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INHIBITION WITHIN THE TRIGEMINAL NUCLEUS INDUCED BY AFFERENT INPUTS AND ITS INFLUENCE ON STIMULUS CODING BY MECHANOSENSITIVE NEURONES

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SUMMARY

1. In decerebrate, unanaesthetized cats two thirds of slowly adapting mechanosensitive neurones sampled in the trigeminal nucleus oralis exhibited inhibition in response to conditioning mechanical stimulation applied beyond their excitatory receptive fields. The influence of this inhibition was examined over the response range of these neurones using controlled, reproducible natural stimulation procedures.

2. The extent of the inhibition was graded according to the intensity of the conditioning stimulus. It was evoked most strongly by vibratory skin indentation which very effectively excites rapidly adapting afferent fibres. Tonic conditioning inputs associated with steady skin indentation were less effective.

3. The slope of stimulus–response relationships constructed from responses to inputs from the excitatory receptive field was reduced in 42 % of trigeminal nuclear cells in the presence of afferent-induced inhibition. In the remainder the slope was unchanged.

4. There was no evidence, in the neurones subject to inhibition, of an expansion of their dynamic range defined as the range of stimulus intensities over which a neurone exhibited a graded responsiveness.

5. The variability in responses of an individual neurone at a given stimulus intensity was unchanged by this inhibition.

6. Analysis of the stimulus–response data using information theory statistics revealed that neurones which underwent a reduction in the slope of their stimulus–response relationship in the presence of inhibition displayed a reduced capacity for defining the intensity of skin indentation. This capacity was not modified in those neurones where the slope was unchanged by the peripherally evoked inhibition.

INTRODUCTION

Inhibition evoked by natural stimulation of cutaneous mechanoreceptors has been observed within the first relay of the somatic afferent system both in the dorsal column nuclei (Gordon & Paine, 1960; Perl, Whitlock & Gentry, 1962; Gordon & Jukes, 1964; Andersen, Etholm & Gordon, 1970) and in the trigeminal nuclear complex (Gordon, Landgren & Seed, 1961; Darian-Smith, 1965).

It has been postulated that this inhibition may aid in the discrimination of spatial attributes of tactile stimuli by limiting and shaping the profile of discharge zones in populations of central neurones (Mountcastle, 1957; Mountcastle & Darian-Smith, 1968). For *individual* neurones, however, little is known about the influence of the inhibition on the transmission characteristics which are important in the coding of tactile stimulus intensity. For example, Jänig, Schmidt & Zimmermann (1968) suggested that presynaptic inhibition at the first synapse of the somatic afferent system may result in a reduction in gain, defined as 'the differential ratio of the neurone output increment to the input increment'. They proposed that this reduction in gain of the neurone may, in turn, result in an expansion of the input range over which the central neurone responds. Changes in the variability of responses to a fixed stimulus intensity could also alter the capacity of somatic afferent neurones to code precisely information about stimulus intensity. These propositions have been specifically investigated in the present study of individual neurones within the trigeminal nucleus oralis. In these cells the influence of inhibition by cutaneous afferents on their capacity for coding stimulus intensity has been quantitatively estimated by the use of information theory statistics.

A preliminary account of some aspects of the present work has already been published (Rowe & Carmody, 1970).

METHODS

Animal preparation

The experiments were performed on twenty-six unanaesthetized adult cats (2·5–4·0 kg), decerebrated surgically at the mid-collicular level. A few days before each experiment a metal cap was attached with dental acrylic to the cat's skull to support the animal during the subsequent experiment. This was in place of conventional stereotaxic fixation of the skull which severely restricts access to the face by the mechanical stimulators. On the day of the experiment the animal was anaesthetized with halothane, the trachea cannulated and the femoral artery and vein catheterized. The animal was then supported in a stereotaxic frame by means of the metal cap and a vertebral clamp. A parietal and occipital craniotomy allowed access for the decerebration and exposed the cerebellum above the trigeminal nucleus oralis. Halothane administration was terminated on completion of the decerebration.

During the recording period animals were immobilized with gallamine triethiodide and artificially ventilated. Blood pressure, rectal temperature and end-tidal P_{CO_2} were monitored continuously.

Recording and stimulation procedures

Tungsten micro-electrodes were used for extracellular recording of responses from single neurones within the oralis division of the trigeminal spinal complex (Olszewski, 1950; Darian-Smith, 1973). Electrode penetrations in the brain stem were made in a grid pattern at intervals of 0·5 mm. Identification of trigeminal nuclear cells was based on the recording location which was verified histologically after the experiment in Nissl stained sections (15 μm in thickness) and on the size of peripheral receptive fields (Darian-Smith, Rowe & Sessle, 1968; Rowe & Sessle, 1972; Darian-Smith, 1973). Identification of trigemino-thalamic relay neurones by antidromic stimulation of the contralateral posterior thalamus was not possible in the present experiments as the animals were decerebrate. However, the majority of neurones within the nucleus oralis project their axons to the contralateral thalamus (Darian-Smith, Phillips & Ryan, 1963; Rowe & Sessle, 1972).

