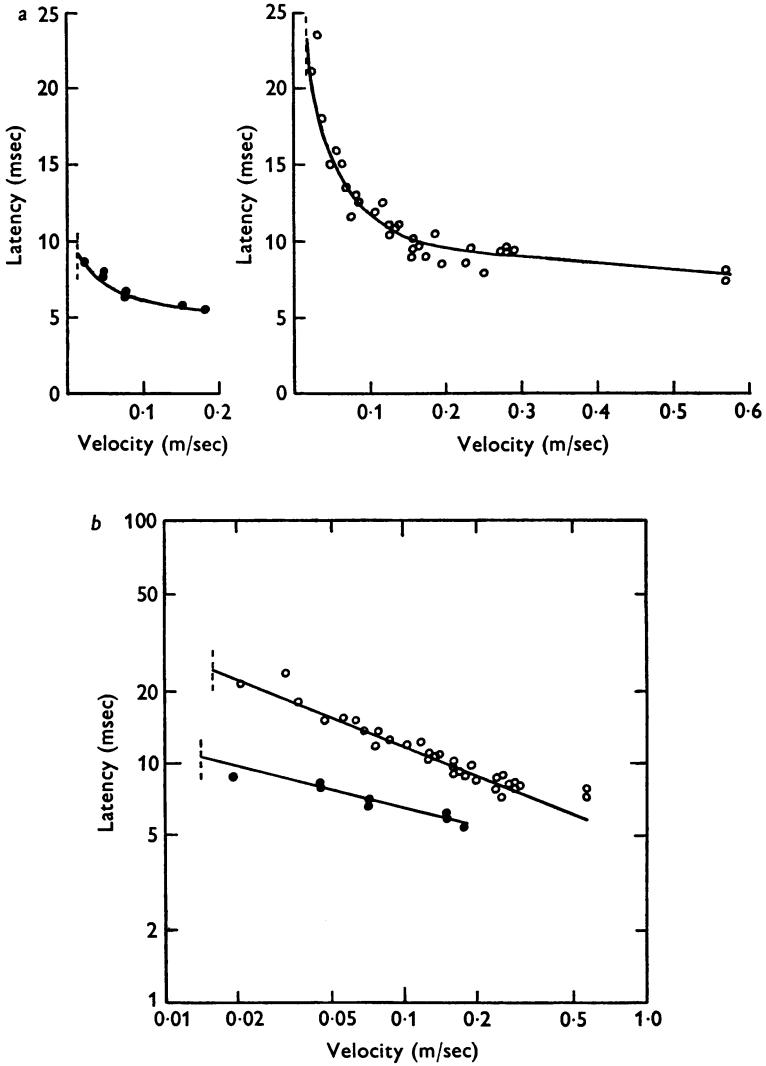

Fig. 8. *a*, Graphs of latency of response (ordinate, msec) against ramp velocity (abscissa, m/sec) for two cells. ●, cell responding to forward movement of whisker B_2; ○, cell responding to upward movement of whisker E_4. Dashed line indicates the critical velocity for each cell.

b, Graphs of latency of response (ordinate, msec) against ramp velocity (abscissa, m/sec) plotted on log. scales for the same two cells as shown in *a*.

values of the exponents (n) and constants (k) measured for the six cells, together with the whisker driving the cell and the amplitude of the ramp. Table 1 also gives the corresponding values for one cell studied with the sinusoidal motor (see later).

TABLE 1. Values of the exponents, n, and constants, k, measured as the slopes and intercepts from the graphs of log. latency against log. velocity for seven cells. The whisker driving each of the cells is given. For the first six cells the whisker was moved with a ramp displacement which was either changing in proportion to the velocity or constant. For the last cell, the whisker was moved sinusoidally and for plotting the graph the latency was measured from the point of maximum velocity forwards and the velocity as the maximum velocity of the sinusoidal movement

Whisker	n	k	Movement wave form and amplitude (Amp.)
C_3	−0·398	7·6	Ramp, Amp. changing
E_4	−0·402	4·6	Ramp, Amp. changing
C_3	−0·449	2·5	Ramp, Amp. 0·8 mm
B_2	−0·185	4·2	Ramp, Amp. changing
D_1	−0·552	1·55	Ramp, Amp. 0·8 mm
C_3	−1·265	0·13	Ramp, Amp. 0·8 mm
E_2	−0·755	2·0	Sinusoid, Amp. 3·0 mm

