QUANTITATIVE ASPECTS OF RESPONSES IN TRIGEMINAL RELAY NEURONES AND INTERNEURONES FOLLOWING MECHANICAL STIMULATION OF SINUS HAIRS AND SKIN IN THE CAT

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SUMMARY

1. Stimulus–response relationships in discharges of trigeminal relay- and interneurones were investigated in the barbiturate anaesthetized cat using controlled sinus hair or skin displacements.

2. In comparison with discharges in slowly adapting primary afferent fibres the responses in all higher order neurones were considerably reduced in firing rate and often revealed modifications suggesting the interaction of mechanisms actively modulating the afferent input.

3. In relay neurones with or without a tonic discharge component the 'dynamic on' response during a trapezoidal displacement of sinus hairs was found to be determined entirely or predominantly by the movement velocity and to be independent of the deflexion angle of a stimulus. In contrast, the static response in tonic relay neurones was determined by both the movement velocity and the displacement amplitude.

4. Spatial summation of afferent input caused either only quantitative changes in the responses of relay neurones leaving the general discharge properties unaltered or caused both qualitative and quantitative changes in the responses.

5. Interneurones consisted of two functional groups. In about 25 % of them the responses were not or only slightly dependent on the intensity of the applied stimulus, often burstlike and of an all or nothing character. In the second group of interneurones the responses showed a quantitative dependence on the applied stimuli. In this group of interneurones responses often increased with the spatial extension of the peripheral stimulus revealing spatial summation of the afferent input.

INTRODUCTION

In several reports on the afferent innervation of facial sinus hairs the responses in single trigeminal nerve fibres have been subjected to detailed quantitative analyses (Zucker & Welker, 1969; Hahn, 1971; Gottschaldt, Iggo & Young, 1973; Dykes, 1975). Stimulus–response relationships were also investigated in single neurones located in different subdivisions of the trigeminal nuclear complex using mechanical stimuli often activating cutaneous and sinus hair afferents simultaneously (Darian-Smith, Rowe & Sessle, 1968; Darian-Smith, 1970; Rowe & Sessle, 1972; Mosso & Kruger, 1973; Carmody & Rowe, 1974; Kirkpatrick & Kruger, 1975; Greenwood & Sessle, 1976). Shipley (1974) and Young (1975) specifically studied quantitative response characteristics of trigeminal neurones responding to sinus hair movements in the rat and cat, respectively, but in these investigations different functional types of neurones (Gottschaldt & Young, 1977) were not clearly distinguished.

The aim of the present paper is to describe stimulus–response relationships in physiologically identified relay neurones and interneurones receiving input from sinus hairs and other mechanosensitive afferents. Particular attention has been paid to the effects of spatial convergence onto the qualitative and quantitative response characteristics in relay neurones and interneurones.

METHODS

The data were obtained from cats in the experiments described in detail in the preceding article (Gottschaldt & Young, 1977). Receptive fields of single neurones were determined by manual exploration. The functional type of a given neurone was determined using cutaneous and thalamic electrical stimulation. Quantitative mechanical stimulation was achieved in three different ways and, whenever possible, it was tried to simulate sinus hair movements as they normally occur in the behaving cat.

(1) Receptors in the skin were activated by the probe of an electromechanical stimulator described previously (Gottschaldt, 1974).

(2) Sinus hairs were stimulated using the 'angle stimulator' (Gottschaldt et al. 1973) in combination with the electromechanical stimulator. Up to fourteen sinus hairs could be moved simultaneously with this technique. Although the actual deflexion angle of a sinus hair at a given position of the angle stimulator could have been determined (Gottschaldt et al. 1973), for the present analysis it was sufficient to measure only the direct excursions of the angle stimulator.

(3) Plasticine balls of different sizes were fixed to the probe of the electromechanical stimulator and then one or several sinus hairs could be moved in a desired direction at controlled velocity and for different angles.

Discharges of single neurones were recorded extracellularly using steel microelectrodes. The potentials were amplified conventionally and led directly to a PDP-12 computer or they were analysed 'off-line' after storage on a FM tape recorder. The data collection program assembled peri-stimulus-time histograms

and an averaged curve analogue to the stimulator movement. Thus the relationship between the response of a neurone and the time course of the stimulus was fully preserved.

In the data analysis a given peri-stimulus-time histogram was divided into a 'dynamic on', a 'static' and a 'dynamic off' response according to the onset and the duration of the respective stimulus components. For each part of the PSTH an average discharge frequency was then calculated using the formula $F = (N \times 1000)/(n \times t)$, where F represents the frequency of discharge, N the number of impulses counted during a given time period t (msec) of the stimulus in n responses. The velocity of a mechanical stimulus was calculated from the rise/fall time and the deflexion amplitude of the angle stimulator or the movement amplitude of the stimulator probe, respectively. Stimulus–response functions were determined by calculating the best fitting regression line, using the method of least squares. For each stimulus–response relationship it was tested whether a linear, logarithmic or power function could be fitted to the data. The highest correlation coefficient r between the experimental data and a given function was considered to indicate the best mathematical description. Most stimulus–response relationships were best described by a power function. Occasionally a linear or logarithmic function described our data better than a power function. In such cases the correlation coefficient of the power function was only a little smaller (< 0.1) than that of the best fitting function.

RESULTS

A quantitative analysis of responses was performed in 46 of 270 synaptically activated neurones. Only those neurones (twenty-seven) were used for a detailed analysis of stimulus response relationships in which the responsiveness did not vary over time as described in the preceding paper (Gottschaldt & Young, 1977). Most of the studied neurones included sinus hairs in their receptive field and responded to slow stimulus velocities. It has been found previously (Gottschaldt *et al.* 1973) that such stimuli would not activate the rapidly adapting high velocity threshold receptors in the sinus hair follicle. Since rapidly adapting low velocity threshold units form only a small proportion of sinus hair afferents it is assumed that most of the investigated neurones received input from slowly adapting sinus hair receptors, either exclusively or in addition to other cutaneous mechanoreceptive afferents with different adaptive properties.

