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STIMULUS–RESPONSE RELATIONSHIPS IN FIRST-ORDER SENSORY FIBRES FROM CAT VIBRISSAE

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SUMMARY

1. In the infraorbital nerve of anaesthetized cat, recordings were made from single units serving the vibrissae. The directional sensitivity of individual units was rather gross, but comparison of the outputs of several units from the same vibrissa could provide information that was more precise about the direction of vibrissa deflexion.

2. Many of the units showed 'spontaneous' activity. The majority of rates were less than 1 impulse/sec, so that this activity is not likely to be an important carrier of information.

3. When sinusoidal deflexions in the frequency range of 0·5–100 Hz were applied, the frequency responses of about half of the units were those to be expected if they were responding to the velocity of the stimulus; most of the remainder responded to both the velocity and the magnitude of the deflexion. This form of information presentation has been shown to be well suited for compensatory tracking tasks, and it is suggested that the vibrissae are important for such tasks in the animal's life, rather than merely serving as obstacle detectors.

4. Greatest deflexion sensitivity typically was at higher frequencies than could be attained in this experiment, but would be greater than the median threshold deflexion angle of 12 min found at 50 Hz. It is suggested that these low thresholds are more appropriate for a tracking system than for an obstacle detector.

INTRODUCTION

A variety of animals possess vibrissae, the sensory accessories that enable the tactile sense in the mouth region to serve as a short-range distance sense. The fact that each vibrissa is innervated by many fibres with a rich supply of nerve terminations (e.g. Ramon y Cajal, 1952) suggests that the vibrissae are an important source of sensory information, but as yet there have been few reported investigations of what sorts of sensory information they provide.

Fitzgerald (1940), studying the response of first-order single units in cat, found that they were directionally sensitive. He reported that they were usually most sensitive to bending of the vibrissa toward the centre of the group of vibrissae, as if they were specialized for detecting stimuli brushing past the animal's face. In single-unit experiments in rat (Zucker & Welker, 1969), this relation between the location of the vibrissae and their directional sensitivity was not confirmed. Moreover, it seems implausible that each vibrissa would have many nerve fibres serving it alone if its function were only that of an obstacle detector. Since Fitzgerald did not present the data on which he based his conclusion, one aim of the present study was to re-examine directional sensitivity of vibrissae in cat.

It would also be of interest to know whether these receptors respond only to rather large displacements or are highly sensitive, since high sensitivity would again suggest that vibrissae are suitable for more precise functions than merely warning that an obstacle has been encountered. Threshold data for cat have not previously been published. In rat, Zucker & Welker (1969) found that over half of the vibrissa thresholds were lower than they could measure. A second aim of the present study was to obtain absolute threshold measurements in cat.

A further question was whether the single units' firing rates are more closely related to displacement amplitude or displacement velocity of the vibrissae, that is, whether these rates are proportional to the location of the stimulus relative to the animal's head, or to the movement of the stimulus. The question was investigated by finding the frequency-amplitude combinations of sinusoidal displacement that yielded the same average firing rates during the first second of stimulation, to see if it were the amplitude or the velocity of displacement at various frequencies that correspondingly remained constant for an initial brief period of stimulation.

In both the studies cited above, about 5% of the units were reported to show 'spontaneous' activity in the absence of experimenter-imposed stimulation. This low percentage suggests that stimulus-produced modulation of such activity would not be an important factor in the transmission of information from vibrissae. Neither paper states, however, whether 'spontaneous' activity was systematically searched for; if not, low rates might not have been noted. Therefore, during the present study any such activity at rates of 0·1 spike/sec or greater was measured.

METHODS

Quantitative data were obtained from eighty-three single units in twenty-seven cats. Cats weighing 2 kg or more were deeply anaesthetized I.P. with sodium pentobarbitone (in some cases, with Dial), supplemental injections being given as needed until the end of the experiment, when euthanasia was performed. Rectal tempera-

ture was maintained within 1° C by a heating pad. After insertion of a tracheal cannula, the animal's head was rigidly fixed in position by means of a rod next to each temporal zygomatic process and a third rod at the premaxillary bone. Rigidity of fixation was subsequently checked by replications of absolute threshold measurements of the vibrissae receptors. After removal of the eye, the infraorbital nerve was exposed by blunt dissection, covered with warmed mineral oil (USP), and small strands were dissected free, severed proximally, and laid over a platinum recording electrode. Action potentials were recorded with respect to grounded nearby tissues by conventional amplification and recording methods.