The ramp amplitude, *per se*, appeared to have little effect on the responses. The responses to the faster ramps were usually over before the maximum amplitude was reached. Also the changes in the number of impulses per ramp and response latency were similar whether amplitude was altered or held constant. However, it was considered possible that the cells were firing to a constant displacement. If this were the case, one would expect the following relationship

$$t = T + \frac{A}{v}$$

where t is the latency of the response in msec, T is the minimum latency following excitation in msec, A is the supposed excitatory displacement in m and v is the velocity of the ramp in m/sec. Graphs of t against $1/v$ were approximately linear for most of the cells and from these graphs the values of T and A were calculated. For half of the cells the values of A were greater than the threshold amplitudes found experimentally. For one such cell, Fig. 9 shows the plot of t against $1/v$ and also the line which would be obtained by using the values of the minimum latency and threshold amplitude found experimentally; the discrepancy is clear. It was therefore concluded that, at least for some of the cells, a constant displacement was not the effective stimulus. This was supported by the fact that on very low velocity ramps (e.g. 0·002 m/sec) some cells fired 200–500 msec after

the maximum amplitude was reached, although the same cell could fire with a much shorter latency (e.g. 8 msec) for faster ramps.

The three cells studied with the sinusoidal motor stimulator (*a*) gave results consistent with those given above. The cells responded with 1–2 impulses per cycle over the whole range of frequencies tried (1–35 Hz, corresponding to maximum velocities of 0·009–0·24 m/sec). There was no consistent or monotonic relationship between the average number of

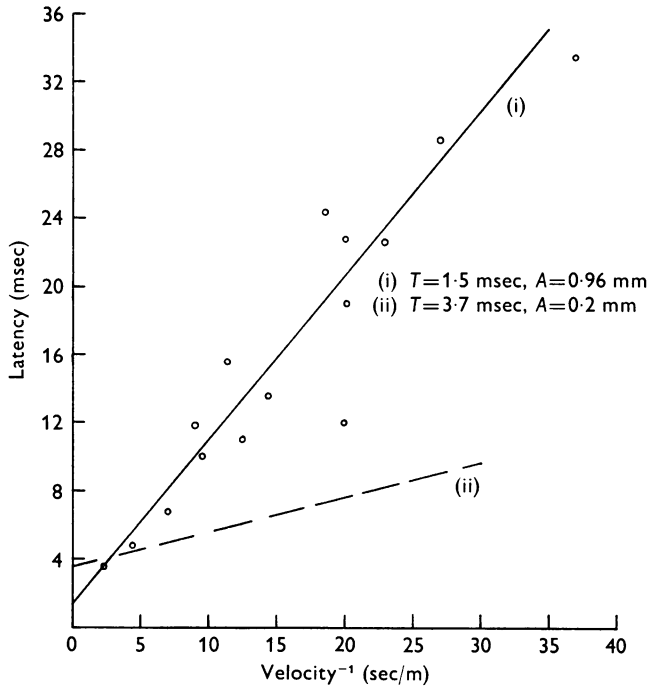

Fig. 9. Graph of the latency, *t*, of the response of a cell (ordinate, msec) to ramp movements of whisker C_4 against the reciprocal of the ramp velocity (abscissa, sec/m). The continuous line (i) is drawn as the best fit (by eye) through the points. The dashed line (ii) is drawn using the values of the minimum latency, *T*, and threshold amplitude, *A*, found experimentally, for the intercept and slope respectively. For each line the values of *T* and *A* are given at the side.

impulses per cycle and the frequency. For comparison with the ramp deflexions, the maximum velocity of the sinusoidal movement was plotted against the latency of the response, measured from the point of maximum velocity. As with the ramp deflexions, the cells showed a decrease in latency with increasing velocity and for one cell the plot of log. latency against log. velocity was proportional (see Table 1).

DISCUSSION

With barbiturate anaesthesia, most workers (e.g. Mountcastle & Henneman, 1949; Davidson, 1965) have reported an increase in background activity when a micro-electrode entered VB. This was not found here; very few cells showed any spontaneous activity, but those that did gave bursts similar to the type of activity reported by others (Andersen & Sears, 1964). It is possible that cells in the vibrissal area are particularly sensitive to anaesthesia. However, another possibility is that many cells only fire in relation to whisker movement, even without an anaesthetic. In the normal rat the whiskers are continually moving back and forth, at least during any exploratory activity. With anaesthetics which do not abolish whisker movements, such as trichloroethylene (Trilene) far more cells show a continual activity (Waite, 1972*b*).

The typical response to movement of a whisker was a rapidly adapting, short latency discharge, similar to that reported for touch cells in other studies at thalamic level (Rose & Mountcastle, 1954). The average minimum latency (5·4 msec) was rather long compared with the values of 1·0–2·0 msec reported for face responses in rat thalamus (Davidson, 1965) and 3·0 msec for the rat trigeminal nucleus (Nord, 1968). However, both these latter studies used electrical stimuli. Also, it should be remembered that the latencies given here were measured from the start of the ramp movement and the full ramp velocity was not reached until about 2 msec later.