When a single neurone was isolated electrophysiologically its receptive field was carefully delineated by gentle mechanical stimulation of the face using a brush or small glass probe. Before the start of each recording period the animal's face had been closely shaved with clippers to allow for maximum accuracy in the application and quantification of mechanical stimuli which were delivered by servo-controlled stimulators (Werner & Mountcastle, 1965; Darian-Smith *et al.* 1968). The positioning of the stimulator probes against the skin was checked with a hand lens and an electrical monitor of contact. Neurones were classified as slowly adapting or rapidly adapting on the basis of their response to a steady indentation (1 sec duration; 30 msec rise time; see Fig. 1) delivered to the point of maximum sensitivity within their excitatory receptive field. Only slowly adapting neurones were selected for study as they are responsible for the coding of indentation intensity (Mountcastle & Darian-Smith, 1968).

Conditioning mechanical stimuli were applied to the skin at a wide variety of sites beyond the borders of the excitatory receptive field to test for inhibition of the neurone. The conditioning stimulus was delivered with every alternate application of the test stimulus and its delivery preceded the test stimulus by 30 msec or occurred coincident with it. Both test and conditioning stimuli were of one second duration and were applied to the skin with probe tips 2–6 mm in diameter. The test stimulus was always a steady indentation of 'rectangular' form, while the conditioning stimulus was usually a vibratory (sinusoidal) indentation (8–200 Hz) superimposed on a rectangular indentation (see Fig. 1). Stimuli were repeated at intervals of 12 sec to allow full recovery of skin position. Ten or more responses were recorded for the test stimulus alone at each intensity and the same number recorded in the presence of the conditioning input. Impulse activity was displayed on an oscilloscope and the number of impulses discharged during the one second stimulation period was counted by means of a differential amplitude discriminator and counter unit. The inhibition produced by the conditioning stimulus was assessed as a reduction in the mean impulse frequency evoked during the one sec period of the response to the test stimulus. Where doubt existed a t test was applied to the conditioned and unconditioned response data.

Stimulus–response relationships were constructed by applying a series of test stimuli over a range which was fractionated into equally spaced steps of indentation. The parameters of the conditioning stimulus were fixed during the investigation of the influence of inhibition over the whole stimulus–response relationship for a neurone.

Analytical methods

Information theory statistics (Miller, 1956; Attneave, 1959; Garner, 1962; Werner & Mountcastle, 1965; Darian-Smith *et al.* 1968) were applied to the stimulus–response data. For this analysis it was assumed that information about the intensity of skin indentation is coded by individual neurones in terms of mean discharge frequency during the period of indentation (Werner & Mountcastle, 1965; Mountcastle, Talbot & Kornhuber, 1966; Darian-Smith *et al.* 1968; Rowe, 1968).

RESULTS

Inhibition of trigeminal nuclear cells by conditioning mechanical stimulation of the skin

Mechanosensitive neurones within the trigeminal nucleus oralis were initially identified by their response to gentle tactile stimulation of the facial skin. The receptive fields of these cells were carefully delineated and were usually confined to restricted areas of the ipsilateral face. Those in the peri-oral region had areas generally in the range of 1·0–1·5 cm^2 while those located beyond this region were larger, usually 3–5 cm^2, findings in agreement with Rowe & Sessle (1972). These tactile receptive field sizes were many times larger than those reported for trigeminal primary fibres whose responses can be recorded from the trigeminal spinal tract which lies immediately lateral to the nucleus (see Fig. 3, also Rowe, 1968; Rowe & Sessle, 1972; Darian-Smith, 1973).

Neurones were classified into slowly and rapidly adapting groups on the basis of their response to a steady indentation applied to the skin with the mechanical stimulator probe (Fig. 1). Those units responding throughout the 1 sec period of indentation were designated slowly adapting neurones (Fig. 1*A*); those which responded only to the dynamic ('on' and 'off') phases of the stimulus were designated rapidly adapting neurones. Only slowly adapting neurones were selected for study and ninety-eight were tested for evidence of inhibition elicited by mechanical conditioning stimuli applied to the skin beyond the excitatory receptive field of the neurone. Of these, 64% (or sixty-three neurones) were effectively inhibited. No systematic study of the spatial organization of the inhibition was made, although surrounding areas of skin, in these studies on the ipsilateral face or contralateral upper lip, were usually the most effective sites. Conditioning stimuli applied more remotely, for example to the ipsilateral forelimb, were rarely effective.

Vibratory indentation always produced greater inhibition than steady indentation. The effectiveness of a vibratory stimulus in producing inhibition is seen in Fig. 1 where the impulse activity is shown for a slowly adapting neurone in response to steady indentation of the vibrissal pad

of the upper lip. The response to this test stimulus alone was an impulse frequency of 77 sec^{-1}, whereas with coincident application of a vibratory conditioning stimulus to the supraorbital skin the impulse frequency was reduced by 35 % to 50 sec^{-1}. This neurone was typical of those analysed in that the reduction in firing frequency resulting from the conditioning stimulus was not confined to the early part of the response period, but occurred throughout the entire period of the response.