When single-unit action potentials resulting from movement of a vibrissa were obtained, adjacent fur was clipped and the vibrissa and adjacent hair stumps were probed under binocular microscopic view (10×) to ensure that the action potentials resulted from movement of the vibrissa itself rather than from vibrissa-produced movement of adjacent hair. There were no instances of a vibrissa unit being activated by movement of fur or of other vibrissae if such movement did not cause visible movement of the vibrissa that was being tested.

Directional sensitivity of the vibrissa was tested by manually deflecting the vibrissa in various directions to establish the limits of the directions in which it would respond. This information was recorded on a sketch of the location of the vibrissa.

Quantitative stimulation was provided by fastening a small metal rod, driven by an electromechanical transducer, to the vibrissa a few mm from its base, perpendicular to the vibrissa and directed to deflect it in a direction to which it was highly responsive. In early preparations the stimulator was attached to the vibrissa by means of sealing wax or collodion; it proved to be difficult to avoid warping or displacing the vibrissa by these methods, and in later preparations the attachment was made with a thin dot of rubber cement. Motion of the vibrissa was observed with stroboscopic illumination under microscopic view (16×) to ensure that the stimulator had remained attached throughout the measurements, and that the motion of the vibrissa between the skin and the point of stimulator attachment was that of a rigid lever pivoted at its base. The stimulus–response relationships to be reported thus do not include the effects of the mechanical properties of the vibrissa in transmitting stimulation from their distal tips. The amplitude of stimulator excursion, calibrated under stroboscopic illumination by means of a microscope with filar micrometer eyepiece, was divided by the measured distance between the skin and the point of stimulator attachment, the quotient being taken as the tangent of the angle of deflexion of the vibrissa.

In early preparations the electromechanical transducer was a Goodmans V-47 vibrator, driven by an audio oscillator and amplifier. For most of the data reported here, the electromechanical transducer was an Agac-Derritron VP2 vibrator, mounted in a heavy modified radial-arm drill press. Driving signals were provided by a low-frequency function generator, repeatability of the amplitude settings being provided by an attenuator with 1-decibel increments. The position of the stimulator was detected by a photocell system that provided constant monitoring of stimulator position and displacement, and that also provided negative feed-back to the power amplifier circuit that drove the stimulator in order to improve fidelity of stimulator response to the driving signals.

The number of action potentials per second as a function of sinusoidal stimulus amplitude was measured at frequencies of 0·5 to 100 Hz. It was felt that this range would provide a reasonably representative sample of the displacement velocities likely to be encountered with naturally occurring stimuli. Latency to a step displacement with 5 msec rise time was also measured at an amplitude such that increasing amplitude did not shorten latency.

In forty-four units, before attachment of the stimulator, the units were observed for 'spontaneous' activity. Units were classed as showing such activity if it occurred at rates of more than one action potential per 10 seconds.

RESULTS

Directional sensitivity. The directions in which a vibrissa responded to deflexion comprised, in some cases, as little as one quarter of a circle with the vibrissa at its centre, in other cases as much as three quarters of such a circle. In only one of seventy-two units was there a response to non-adjacent directions; in this case, the unit responded to deflexion in the

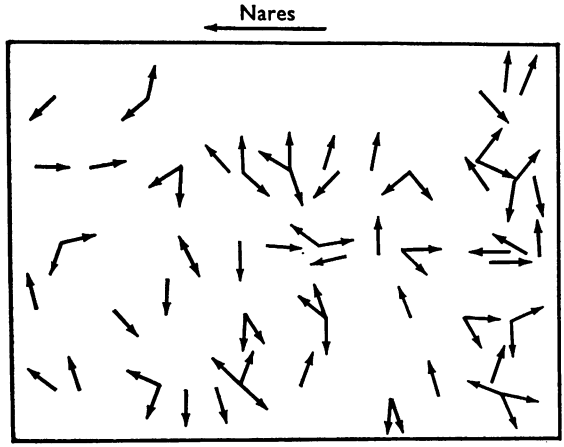

Fig. 1. Location and directional sensitivity of vibrissa single units, pooled data. Each unit is represented by an arrow indicating the location of the vibrissa in the group and the median direction of deflexion to which the unit responded. Arrows with a common origin represent units from the same vibrissa in the same cat.

direction of either of two opposed quadrants. Units that showed 'spontaneous' activity responded by increasing or decreasing their rate of firing according to the direction in which they were deflected.