If, in a higher order neurone, each sinus hair in the receptive field was stimulated individually, several possibilities existed as to the nature of the neurone's response. One or two sinus hairs were often more effective in evoking a tonic discharge than others, or alternatively, movement of each sinus hair produced approximately the same response. In some neurones the responses were strictly phasic although the sensitivity of the neurone to slow sinus hair movements suggested input from slowly adapting receptors. In other cases stimulation of each single sinus hair yielded a phasic response but movement of several sinus hairs together resulted in a sustained discharge.

Stimulus–response relationships in relay neurones

Fig. 1 illustrates responses in a tonic relay neurone which exhibited directional sensitivity and a clear dynamic and static component (Fig. 1*B*, *C*) following stimulation of only one sinus hair (crossed in Fig. 1*A*). The receptive field comprised also seven other sinus hairs (black in Fig. 1*A*) from each of which a comparable phasic-tonic discharge could be elicited.
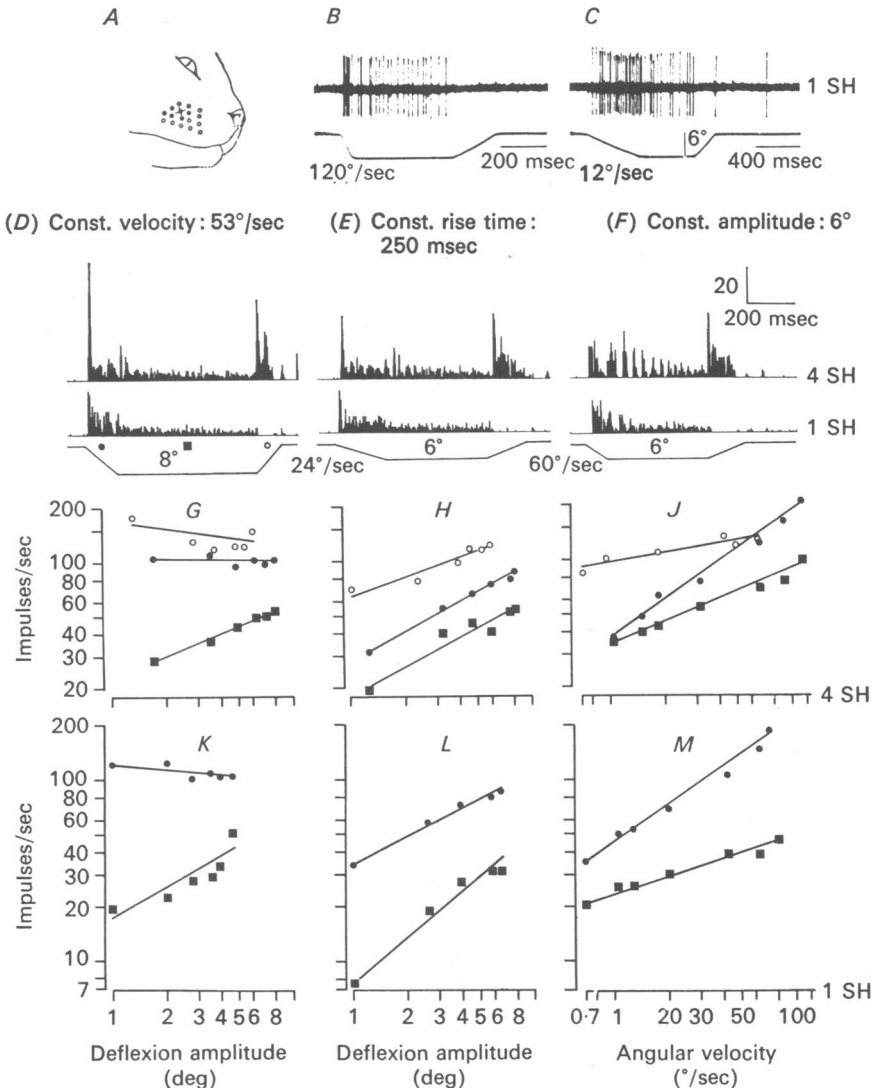

Fig. 1. For legend see facing page.

In order to establish the effect of afferent convergence on to the qualitative and quantitative response characteristics the same series of stimuli were applied first to one sinus hair and then to three further, neighbouring, ones. Stimulus–response relationships were determined for three modes of stimulation: (*a*) variation of the movement amplitude at constant velocity (Fig. 1*D*, *G*, *K*); (*b*) variation of both the velocity and the amplitude over a constant rise time (Fig. 1*E*, *H*, *L*); and (*c*) variation of the movement velocity at constant displacement amplitude (Fig. 1*F*, *J*, *M*).

The six peri-stimulus-time histograms in Fig. 1 contrast responses to three identical movements of one and four sinus hairs, respectively. With four sinus hairs stimulated a new response component is conspicuous during the 'off' phase of the stimulus and a slight increase of the 'dynamic on' and the 'static' response can just be recognized. The graphs in Fig. 1 show for each mode of stimulation the stimulus–response relationship, plotted on logarithmic co-ordinates, for the 'dynamic on' response (filled circles), the 'static' response (squares) and the 'dynamic off' response (open circles). An analysis of these stimulus–response relationships reveals an interaction of velocity and amplitude responses with a dominating velocity response. Where the velocity was held constant (Fig. 1*G*, *K*) the 'static' response increased with the deflexion amplitude but the 'dynamic on' response and, when four sinus hairs were stimulated together, the 'dynamic off' response appeared to be independent of the deflexion amplitude. Where both the velocity and the amplitude of the stimuli were changed (Fig. 1*H*, *L*) the 'dynamic' and 'static' response