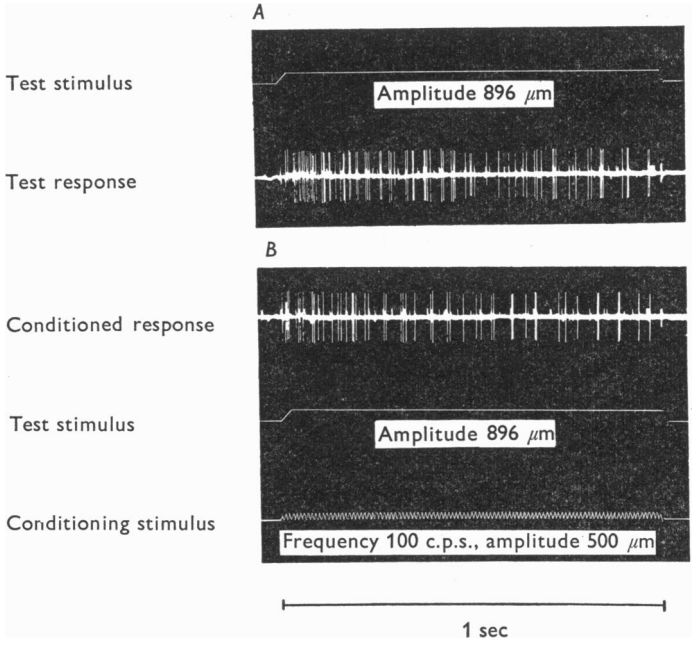

Fig. 1. Inhibition induced in a trigeminal nuclear cell by vibratory cutaneous indentation. *A*, response to steady indentation of the skin (896 μm) on the vibrissal pad of the upper lip. *B*, inhibition induced by stimulation of the ipsilateral supraorbital region by a vibratory conditioning stimulus (100 Hz; 500 μm amplitude). Negativity upwards in spike records.

Each histogram in Fig. 2 shows the distribution of eighty successive responses of a trigeminal nuclear cell to a steady indentation of 448 μm applied to the supraorbital skin. The distributions represented by the continuous lines were obtained when the test stimulus was applied alone; those represented by the broken lines were obtained in the presence of a conditioning stimulus, which in *A* was a *steady* indentation and in *B* a *vibratory* indentation. There is no shift to the left in the distribution of responses in Fig. 2*A*, whereas clear inhibition induced by the vibratory stimulus is evident in Fig. 2*B*. In this latter case the mean response over

the 1 sec period of the test stimulus was reduced from 46·6 to 27·8 impulses sec^{-1}. These observations are consistent with the findings of Andersen *et al.* (1970) that stimuli, such as blowing, which evoke a continuous activation of rapidly adapting afferents, are more effective than steady stimuli in producing primary afferent depolarization in the dorsal column nuclei. In fact, vibratory stimuli of the type employed for conditioning in the present study are particularly effective in activating rapidly adapting primary afferent fibres supplying the facial skin (Fig. 3). The responses

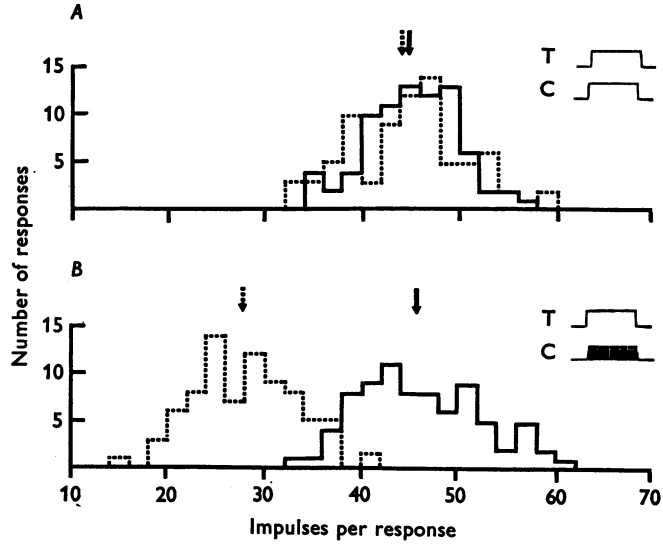

Fig. 2. Distribution of responses of a trigeminal nuclear cell with receptive field in the supraorbital area of the skin. Each histogram represents eighty responses. Those indicated by the continuous lines (in *A* and *B*) show the distribution of responses to the test stimulus (steady indentation, 448 μm amplitude). The histograms represented by the broken lines show the distribution of responses to the combined application of test and conditioning stimuli. The conditioning stimulus was applied to the ipsilateral upper lip and in *A* was a steady 1 sec indentation (448 μm) and in *B* a vibratory stimulus (50 Hz) of the same amplitude. The vertical arrows indicate mean firing frequency for each histogram. Test (T) and conditioning (C) stimulus wave forms are shown on the right side.

for the unit illustrated in Fig. 3 were recorded from the central division of its axon near the lateral border of the trigeminal nucleus. This unit displayed the typical characteristics of a rapidly adapting neurone in responding only to the dynamic components of the stimulus (Rowe & Sessle, 1972). In both cases a one-to-one discharge was evoked during the period of vibration, i.e. one impulse was elicited by each cycle of the vibratory stimulus.

Whereas 64 % of the slowly adapting nuclear cells were inhibited by vibratory conditioning stimuli very few displayed inhibition in response to a steady conditioning stimulus even with the use of the largest stimulus probes (5 or 6 mm diam.). The extent of the inhibition evoked by a conditioning stimulus was graded according to the amplitude of the conditioning stimulus (Fig. 4) as was also observed (Jänig *et al.* 1968) for the primary afferent depolarization of slowly adapting afferents of the dorsal horn.