In Fig. 1 are presented the pooled data on the relationship between directional sensitivity and position of the vibrissa relative to the group of vibrissae. Each arrow bisects the zone of directional sensitivity of a vibrissa unit, the zones themselves being omitted from the diagram for clarity. Arrows originating at the same point represent different single units innervating the same vibrissa in the same animal. These data, like those of Zucker & Welker (1969) for rat vibrissae, are not in agreement with Fitzgerald's (1940) reported correlation between directional sensitivity of cat vibrissae and their location in the group of vibrissae. The number of

units he studied is not given, and his report was that the directional sensitivity was 'usually' inward, so it is difficult to assess how much disagreement there is between his findings and later data.

The differing directional sensitivities of different units from the same vibrissa suggest that the central nervous system, by comparing the inputs from such units, could obtain more precise information about the direction of vibrissa deflexion than is available in the input from any one of the units. The data from the first-order afferents do not, of course, show whether it actually does so.

'Spontaneous' activity. Activity in the absence of experimenter-imposed stimulation was measured in forty-four units, and observed to occur in 77 % of them. In two thirds of these units, the rates of firing were between 0·1 sec and 1 per sec, in 22 % the rates were between 1 and 10/sec, and in 11 % the rates were above 10/sec; 28/sec was the highest rate observed. Zucker & Welker reported 6–7 % of their rat vibrissa units to show such activity, and Fitzgerald reported about the same percentage in cat. The higher incidence of such activity in the present study presumably resulted from the inclusion in the count of units with lower 'spontaneous' activity rates than were counted in the previous experiments.

Background vibrations are not likely to be the explanation of this activity. The activity was not related to pulse, respiration, or to the resonant frequency of the table holding the preparation. Moreover, high rates were observed in units whose measured thresholds were high as well as in those with low thresholds. Zucker & Welker suggest mild tonus of the facial muscles as a possible explanation, because they did not see such discharge in preliminary observations on unanaesthetized rats under the influence of Flaxedil. Corresponding information for the cat is not available, but even if the rates found in the present study do occur in the awake, behaving animal, the majority of rates are too low to carry much information by their modulation.

Rate-intensity functions. The rate-intensity functions of seventeen vibrissa units in response to sinusoidal stimuli were obtained in the frequency range 0·5–100 Hz. An example is shown in Fig. 2. The slopes of the functions increased with increasing frequency in the range studied. Particularly at frequencies of 20 Hz and above, there were likely to be plateaus in the functions at those intensities at which the number of action potentials per stimulus cycle was an integer. Such non-linearities have also been found in other cutaneous mechanoreceptors (Lindblom & Tapper, 1967; Talbot, Darian-Smith, Kornhuber & Mountcastle, 1968).

Absolute thresholds. Absolute thresholds for these units for sinusoidal stimulation depended upon stimulus frequency. In occasional instances, maximum sensitivity was reached at frequencies as low as 20 Hz, but in

most cases, maximum sensitivity was at frequencies higher than the 100 Hz available from the stimulator without distortion. As an illustration of the order of magnitude of these thresholds, however, Fig. 3 presents the 50 Hz thresholds for fifty-one vibrissa units. Over half of the units