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Fig. 1. Responses and stimulus–response functions in a relay neurone after movement of one and four sinus hairs (SHs). *A*: face figurine depicting the number and location of sinus hairs forming the receptive field of this relay neurone. *B*, *C*: single responses following stimuli at two movement velocities applied to one sinus hair (crossed in *A*). *D*–*F*: peri-stimulus-time histograms of responses to three different stimuli applied to one sinus hair (lower histograms) and four sinus hairs (upper histograms). Each pair of histograms was taken from a series in which the deflexion amplitude was varied either at a constant movement velocity (*D*), or at a constant rise time (*E*), or the final deflexion amplitude was kept constant but attained at different movement velocities (*F*). Movement velocities and deflexion angles in *B*–*F* were as indicated at the monitored stimulus records. Stimulus–response relationships plotted on log–log co-ordinates, corresponding to the variation of stimulus parameters as in the histograms shown above them, are plotted for movements of four sinus hairs in *G* to *J* and of one sinus hair in *K* to *M*. Regression lines are hand-fitted. Symbols as indicated in *D*. Filled circles: 'dynamic on' response, filled squares: 'static' response, open circles: 'dynamic off' response. Twenty-five responses in each histogram, bin width 2 msec. Cutaneous latency: 2·2 msec, antidromic latency 0·8 msec.

changed proportionately and this was also the case for stimulation of a single or four sinus hairs, if only the movement velocity was varied and the amplitude remained constant (Fig. 1*J*, *M*).

The strong velocity dependence of the 'dynamic on' response was also confirmed by substituting the velocity of 53°/sec, used for the amplitude variation as shown in Fig. 1*D*, *G* and *K*, into the equation of the 'dynamic on' response in Fig. 1*J* ($R = 7.2\,S^{0.67}$) derived from a pure velocity variation. Assuming the 'dynamic on' response was determined
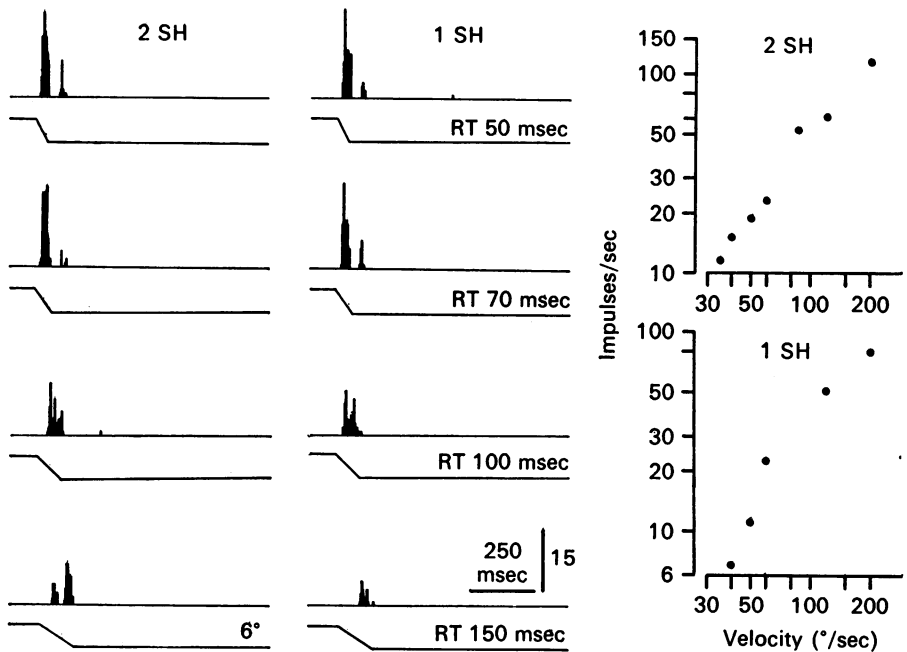

Fig. 2. Responses and plotted stimulus–response relationships in a phasic relay neurone after movement of one and two sinus hairs. The right column of peri-stimulus-time histograms shows responses at four movement velocities following stimulation of one sinus hair, the histograms in the left column show responses to the same stimuli if two sinus hairs were moved simultaneously. Rise time and amplitude of the sinus hair movements are given with the stimulus records. The relationship between the stimulus velocity and the mean frequency of discharge is plotted on log–log co-ordinates in the two graphs for a movement of two (top) and one sinus hair (bottom). Cutaneous latency 2·2 msec, antidromic latency 1·5 msec, 25 responses in each histogram, bin width 4 msec.

only by the stimulus velocity the predicted discharge frequency at the velocity of 53°/sec would be 102·9 impulses/sec, which is almost exactly the average discharge frequency obtained over the whole range of applied stimulus amplitudes for the 'dynamic on' response in Fig. 1*G* (102 ± 5·6

impulses/sec). It should be emphasized that in slowly adapting primary afferent fibres from sinus hairs the 'dynamic on' response is always determined by the velocity and by the amplitude of a displacement (K.-M. Gottschaldt, unpublished results).

In Fig. 2 an example is illustrated for those relay neurones which responded only with a phasic discharge during the movement part of the stimulus. This relay neurone could be excited from four neighbouring sinus hairs, each of which gave an approximately equal and directionally sensitive response. Stimulus–response relationships were established by moving first one and then two sinus hairs at different velocities and constant deflexion amplitudes. The pairs of peri-stimulus-time histograms for each of four rise times show only a slightly larger response if two sinus hairs were stimulated together. The directional sensitivity and the elicitation of responses by slower sinus hair movements in this relay neurone suggest that it received input from slowly adapting sinus hair afferents. A virtual absence of any spontaneous activity was characteristic for all relay neurones showing this type of response and may indicate the presence of a continuous inhibition by which all but the dynamic part of the slowly adapting primary afferent response is eliminated in the process of synaptic transmission.