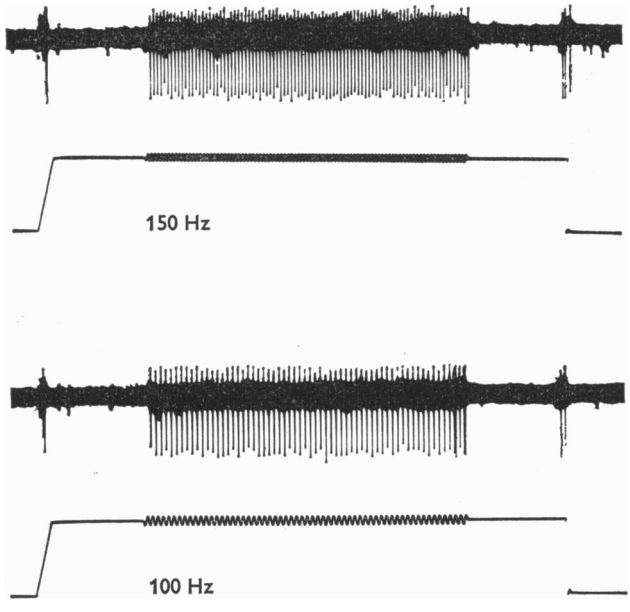

Fig. 3. Responses of a rapidly adapting trigeminal primary fibre which innervated a single vibrissal follicle on the upper lip. At both frequencies (150 and 100 Hz) the neurone followed the stimulus faithfully, i.e. there was one spike for each sine wave of the stimulus. The amplitude of the vibration was 75 μm at 150 Hz and 100 μm at 100 Hz. In each case it was superposed on a steady indentation of 960 μm. Negativity upwards in spike records.

Functional effects of afferent-induced inhibition

Influence of inhibition on the slope of stimulus–response relationships of slowly adapting trigeminal nuclear cells

The test stimuli used in the present investigation will themselves induce inhibition of the neurone under study within 10–20 msec of their onset (Schmidt, Senges & Zimmermann, 1967). However, to evaluate in a controlled way the influence of the inhibition on coding parameters it

was necessary that it be evoked from beyond the excitatory receptive field of the neurone.

The influence of afferent-induced inhibition on the stimulus–response relationships of slowly adapting trigeminal nuclear cells was examined carefully in nineteen units by comparing the normal stimulus–response relationship (triangles in Figs. 5*A* and *B*) with that obtained in the presence of inhibition (circles in Figs. 5*A* and *B*). It was found that in the

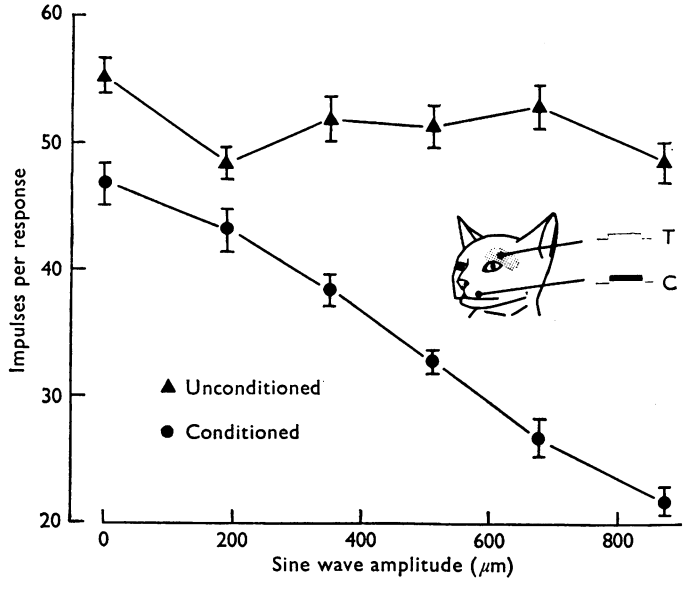

Fig. 4. Effect of the intensity of the conditioning stimulus on the degree of inhibition. The vertical axis shows the firing frequency of a trigeminal cell in response to a steady 1 sec indentation (T; 960 μm) of the supraorbital skin. The conditioning stimulus (C) was applied to the ipsilateral upper lip. A steady rectangular conditioning stimulus (960 μm, indicated as 0 μm on the abscissa) induced some reduction in firing frequency, but when a 50 Hz conditioning stimulus was superposed the magnitude of the inhibition increased virtually linearly with increasing amplitude of the vibratory conditioning stimulus. Each point on the graph is the mean of twenty responses; the vertical lines represent $\pm$ 1 S.E. of mean.

majority of these neurones (eleven out of nineteen) the slope over the linear region of the stimulus–response relationship was unchanged while the inhibition was operating. For the unconditioned stimulus–response relationship illustrated in Fig. 5*A* this slope was 12·9 impulses/100 μm indentation, and that for the stimulus–response relationship obtained under conditions of inhibition was 12·2 impulses/100 μm indentation. The regression coefficients for these two slopes in Fig. 5*A* were not significantly different

($P > 0{\cdot}4$). For neurones such as this, where the slope of the stimulus–response relationship was unchanged, the extent of the inhibition was approximately constant over the whole stimulus–response range. In the remaining eight neurones (42 %) a significant reduction in slope of the stimulus–response relationship accompanied the inhibition (Fig. 5*B*). In these cells the extent of the inhibition always increased through the stimulus–response range. For the unit illustrated in Fig. 5*B*, the slope over the linear part of the unconditioned stimulus–response relationship was 6·2 impulses/100 μm indentation and during the operation of the inhibition was 4·4 impulses/100 μm indentation. This 29 % reduction in slope was highly significant ($P < 0{\cdot}001$).