The phasic nature of the responses found here was surprising. All workers recording from the afferents from vibrissae in both rats and cats, under barbiturate anaesthesia, have found that the majority give slowly adapting responses although some are phasic (Fitzgerald, 1940; Kerr & Lysak, 1964; Zucker & Welker, 1969; Hahn, 1971). Most afferents from the carpal sinus hairs, which are anatomically similar to vibrissae, also give slowly adapting responses (Nilsson & Skoglund, 1965), although afferent responses from all other types of hairs, including tylotrich hairs, are rapidly adapting (Brown & Iggo, 1964, 1967).

The difference in adaptation rates between the afferent fibres and the thalamic responses could be (*a*) an effect of the anaesthetic, or (*b*) represent a naturally occurring 'analysis'. A third possibility, that the responses here were all from injured cells, is most unlikely. The responses commonly lasted for several hours with repeatable results and the small amplitude responses from cells at a distance from the electrode tip were also phasic. On the other hand, a few slowly adapting responses were found but these were seldom consistent and the cell often died.

(*a*) If the change in adaptation rate occurs in the unanaesthetized

animal it does not necessarily mean a loss of information for the rat. It is possible that the information from the static components of the response, e.g. about the magnitude and duration of static deflexions of the whiskers, is analysed at the trigeminal level or in other paths, not involving VB. These could be via other brain stem nuclei or the intralaminar nuclei of the thalamus (Torvik, 1956; Nauta & Kuypers, 1958). It is also worth considering that a static displacement of a whisker may be a quite 'unnatural' stimulus, for the whiskers are only stationary when a rat is not exploring and apparently paying no attention to their input. During exploratory behaviour, the whiskers are vibrating so that static deflexions would not occur. Perhaps when a rat is not exploring, the whiskers are used simply for an alerting system; if so, the static component of the afferent input might be irrelevant and it may be 'filtered out' by central mechanisms.

(*b*) That the change could be an artifact of the anaesthesia seems unlikely. VB is a nucleus of the 'lemniscal' path and this path is remarkable for the constancy of its responses at all levels (Albe-Fessard, 1967). There have been no previous reports of marked changes in adaptation rate with anaesthesia. Responses from hair movement remain phasic at all levels (Gordon & Jukes, 1964; Mountcastle, 1956, 1957; Mountcastle & Powell, 1959*b*). Although slowly adapting responses have not been studied in detail at thalamic level, Poggio & Mountcastle (1963) found anaesthesia did not alter the excitatory angles over which most joint units, in monkey VB, gave a steady-state discharge. Also the responses in VB from the carpal sinus hairs in cats under barbiturate are slowly adapting (Gordon G. & Manson J., personal communication). In the cortex, slowly adapting responses to skin indentation and joint rotation were found in cats (Mountcastle, 1956, 1957) and monkeys (Mountcastle & Powell, 1959*a*) under light barbiturate anaesthesia. All the above studies were in cats or monkeys and there may be a species difference in the susceptibility to anaesthesia. It is also possible that vibrissal responses are particularly susceptible. Barbiturates are known to prolong recovery times following a response (Bard, 1938; Poggio & Mountcastle, 1963) and their depressive effect might prevent the later components of a response. Studies at the trigeminal level are rather conflicting. In rats, under barbiturate, Nord (1968) reported that responses were both tonic and phasic. In decerebrate cats, Kruger & Michel (1962) found most responses were rapidly adapting while other workers, using barbiturate anaesthesia, found that over half of the responses were slowly adapting (Gordon *et al.* 1961; Eisenman *et al.* 1963). Kruger & Michel's results are surprising if the change in adaptation is due to anaesthesia. Also some experiments currently in progress in this laboratory, recording vibrissal responses from the trigeminal nucleus in

decerebrate rats, suggest that many responses are phasic at this level. Thus the question of the anaesthetic effect on adaptation must await further studies.

Two other effects of anaesthesia should be mentioned. Firstly, some workers have found that receptive fields were reduced under barbiturate (Towe & Kennedy, 1961; Ohye & Narabayashi, 1971) and in this study localization was also less precise with lighter levels of pentobarbitone. However, it should be noted that Mountcastle & Powell (1959*b*) found no change in receptive field size. Secondly, a similar increase in latency, with deepening anaesthesia, to that found here has also been reported before in thalamus and cortex but does not occur in the dorsal column nuclei (Angel & Unwin, 1970).