In the relay neurone shown in Fig. 2 an increase of the number of stimulated sinus hairs was expressed only by a small increase in the response but was not accompanied by qualitatively different response patterns. Such qualitative changes were observed in several instances and are illustrated in Fig. 3 which shows responses of another relay neurone also activated only from four neighbouring sinus hairs. In this case movement of each individual sinus hair yielded a directionally sensitive and phasic response but if all four sinus hairs were moved together a strong tonic and still directionally sensitive response resulted. The pairs of histograms in Fig. 3A demonstrate this effect for a variation of the movement velocity at constant deflexion amplitude and in Fig. 3B for a variation of the deflexion amplitude at constant rise time. Moving four sinus hairs at a time and increasing the stimulus amplitude (Fig. 3B, left column) the response was purely phasic at small angular deflexions. With increasing angle of the sinus hair bending an increasingly tonic response appeared. The stimulus threshold for a response was clearly lower if four sinus hairs were stimulated. Thus, at deflexion amplitudes of three degrees, movement of any one of the four sinus hairs alone caused no response in the relay neurone but a phasic-tonic discharge appeared if all four sinus hairs were stimulated together (Fig. 3B).

The filled circles in Fig. 3C show the stimulus–response relationship for the 'dynamic on' response after variation of only the movement

velocity. The open circles show the relationship between the frequency of discharge in the 'dynamic on' response and increasing movement velocities which resulted if different angular deflexions were attained in a constant rise time. As in the case of the relay neurone shown in Fig. 1
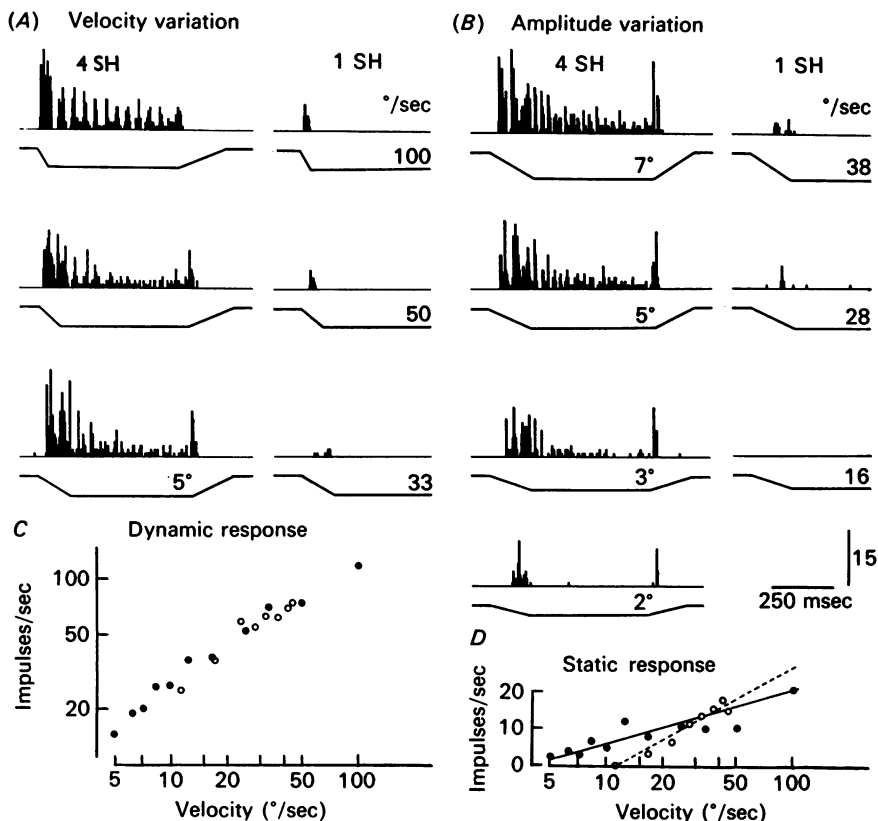

Fig. 3. Responses in a relay neurone after movement of one and four sinus hairs. The peri-stimulus-time histograms show responses to stimuli of changing movement velocity but constant angular displacement (*A*) and of changing displacement amplitudes but constant rise time (*B*), i.e. the movement velocity increased with the angular displacement. Responses after movement of four sinus hairs are shown on the left side of *A* and *B* and after movement of only one of the four sinus hairs on the right side. The stimulus–response function for the 'dynamic on' response and stimulating four sinus hairs together is plotted in *C* for different movement velocities in the pure velocity variation (filled circles) and in the amplitude variation (open circles). In *D* the static response is plotted as a function of the movement velocity for stimuli leading to a constant (filled circles) and to increasing angular deflexions (open circles). Twenty-five responses in each histogram, bin width 4 msec. Cutaneous latency 2·2 msec, antidromic latency 1·5 msec.

the discharge frequencies in the dynamic responses were virtually identical (Fig. 3C), and apparently independent of whether the movement led to a small or a large sinus hair deflexion. The discharge frequency in the static response was also related to the movement velocity (Fig. 3A and D, filled circles) but, in addition, increased with the stimulus amplitude (Fig. 3D, open circles). Therefore it can be concluded that in this relay neurone also the amplitude of the movement of four sinus hairs was expressed quantitatively only in the 'static' response but scarcely in the velocity dependent 'dynamic on' response.
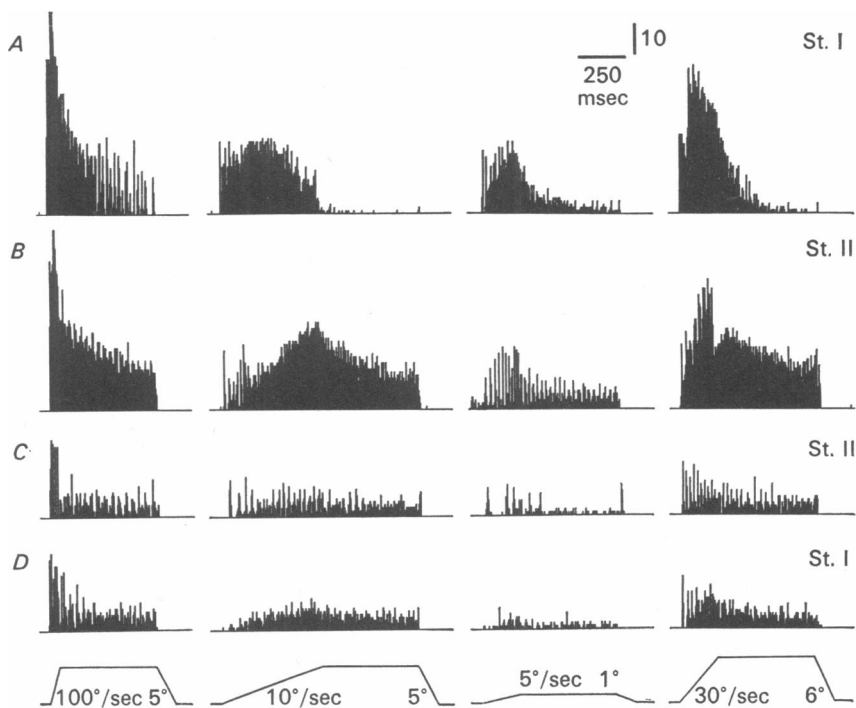