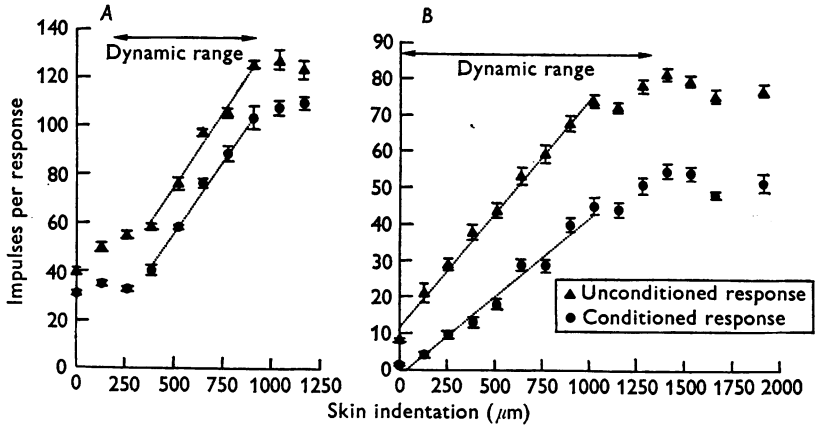

Fig. 5. Stimulus–response relationships for two trigeminal nuclear cells. Each point represents the mean of ten responses and the vertical lines indicate ± 1 S.E. of mean. In the linear portions of these relationships the dotted lines indicate the lines of best fit calculated by the method of least squares. In *A* the two slopes were not significantly different, whereas in *B* the conditioning input has significantly reduced the slope. In neither neurone has the dynamic range of responsiveness (see text) been altered by the inhibitory conditioning input.

Influence of inhibition on the range of responsiveness of slowly adapting trigeminal nuclear cells

The proposal that inhibition operating at the first synapse of the somatic pathway may result in an expansion of the dynamic range of responsiveness of secondary neurones (Jänig *et al.* 1968) has been specifically investigated by studying the stimulus–response relationships of slowly adapting trigeminal nuclear cells over a sufficient range for the stimulus–response relationship to attain a plateau. We define the dynamic range of a neurone as the range of stimulus intensity over which the

neurone exhibits a graded responsiveness. For both the neurones illustrated in Fig. 5 the dynamic range of responsiveness was unchanged during the action of the inhibition. In Fig. 5*A* both curves reach a plateau at a stimulus intensity of approximately 900 μm indentation, and, at the lower end of the curves, begin to display increases in firing frequency at approximately 250 μm indentation. The dynamic range thus extended over about 650 μm of skin indentation for both unconditioned and conditioned curves. For the unit displaying a reduced slope in its stimulus–response relationship in Fig. 5*B*, again the dynamic range was unchanged by inhibition; for both conditioned and unconditioned curves it was approximately 1400 μm. In none of the neurones studied in this detailed aspect was there a clear change in dynamic range associated with the inhibition.

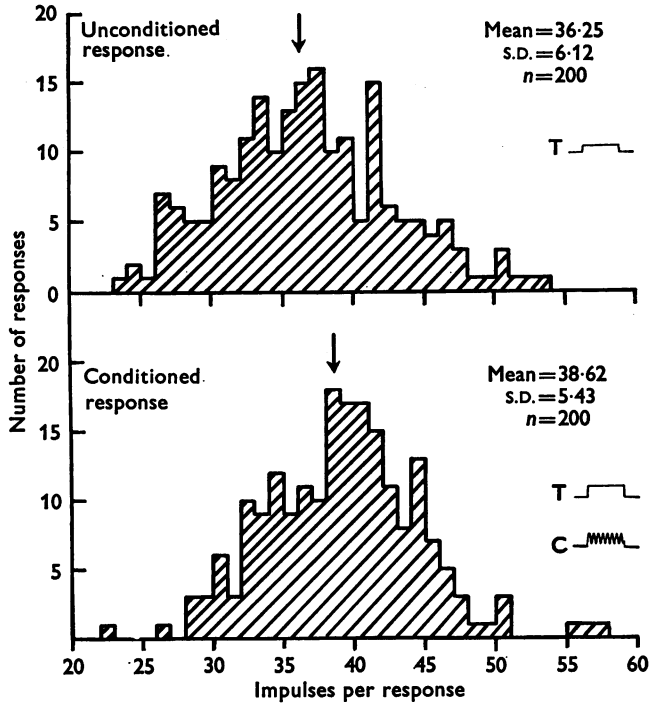

Fig. 6. Histograms of responses of a trigeminal nuclear cell. Supraorbital receptive field. Upper panel: distribution of 200 unconditioned responses to a 1 sec steady test indentation (576 μm). Lower panel: distribution of 200 conditioned responses to a 1 sec steady test indentation (960 μm). The conditioning stimulus applied to the ipsilateral upper lip was an 8 Hz vibratory indentation (amplitude 900 μm). The variances in the two distributions were not significantly different (F test, $P > 0{\cdot}05$). The wave forms of test (T) and conditioning (C) stimuli are indicated on the right side of the Figure.