The fact that small static displacements of a whisker did little to modify the response to a superimposed movement is consistent with the results of Höglund & Lindblom (1961) for phasic responses from frog skin. The response was abolished by extreme displacements and it was also reduced when large amplitude ramps (about 5 mm), which pulled on the skin, were given; a similar effect was noted by Zucker & Welker (1969). Perhaps these large movements reduce the relative distortion within the follicle by moving the skin around the follicle as well as the hair within it. This study agreed with others (Fitzgerald, 1940; Zucker & Welker, 1969) in finding that pushing or pulling along the shaft of the whisker was a relatively ineffective stimulus compared to movements at right angles to the shaft.

Three-quarters of the cells were found to have a direction sensitivity, usually restricted to one quadrant. This is very similar to the results from the afferent nerves and trigeminal nucleus in both rats and cats. All studies found that approximately half the units showed a direction sensitivity and the sensitivity was usually for movements in one, two, or three adjacent quadrants (Zucker & Welker, 1969; Eisenman *et al.* 1963; Kerr & Lysak, 1964). However, in the rat cortex, Welker (1971) did not find that the cells showed any direction sensitivity.

Fitzgerald (1940), working on cats, found that the direction sensitivity of an afferent nerve fibre from a whisker was related to the position of the whisker on the face, so that it was more sensitive to movements towards the centre of the whisker field. This clear relationship for individual afferents has not been found in later studies on either cats (Hahn, 1971) or rats (Zucker & Welker, 1969), nor was it found here for individual thalamic cells. However, the average responses did show a slight preference for movements towards the centre of the whisker field. The slight predominance of units sensitive to downward movements has not been reported by others and was probably due to a sampling error. Direction

sensitivity is not common in afferents from ordinary hairs (Brown & Iggo, 1964, 1967) although it does occur in the carpal sinus hairs (Nilsson, 1969) and in the rapidly adapting responses from the hairs of the blow-fly (Wolbarsht & Dethier, 1958). The mechanism giving direction sensitivity in vibrissal afferents is unknown although it may have an anatomical basis, for instance, depending on the position of the nerve endings.

The decrease in latency with increasing intensity of stimulation (in this case increasing ramp velocity and amplitude) is consistent with earlier studies (Rose & Mountcastle, 1954; Mountcastle, Davies & Berman, 1957; Mountcastle & Powell, 1959*b*; Towe & Kennedy, 1961). However, previous studies have usually found that increases in stimulus strength also increased the number of impulses per response. This was only found for one-third of the cells here. This may have been an effect of the anaesthetic, if, for instance, it was abolishing the later impulses in a response. It is also possible that amplitude and velocity are not commonly coded in this system by the number of impulses in one cell but by the number of active cells. The large number of cells involved would be sufficient for this, especially since different cells had different critical velocities.

In this study, critical velocities were measured at 1 cm from the whisker base, while other studies (Zucker & Welker, 1969; Hahn, 1971) gave threshold values at 5 mm out. The difference between critical (defined as the highest velocity which produced no response) and threshold (defined as the velocity halfway between that which produced one impulse and that which produced none) was small (about 0·01 m/sec). If one assumes that the whisker is a stiff lever, then the range of critical velocities found here would correspond to 0·5–20 mm/sec at 5 mm from the whisker base; the fact that the whisker is not stiff would reduce these values. This range compares with threshold values of less than 5 mm/sec (for 60 % of the cells) to 130 mm/sec (for 10 % of the cells) for the afferent responses in rats (Zucker & Welker, 1969) and less than 6 mm/sec (for over half of the cells) for afferents in cats (Hahn, 1971). It should be noted that Zucker & Welker's figures are for amplitudes of 2 and 4 mm, while the values here were measured at 0·8 mm. They reported that threshold velocities were higher at lower amplitudes as has been found in this study. Thus the values in the thalamus are similar to those for the most sensitive afferents. The higher values reported for the afferents may have been missed here because of the small number of cells studied, but it is also possible that the higher values have been lost by convergence.

It is not clear whether the power relationship between latency and velocity found for half the cells has any functional significance. Many sensory responses show a power relationship between frequency of firing, or number of impulses, and stimulus velocity (Stevens, 1966) with the

exponents for hair responses ranging from 0·5 to 1·1 (Brown & Iggo, 1967; Nilsson, 1969; Zucker & Welker, 1969). A latency, by itself, can obviously not provide any information about the magnitude of a stimulus. However, in the normal rat, information about the active movement of the whiskers is probably available and the power relationship between the latency and velocity could possibly be relevant.

For the afferent responses from the whiskers, both the amplitude and velocity are important, while for the thalamic responses, the velocity, rather than the amplitude, of the movement appeared to be the effective stimulus. However, the small number of cells and the uncertainty about the anaesthetic effects do not allow any definite conclusions to be made on this point.

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