Fig. 4. Peri-stimulus-time-histograms of responses in four slowly adapting primary afferent fibres (A–D). Stimulus conditions in all four units were made as similar as possible and corresponded to the stimulus conditions used for excitation of the relay neurone illustrated in Fig. 3. Responses to two movement velocities at constant final angular deflexion and to two deflexion amplitudes attained at constant rise time are shown. Twenty-five responses in each histogram, bin width 4 msec.

A comparison of responses in slowly adapting primary afferent fibres with those in relay neurones can further illustrate some of the general characteristics of the synaptic relay in the rostral trigeminal nuclei. In Fig. 4 responses in the two kinds of slowly adapting sinus hair afferents

are displayed. Each unit was stimulated under the same conditions as the relay neurone illustrated in Fig. 3 and responses to four different stimulus parameters are shown. It is immediately apparent that great variations exist in the responses of individual receptors and that the discharge pattern in a given afferent fibre can change enormously with different stimulus parameters. However, in no synaptically activated neurone did we ever observe responses of the magnitude of those shown in Fig. 4A, B and even responses such as illustrated in Fig. 4C, D were rare in higher order neurones. This is all the more striking in view of the strong spatial summation which we observed in some synaptically activated neurones.

Another feature of second order responses, not observed in primary afferent fibres, are the strongly periodic discharges as seen in Figs. 1F and 3A. It is conceivable that under certain stimulus conditions such oscillatory responses result from the activation of inhibitory feed-back loops initiated by the first impulses in a given response. The consequence of the interaction of such feed-back loops with tonic discharges can be a damped oscillatory response, as mathematically demonstrated in model neurones by Wilson & Cowan (1972).

Stimulus–response relationships in interneurones

With respect to the characteristics of the stimulus–response relationship, trigeminal interneurones could be subdivided into two different types. In one type, representing about 25 % of our interneurone population, the responses to tactile stimuli occurred only during the movement components in the stimulus and, characteristically, consisted of a brief burst of impulses. These interneurones responded in an all or nothing fashion to stimuli applied anywhere inside of the receptive field and most of them were extraordinarily sensitive towards tactile stimulation. Responses in this first type of interneurone are illustrated in Fig. 5A and the receptive field which included sinus hairs, glabrous skin and fur is delineated in Fig. 5C. The records of the 'dynamic on' response demonstrate that with slower movement velocities individual responses to a given stimulus varied considerably but the mean discharge frequency or the number of elicited impulses during the rise time of the displacement did not change systematically with the stimulus velocity. The plotted stimulus–response relationship (Fig. 6B) confirmed the impression obtained from the original records that in this type of interneurone the response was not systematically related to the stimulus velocity as would be expected from the all or nothing character of the responses.

In the second group of interneurones it was evident even with manual stimulation that the discharge frequency in the responses was quantitatively related to the stimulus. In this type of interneurone spatial and

temporal summation was observed as well as many units with tonic responses during sustained stimuli. Pure phasic responses, however, were seen more often (Fig. 6*A*, *C* and *D*). The upper record in Fig. 6*C* shows a phasic 'dynamic on' and 'off' response which, at sufficiently fast movement velocities, could reach mean discharge frequencies of over 900 impulses/sec (lowest record in Fig. 6*C*).
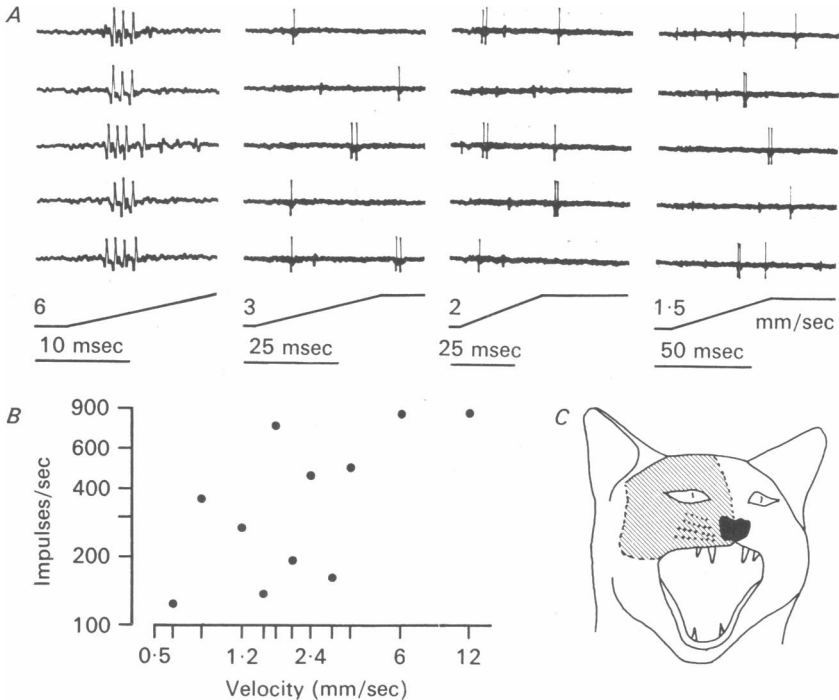

Fig. 5. Response characteristics in one functional type of trigeminal inter-neurone. *A*: five successive responses to four different stimuli. Movement velocities as indicated at the stimulus trace. Constant stimulus amplitude of 1 mm. *B*: a plot of the mean discharge frequencies per burst of impulses in twenty responses to an identical stimulus (ordinate) against the movement velocity of that stimulus (abscissa). The shaded area in *C* delineates the receptive field. The stimulus was a direct displacement of skin in the frontal sinus hair field.