Influence of inhibition on the variability of responses

Figs. 2*B* and 5 suggest that the variability of responses in the presence of afferent-induced inhibition was unchanged. However, in Fig. 5 each S.E. was based on ten responses, and although larger samples were compared in Fig. 2*B* the mean responses differed considerably in value. This fact raises the difficulty, in the application of the Snedecor *F* test, that the variance of the group with the larger mean may spuriously influence the numerical value of *F*. Accordingly, the variability of responses was studied more thoroughly using either 100 or 200 responses, and the comparison between conditioned and unconditioned responses made for responses of approximately equal magnitude. Thus, when the response was inhibited by the conditioning stimulus the intensity of the test stimulus was increased until the response magnitude approximated that of the unconditioned response (Fig. 6). In addition, Bartlett's test for the homogeneity of variance permits variance comparisons in a number of groups and may be applied to stimulus–response matrices. Fifteen cells were analysed by these methods and in none was there any significant change in response variability.

Influence of conditioning stimuli on information transmission capacity of trigeminal nuclear cells

The capacity of individual somatosensory neurones to code information about the intensity of skin indentation will depend on the parameters discussed earlier, viz. the slope of the stimulus–response relationship, the dynamic range of responsiveness and the variability of responses at a particular stimulus intensity. None of these individual parameters, however, provides a quantitative evaluation of the capacity of the neurone to define, in terms of its mean firing frequency, the intensity of skin indentation. This knowledge can be achieved, though, by using information theory statistics (Werner & Mountcastle, 1965; Darian-Smith *et al.* 1968).

These statistical procedures were employed for sixteen slowly adapting nuclear cells whose mean channel capacity was 2·0 *bits* which is in close agreement with the previously reported value of 2·1 *bits* for nucleus oralis cells (Darian-Smith *et al.* 1968). When the analysis was made for each of these neurones in the presence of inhibition the differences in the paired observations from each neurone were pooled and were not significantly different from zero ($P > 0{\cdot}4$). Among these 16 neurones, however, were eight neurones whose stimulus–response slopes were reduced by inhibition, and eight neurones which displayed no change in slope. One might predict some alteration in channel capacity for the former group since the slope of the stimulus–response relationship was reduced while response variability

and dynamic range were unaltered. When the channel capacities were re-examined for these two separate groups it was found that those cells with no reduction in slope showed no significant change in channel capacity (Fig. 7). In other words, their capacity for defining the intensity of the skin indentation was unchanged ($P > 0{\cdot}3$) in the presence of the inhibition; but, in the eight cells which displayed a reduced slope in their stimulus–response relationship, a small, but consistent, reduction in

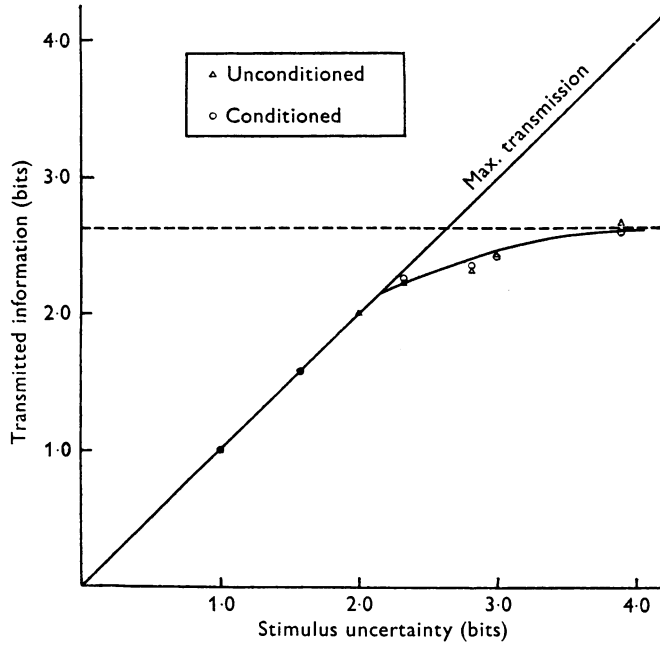

Fig. 7. Information transmission by a trigeminal nuclear cell. The points on the graph were obtained by the statistical techniques of information theory. The single dotted horizontal line indicates the estimated channel capacity of the neurone (2·6 bits) for both the unconditioned and conditioned data. The 45° line indicates the maximum attainable transmitted information for increasing stimulus uncertainty. For this neurone, which had no change in the slope of its stimulus–response relation with inhibition, the conditioning input did not change the channel capacity.

channel capacity was seen (Fig. 8) which was statistically significant ($P < 0{\cdot}01$). For the neurone whose result is depicted in Fig. 8 the transmitted information calculated from the unconditioned stimulus–response relationship gives an estimated channel capacity of 2·22 *bits*, indicating that the neurone could unequivocally differentiate about five stimulus categories over its stimulus–response range. For the conditioned stimulus–