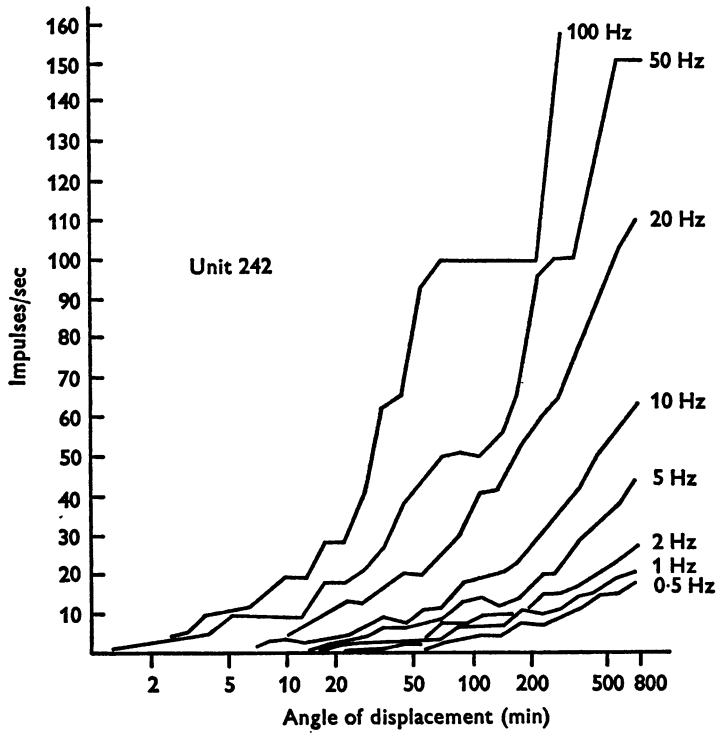

Fig. 2. Rate of firing as a function of amplitude and frequency of sinusoidal displacement. The abscissa values, plotted on a logarithmic scale, are measured from resting position to peak displacement. Data not averaged.

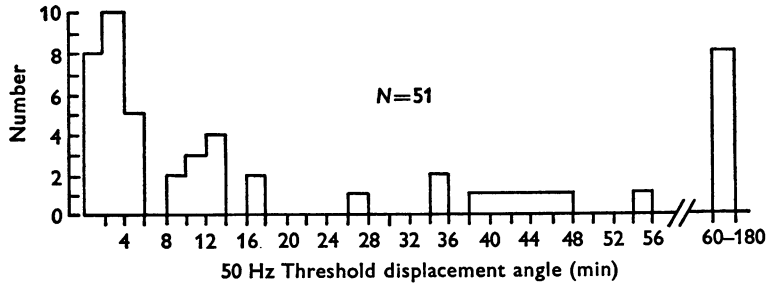

Fig. 3. Frequency distribution of absolute thresholds for sinusoidal displacement at 50 Hz. Abscissa values are peak displacement from resting position.

responded to bending of the vibrissa through an angle of less than one fifth of 1 degree at this stimulus frequency. This is equivalent to a peak velocity of 4 min of arc per millisecond. If this value is expressed as the deflexion velocity of a point on the vibrissa 5 mm from the skin, which is how Zucker & Welker reported thresholds for rat vibrissae, then over half the units in cat were found to have velocity thresholds at 50 Hz of less than 6 mm/sec. The majority of low-velocity thresholds in rat were below

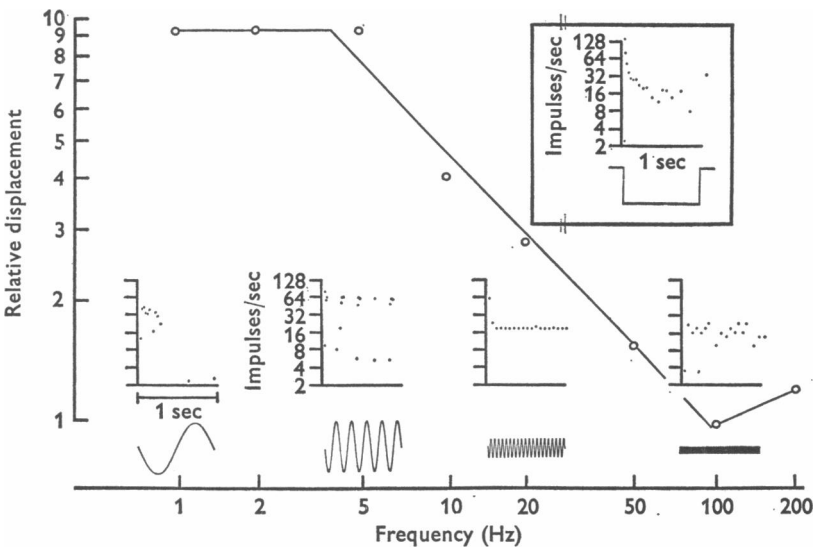

Fig. 4. Frequency response of a single unit. Frequency-intensity combinations are plotted that yielded approximately the same average firing rates. The small inset graphs show the momentary firing rates, each filled circle corresponding to an action potential. The wave forms below show the corresponding stimuli as recorded from the photocell monitor of stimulus position. The inset at upper right is a similar display showing response to a displacement step. Data not averaged.

0·25 mm/sec, but the two sets of data are not directly comparable. Zucker & Welker observed that velocity thresholds were affected by the displacement amplitudes at which measurements were made, and the smallest displacement amplitude available in their experiment was some 14 times larger than the amplitudes at which the 50 Hz thresholds reported here were found. Moreover, it will be argued below that, at least in cat, there is a class of units for which deflexion velocity is not the appropriate measure of the stimulus.