The series of peri-stimulus-time-histograms in Fig. 6*A* shows averaged responses of the same interneurone to stimuli of different movement velocities. For stimulation a plasticine ball of 5 mm in diameter was attached to the probe of the electromechanical stimulator (see Methods) and was moved tangentially across the receptive field. The resulting stimulus response relationship is plotted in Fig. 6*B*. The receptive field

of this interneurone, depicted by the hatched area in the face cartoon, did not include sinus hairs but very similar response properties were also observed in interneurones which included sinus hairs in their receptive field (Fig. 6D).
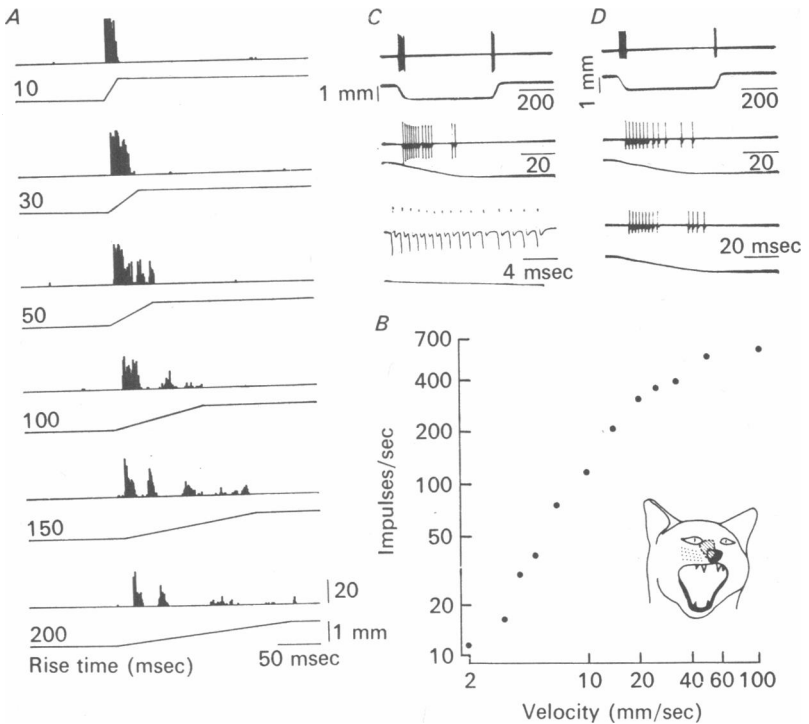

Fig. 6. Responses and stimulus–response relationship in an interneurone of the second functional group. A: peri-stimulus-time histogram of 'dynamic on' responses to displacements of constant amplitudes (1 mm) attained in different rise times. Twenty-five responses in each histogram, bin width 5 msec. B: the mean frequency of discharge during the dynamic part of the 'on' stimulus is plotted as a function of the movement velocity, the shaded area in the face figurine depicts the location of the receptive field. C: three single responses of the same interneurone to an identical stimulus displayed at different sweep velocities. The stimulus velocity was 25 mm/sec. D: single responses of another interneurone with similar discharge properties. Responses to the same stimulus (displacement rate 25 mm/sec) are shown in the upper and middle record at two speeds of beam deflexion, the lowest record shows a response to a slower stimulus velocity of 20 mm/sec. The displacement amplitude was 1 mm.

In several interneurones it was found that the site of stimulation within a large receptive field determined the intensity and the pattern of the responses. In the interneurone of Fig. 7 the receptive field included all

maxillary and supraorbital sinus hairs, fur and the glabrous skin of the nose. Responses to a direct displacement of hairy skin (Fig. 7A) were compared with responses to movements of a single maxillary (Fig. 7B) and a single supraorbital sinus hair (Fig. 7C). Although in this interneurone the evoked discharge was always phasic, the directional sensitivity
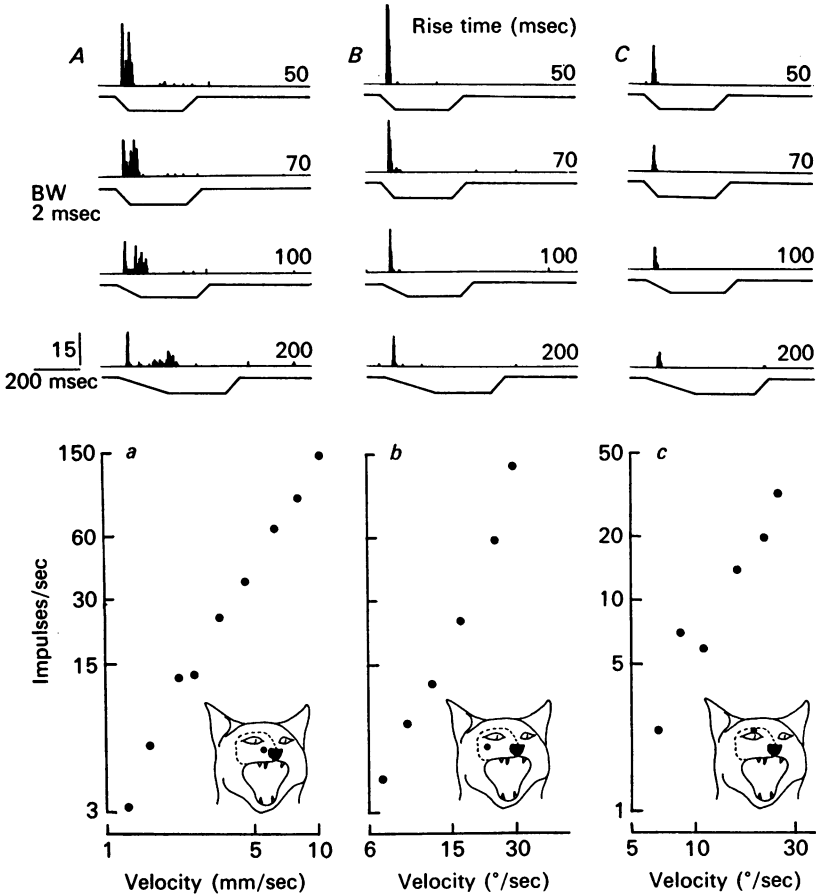