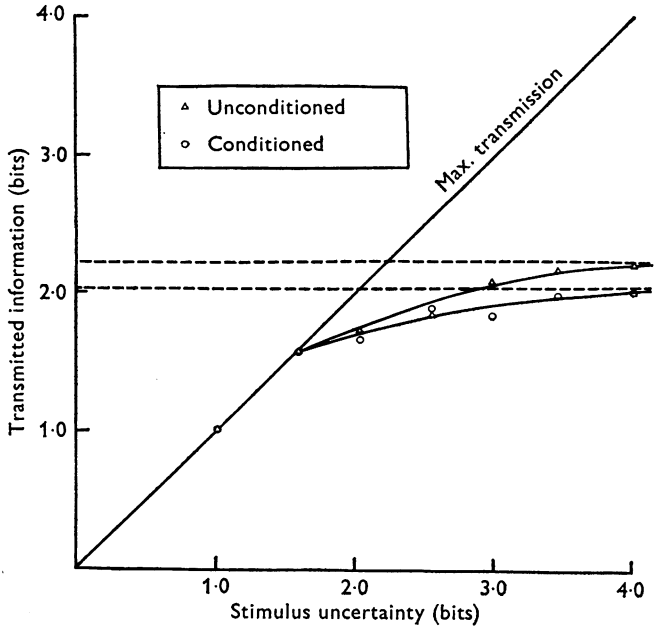

Fig. 8. Information transmission by a trigeminal nuclear cell for which the slope of the stimulus–response relation was reduced by the conditioning input. Details as in Fig. 7. There is a small reduction in channel capacity during the operation of the inhibition.

response relationship, on the other hand, the channel capacity was reduced to 2·05 *bits*, enabling unequivocal indentification of only four stimulus categories.

DISCUSSION

The observation that approximately two thirds of trigeminal slowly adapting neurones displayed inhibition following conditioning mechanical stimulation of the skin contrasts with previous studies made within the dorsal column nuclei which reported that slowly adapting mechanosensitive neurones were not subject to afferent-induced inhibition (Gordon & Jukes, 1962, 1964; Perl *et al.* 1962; Andersen *et al.* 1970). However, for two reasons we cannot be certain that these results reflect a real difference between the slowly adapting neurones of these two regions.

Firstly, in our study the adaptive characteristics of trigeminal neurones were tested by servo-controlled steady skin indentation whose parameters were precisely known and reproducible, in contrast to the other studies which used hand-held stimulus probes and manual stimulation. These, unavoidably, include some tremor which could have activated rapidly adapting units.

Secondly, the present study employed decerebrate animals which were

unanaesthetized except for a short initial period of halothane anaesthesia. We observed in some preliminary experiments with chloralose-anaesthetized cats that, in agreement with Darian-Smith & Yokota (1966), slowly adapting neurones were encountered relatively infrequently. This interference by anaesthesia accords with the observations of Rose & Mountcastle (1959) that the temporal characteristics of a unit's response are particularly susceptible to anaesthetics. As barbiturate anaesthesia was employed during the experiments by Gordon and his colleagues and before decerebration by Perl *et al.* (1962) it is possible that the slowly adapting neurones investigated in their studies may represent a restricted sample, e.g. they might have been cells of the kind which constituted about one third of our sample of slowly adapting cells viz. those uninfluenced by our conditioning inputs. A further complication in the anaesthetized animals could have been a blockade of the inhibitory action normally produced by the conditioning input to the slowly adapting nuclear cells. Certainly, within the thalamus the mechanisms involved in surround inhibition seem to be differentially sensitive to anaesthetics since quite diverse values have been reported for the proportion of thalamic cells subject to this inhibition (Gordon, 1973).

Our finding that dynamic conditioning inputs induced inhibition most effectively is consistent with some previously reported results. Andersen *et al.* (1970) demonstrated that primary afferent depolarization within the dorsal column nuclei is derived, largely, from rapidly adapting afferents. Further, Schmidt, Trautwein & Zimmermann (1966) found that phasic inputs were very much more effective than tonic inputs in producing prolonged dorsal root potentials, although Jänig *et al.* (1968) have since demonstrated that tonic inputs are capable of inducing maintained primary afferent depolarization of individual dorsal root afferents.

The postulate of Jänig *et al.* (1968) that inhibition at the first synapse in the somatic afferent system may reduce the gain of neurones within this system has been confirmed for 42% of the trigeminal slowly adapting mechanosensitive neurones by examining the slope of their stimulus–response relationships. However, this reduction in slope was not accompanied by an expanded dynamic range as they also suggested. The input range over which trigeminal neurones displayed increments in response magnitude was unchanged by the inhibition. An expanded dynamic range for mechanosensitive cells of the dorsal horn has, however, previously been reported by Wall (1967), although this occurred following block of descending activity from the brain stem.

The variability of responses, another determinant of coding capacity of individual neurones was also unchanged by the conditioning inputs. This contrasts with the observation that a reduction occurs in the varia-

bility of post-synaptic field responses in the trigeminal nucleus oralis in the presence of peripheral conditioning inputs which produce inhibition (Rowe, 1970). However, this latter reduction in the variability of the population response may be due to a change in correlation between the excitability of individual neurones contributing to the population response.

In those neurones in which afferent-induced inhibition elicited no change in slope of the stimulus–response relationship there was also no change in channel capacity, a not unexpected finding considering that both response variability and dynamic range, as well as slope, were unaltered by the conditioning inputs. However, in the group of neurones which displayed a reduction in the slope of the stimulus–response relationship in association with inhibition, there was a significant reduction in information transmitting capacity. Thus, for this group of trigeminal nuclear cells the number of stimulus categories over the stimulus–response range which could be differentiated without error is reduced in the presence of afferent-induced inhibition. This small impairment in the domain of intensive coding by individual neurones suggests that if inhibition of the kind under study is to be of functional value in the somatic sensory system it is likely to be through an effect on over-all population responses, for example by sculpting the spatial profile of these responses as has been suggested by Mountcastle & Darian-Smith (1968).