Frequency response. Fig. 4 shows, for a single vibrissa unit, the sinusoidal frequency-intensity combinations that produced approximately the

same average firing rates. The stimulus amplitude at 1 Hz was set at a level that produced 12–15 action potentials in 1 sec, the amplitudes at other frequencies then being adjusted to within 1 db of the amplitude level that would produce the same number of action potentials in 1 sec. The smaller inset graphs are included to illustrate for various frequencies the temporal variations in rate of firing that produced equivalent average firing rates. Also shown is a representative example of the vibrissa unit's response to a step displacement.

These data provide a means of answering the question of whether the response of the unit, measured as the number of action potentials per second, is to the magnitude or to the velocity of displacement. Response solely to the magnitude of displacement would produce a horizontal frequency reponse function; response solely to velocity of displacement would yield a function with a slope of -1 on log-log co-ordinates, so that a doubling of frequency would require a halving of displacement to yield the same response. In the case of the unit shown in Fig. 4, over most of the frequency range the function is that to be expected of a unit responding to velocity of the stimulus.

In Fig. 5 are shown the frequency–response functions for seventeen units, at the level required to produce average firing rates of 10 action potentials per second. (The frequency–response functions are similar at the level of 30 action potentials per second, but it was not always possible to obtain the functions for the lower frequencies because of the large amplitudes required to produce this firing rate at low frequencies. The frequency–response functions in this figure were obtained from rate-intensity functions for the units, rather than from direct matchings as in Fig. 4.) The functions have been sorted into two groups and displayed separately: the lower graph shows frequency–response functions whose slope over part of the frequency range is such that halving their amplitude accompanies a doubling of the frequency, while the upper graph contains functions whose slope is less than this. The frequency responses of the two groups of units were most dissimilar in the 2–20 Hz region. The relative sensitivities of these units at these two frequencies, and those of an additional 16 units measured at comparable firing rates, are shown in the frequency distribution of Fig. 6.

About half of the units maintained the same average firing rate when a tenfold reduction in displacement amplitude accompanied a tenfold increase in frequency, indicating that it was displacement velocity to which they responded. This relationship was not simply a result of more cycles per second producing more action potentials per second, for if it were, the result above would imply that at any given frequency, reducing amplitude by a given ratio would reduce the firing rate by the same ratio, and this

was not the case. It should be emphasized that the conclusion that these units were responding to the velocity of the stimulus applies only to the tested frequency range, and does not imply that their response to a long-maintained deflexion of the vibrissa need drop to zero.

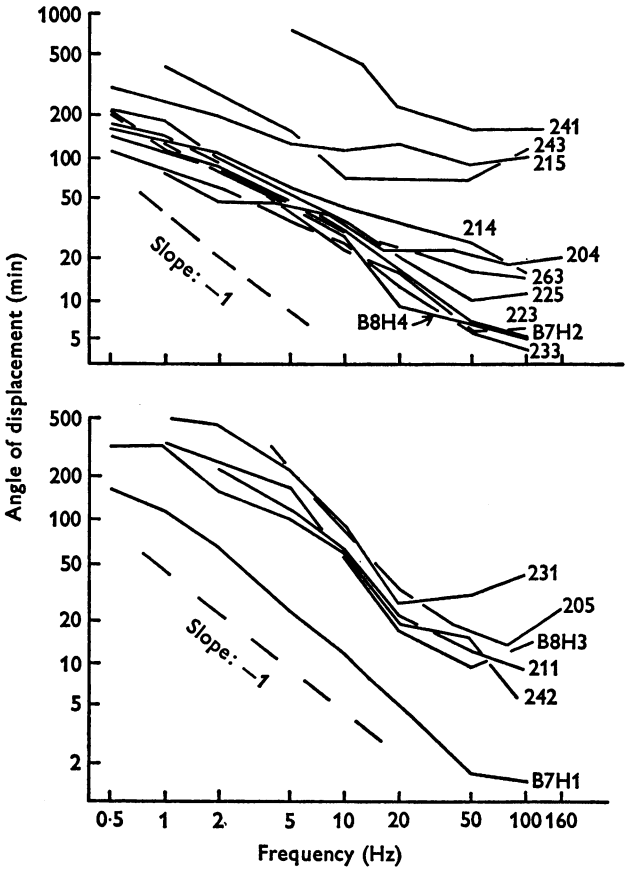

Fig. 5. Log-log plots of sinusoidal frequency responses of seventeen vibrissa units at the level of 10 impulses/sec. Upper graph: units with slopes less steep than −1. Lower graph: units with slopes of −1 or steeper. Displacement angles measured from resting position to peak. Data not averaged.