Fig. 7. Responses of an interneurone to stimuli applied at three different sites in its receptive field. The dashed line in the face figurines indicates the extent of the receptive field and the black dots the sites at which the stimuli were applied. The peri-stimulus-time histograms in A show responses to direct skin displacements of hairy skin, in B to angular movements of a single maxillary sinus hair and in C of a single supraorbital sinus hair. The rise times of the respective displacements are indicated to the right of each histogram which consists of twenty-five responses collected at a bin width of 2 msec. The mean discharge frequency during the movement part of the stimulus is plotted against the displacement velocity for the responses at each site of stimulation in a, b and c.

and the requisite slow movement velocities suggest that in the case of the sinus hair stimulation slowly adapting receptor afferents were activated.

For the three stimulation sites, activating either cutaneous or sinus hair follicle receptors, the magnitude of the responses showed some differences but stimulus-response relationships could be established for all three
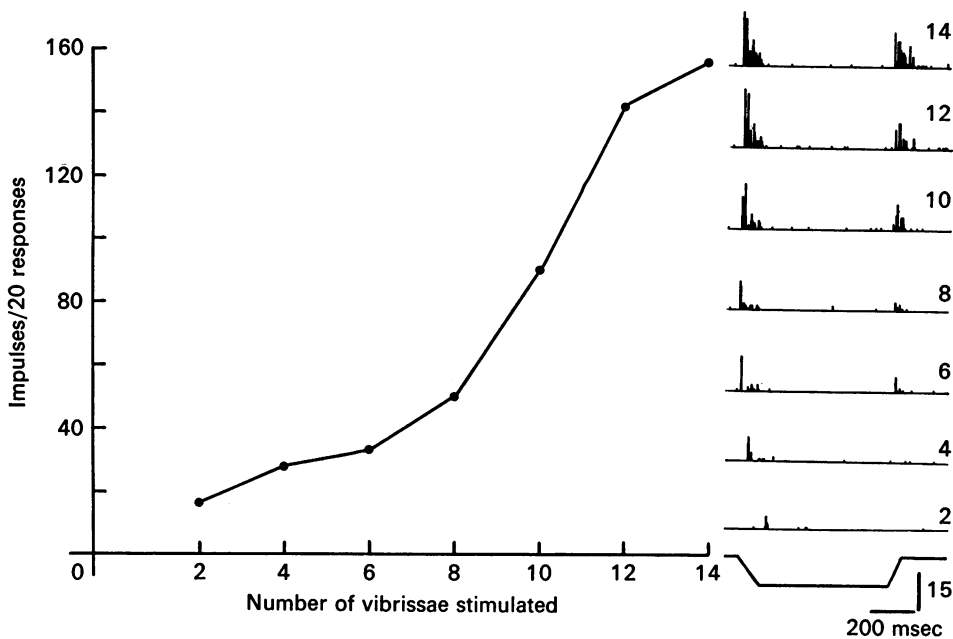

Fig. 8. Spatial summation in an interneurone. Two to fourteen sinus hairs were moved simultaneously. The resulting peri-stimulus-time histograms of twenty responses with the respective number of stimulated sinus hairs are given to the right with the time course of the stimulus at the bottom. The plotted curve represents the number of impulses counted in twenty 'dynamic on' responses for each number of stimulated sinus hairs. Twenty responses in each histogram, bin width 5 msec.

stimulus situations (Fig. 7a–c). The stimulus–response functions, however, were not identical, revealing the highest slope and thus the greatest sensitivity to a change of the displacement velocity for the movement of the maxillary sinus hair. The exponents of the stimulus–response functions were 1·74 for the curve plotted in Fig. 7a, 2·22 in Fig. 7b and 1·64 in Fig. 7c. Since in this interneurone, qualitatively similar responses were obtained following activation of presumably rapidly and slowly adapting receptors, it is suspected that the phasic response characteristics

were determined more by central control mechanisms than by the kind of the afferent inputs.

The effect of spatial summation in interneurones is illustrated in Fig. 8. This interneurone responded only to movements of all large maxillary sinus hairs. Using an identical stimulus, two to fourteen sinus hairs were moved simultaneously with the angle stimulator. The plotted curve and the peri-stimulus-time histograms in Fig. 8 demonstrate that the number of impulses in the 'dynamic on' and the 'dynamic off' responses increased steadily though not arithmetically with the number of stimulated sinus hairs. The sigmoid course for the 'dynamic on' response suggests a non-linear summation process but this is difficult to ascertain since the non-linearity may have resulted from a sequential activation of receptors in individual sinus hair follicles responding differently to the given stimulus.

DISCUSSION

In this paper we have described some examples of stimulus–response relationships in higher order neurones of the rostral trigeminal nuclei which were usually excited by movements of facial sinus hairs, either exclusively or in addition to other cutaneous mechanoreceptive afferents. For two reasons we were specifically interested in the responses of relay neurones and interneurones. Firstly, relay neurones provide the direct input for the thalamo-cortical projection system and, secondly, interneurones seem to belong to systems which modulate the response characteristics of relay neurones.

Previous investigators also described stimulus–response relationships in trigeminal neurones (Mosso & Kruger, 1973; Shipley, 1974; Kirkpatrick & Kruger, 1975), often under specific aspects, such as information transmission capacity (Darian-Smith *et al.* 1968; Darian-Smith, 1970) or the changes in stimulus–response relationships induced by interacting inhibitory or disinhibitory mechanisms (Carmody & Rowe, 1974; Greenwood & Sessle, 1976). With one exception (Greenwood & Sessle, 1976), in which responses to sinus hair stimulation were not specifically investigated, different functional types of neurones were not clearly distinguished in these studies.

In the trigeminal nuclei almost no information is available to what extent the movement velocity of a mechanical stimulus alone determines the response in a given higher order neurone. In most of the previous investigations rectangular displacements of different amplitudes were used for mechanical stimulation in which the movement velocity always changed with the displacement amplitude. For this reason we have separated the dynamic from the static response and established stimulus–

response relationships in each response component as a function of both the movement velocity and the displacement amplitude. Our results show that the dynamic responses in relay neurones receiving input from slowly adapting sinus hair afferents could be determined primarily by the velocity of a displacement while the static responses were determined by both the stimulus velocity and amplitude. This contrasts to response characteristics in slowly adapting primary afferent fibres from cutaneous and sinus hair follicle receptors in which the dynamic as well as the initial static responses depend on both the stimulus velocity and the amplitude (Iggo & Muir, 1969; Chambers, Andres, v. Düring & Iggo, 1972; Pubols & Pubols, 1976; K.-M. Gottschaldt, unpublished results). These findings imply that inaccurate stimulus–response relationships will be obtained if the analysis does not account for different response components, as is the case if rectangular skin displacements of different amplitudes are used and an average discharge frequency is determined during a period of time which includes both the dynamic and static response.

In the sinus hair system of the cat rapidly adapting receptors coding stimulus velocity are not very frequent (Gottschaldt et al. 1973) but a velocity response is contained in the dynamic discharge of slowly adapting afferent fibres. Schultz, Galbraith, Gottschaldt & Creutzfeldt (1976) suggested that perhaps already at the level of the trigeminal nuclei the complex information in slowly adapting afferent responses about the velocity, amplitude, direction and duration of a sinus hair movement can be segregated by neuronal mechanisms into simpler components which then are passed on through different channels to higher centres of the brain. In fact, we have observed relay neurones and interneurones which either responded only with a tonic discharge lacking a dynamic response (Gottschaldt & Young, 1977) or displayed only a dynamic response without a static discharge. In other cases a tonic discharge was qualitatively preserved but the dynamic response was seemingly determined entirely on the movement velocity. Presumably the isolation of a particular response component is achieved by specific inhibitory mechanisms eliminating other response components as recently discussed by Yin & Williams (1976) for phasic thalamic neurones receiving input from slowly adapting joint afferents.

The comparison of responses to identical stimuli in primary afferent fibres and trigeminal relay neurones has demonstrated a considerable reduction of discharge rate in the latter, particularly in the static responses. It is possible that the use of an anaesthetic agent accounts for the general attenuation of post-synaptic tonic discharges. However, the dynamic ranges of static responses, extending over 0·5–1 log unit of stimulus

intensities in our experiments, were in a similar order of magnitude as reported by Carmody & Rowe (1974) who used unanaesthetized, decerebrate preparations. It should also be considered that anaesthetic agents may diminish the effectiveness of those inhibitory mechanisms which in the waking animal would reduce the afferent input. Thus, it usually remains uncertain whether in an anaesthetized preparation a given response is stronger or weaker or a given receptive field larger or smaller than it would be in an awake animal.

No data about stimulus–response relationships in identified trigeminal interneurones have previously been available. The quantitative response characteristics of these interneurones are particularly interesting, for, if they were part of neuronal circuits controlling the input to and the output from relay neurones, it would be expected that also the discharges in interneurones are quantitatively related to peripheral stimuli. For instance, afferent inhibition may be relayed by interneurones and in cuneo-thalamic relay neurones it was found to increase with the strength of peripheral stimuli (Jänig, Schoultz & Spencer, 1977). In the majority of our interneurones stimulus–response relationships could be established. It is more difficult to ascribe a functional role to those interneurones in which the responses did not correlate quantitatively with the intensity of the applied stimulus.

The influence of spatial convergence onto the quantitative response properties in higher order neurones has previously been studied in the spinal afferent system (Armett, Gray, Hunsberger & Lal, 1962; Brown, 1969; Gardner & Spencer, 1972) but not in the trigeminal system. The presence of sinus hairs in the cat's face and the characteristics of the innervation of their follicles facilitates a study of this problem since the excitability of a central neurone by stimulation of more than one sinus hair provides some measure of the degree of afferent convergence. Our data indicate that afferent convergence may be reflected in the responses of relay neurones in two different ways. In some relay neurones the qualitative response characteristics remain unchanged but spatial summation results in a higher discharge frequency of the response. In other cases the progressive recruitment of cutaneous afferents results in qualitative changes of the responses in relay neurones, such as an additional tonic discharge component or the origin of a new response component (Fig. 1). Suppose the detection of the velocity of sinus hair movements bears significance for the cat's tactile orientation, then the stimulus response functions for the velocity dependent 'dynamic on' discharge in relay neurones should be independent from the spatial extent of a stimulus. Although this must not be the case in all relay neurones in one of our examples (Fig. 1) the stimulus response functions for the 'dynamic on'

response in this relay neurone did not differ significantly whether one or four sinus hairs were stimulated.

Our results indicate that in the rostral trigeminal nuclei tactile information from sinus hair receptors is not transmitted in a passive manner. Individual relay neurones can receive, extract and transmit precise information about dynamic stimulus parameters and also have the additional capacity to convey information about the amplitude, direction, duration and the spatial extent of peripheral mechanical stimuli.

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