The remainder of the units showed frequency responses intermediate between a velocity response and a displacement response, with slopes of about −0·4. The average firing rates of these units were thus a function of both the velocity and the amplitude of displacement. Since they were transmitting information about both aspects of the stimulus, neither by itself is a sufficient description of the stimulus, and both need to be speci-

fied. The same may be true also of the first group of units at frequencies outside the range studied here.

The two groups of units did not differ consistently from one another in the range of deflexion directions to which they responded, the location of the vibrissa in the group of vibrissae, the amount of 'spontaneous' activity, or the quotient of measured nerve length divided by the shortest latency obtainable with a mechanical pulse stimulus.

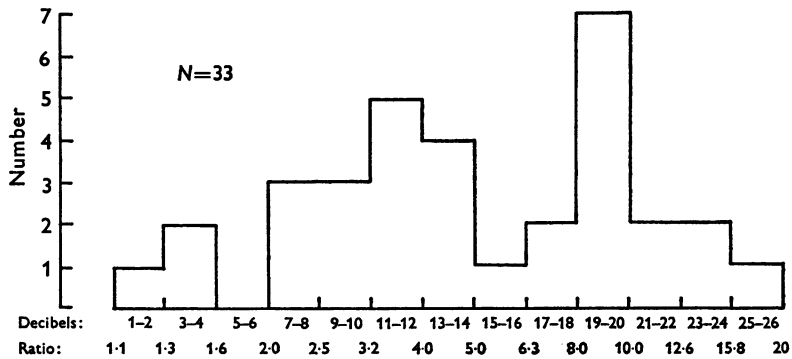

Fig. 6. Frequency distribution of vibrissa units' relative sensitivities. Abscissa values indicate sensitivity at 20 Hz relative to that at 2 Hz.

DISCUSSION

It appears hazardous to attempt a structural explanation of the differences in frequency response obtained among the vibrissae receptors. The fine structure of the Merkel cells serving vibrissae has been studied by Patrizi & Munger (1966) and Andres (1966), and the latter has included study of the lancet- and club-like sensory endings and the encapsulated lamellated corpuscles of the inner hair follicle, but it would be quite speculative to infer a particular frequency response from these data or from the differences in location of the various endings in the tissues surrounding the vibrissae.

The picture of vibrissae function in cat that emerges from the present study differs to some extent from that suggested by Fitzgerald (1940). Rather than being a group of sensory hairs designed to report the passage of a stimulus from the outside of the group toward the centre, as when brushed by an obstacle, the vibrissae are innervated in a manner that provides information about the direction of deflexion of each one. Because of the differing directional sensitivities of the single units serving the same vibrissa, a mechanism that compared their inputs could obtain directional information more precise than that provided by one unit.

The two studies agree in finding that the preponderance of units show a tonic response, and in the relative unimportance of 'spontaneous' activity as a carrier of information.

It is difficult to compare the absolute sensitivity of vibrissae receptors to the sensitivities reported for other tactile receptors, because stimulation of vibrissae involves a lever system. An appreciation of their sensitivity can be gained, however, from the observation that the threshold of the Pincus touch corpuscle, a quite sensitive tactile receptor, is about 20 μm at 50 Hz (Lindblom & Tapper, 1967). Half of the single units in the present study would respond to such a stimulus applied to the vibrissa 6 mm from the skin. The stimulus at the receptor is probably weaker.

The functional utility of units that are responsive both to displacement and velocity characteristics of the stimulus may be suggested by the concept of 'quickening', as developed in research on systems designed to aid humans in tasks that involve tracking a moving target (Birmingham & Taylor, 1954; McCormick, 1964). It is frequently found that if the operator's magnitude of error and its first derivative are combined and displayed to him in a suitably weighted sum, his tracking performance is superior to that obtained when only the magnitude of error is displayed. By analogy, one might suspect that if a vibrissa unit's output is a weighted sum of the displacement magnitude and velocity of the stimulus, this might improve the animal's ability to track that stimulus, whether the stimulus be an obstacle with respect to which the animal's head is moving, or struggling prey.

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