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REFERENCES

ANDERSEN, P., ETHOLM, B. & GORDON, G. (1970). Presynaptic and post-synaptic inhibition elicited in the cat's dorsal column by mechanical stimulation of the skin. *J. Physiol.* **210**, 433–455.

ATTNEAVE, F. (1959). *Applications of Information Theory to Psychology*. New York: Holt, Rinehart and Winston.

DARIAN-SMITH, I. (1965). Presynaptic component in the afferent inhibition observed within trigeminal brain stem nuclei of the cat. *J. Neurophysiol.* **28**, 695–709.

DARIAN-SMITH, I. (1973). The trigeminal system. In *Handbook of Sensory Physiology*, vol. II, *Somatosensory System*, ed. IGGO, A., pp. 271–314. Berlin: Springer-Verlag.

DARIAN-SMITH, I., PHILLIPS, G. & RYAN, R. D. (1963). Functional organization in the trigeminal main sensory and rostral spinal nuclei of the cat. *J. Physiol.* **168**, 129–146.

DARIAN-SMITH, I., ROWE, M. J. & SESSLE, B. J. (1968). 'Tactile' stimulus intensity: information transmission by relay neurons in different trigeminal nuclei. *Science, N.Y.* **160**, 791–794.

DARIAN-SMITH, I. & YOKOTA, T. (1966). Corticofugal effects on different neuron types within the cat's brain stem activated by tactile stimulation of the face. *J. Neurophysiol.* **29**, 185–206.

GARNER, W. R. (1962). *Uncertainty and Structure as Psychological Concepts*. New York: Wiley.

GORDON, G. (1973). The concept of relay nuclei. In *Handbook of Sensory Physiology*, vol. II, *Somatosensory System*, ed. IGGO, A., pp. 137–150. Berlin: Springer-Verlag.

GORDON, G. & JUKES, M. G. M. (1962). Correlation of different excitatory and inhibitory influences on cells in the nucleus gracilis of the cat. *Nature, Lond.* **196**, 1183–1185.

GORDON, G. & JUKES, M. G. M. (1964). Dual organization of the exteroceptive components of the cat's gracile nucleus. *J. Physiol.* **173**, 263–290.

GORDON, G., LANDGREN, S. & SEED, W. (1961). The functional characteristics of single cells in the caudal part of the spinal nucleus of the trigeminal nerve of the cat. *J. Physiol.* **158**, 544–559.

GORDON, G. & PAINE, C. H. (1960). Functional organization in nucleus gracilis of the cat. *J. Physiol.* **153**, 331–349.

JÄNIG, W., SCHMIDT, R. F. & ZIMMERMANN, M. (1968). Two specific feedback pathways to the central afferent terminals of phasic and tonic mechanoreceptors. *Expl Brain Res.* **6**, 116–129.

MILLER, G. A. (1956). The magical number seven, plus or minus two. *Psychol. Rev.* **63**, 81–97.

MOUNTCASTLE, V. B. (1957). Modality and topographic properties of single neurons of cat's somatic sensory cortex. *J. Neurophysiol.* **20**, 408–434.

MOUNTCASTLE, V. B. & DARIAN-SMITH, I. (1968). Neural mechanisms in somesthesia. In *Medical Physiology*, ed. MOUNTCASTLE, V. B., pp. 1372–1423. St Louis: C. V. Mosby Company.

MOUNTCASTLE, V. B., TALBOT, W. H. & KORNHUBER, H. H. (1966). The neural transformation of mechanical stimuli delivered to the monkey's hand. In *Touch, Heat and Pain*, ed. DE REUCK, A. V. S. & KNIGHT, J., pp. 325–345. London: Churchill.

OLSZEWSKI, J. (1950). On the anatomical and functional organization of the spinal trigeminal nucleus. *J. comp. Neurol.* **92**, 401–413.

PERL, E. R., WHITLOCK, D. G. & GENTRY, J. R. (1962). Cutaneous projection to second-order neurons of the dorsal column system. *J. Neurophysiol.* **25**, 337–358.

ROSE, J. E. & MOUNTCASTLE, V. B. (1959). Touch and Kinesthesis. In *Handbook of Physiology*, Section 1, Neurophysiology, vol. I, ed. MAGOUN, H. W., pp. 387–429. Washington: American Physiological Society.

ROWE, M. J. (1968). Trigeminal neural mechanisms of facial tactile sensation. Ph.D. Thesis, University of New South Wales.

ROWE, M. J. (1970). Reduction of response variability in the somatic sensory system by conditioning inputs. *Brain Res.* **22**, 417–420.

ROWE, M. J. & CARMODY, J. J. (1970). Afferent inhibition over the response range of secondary trigeminal neurones. *Brain Res.* **18**, 371–374.

ROWE, M. J. & SESSLE, B. J. (1968). Somatic afferent input to posterior thalamic neurones and their axon projection to the cerebral cortex. *J. Physiol.* **196**, 19–35.

ROWE, M. J. & SESSLE, B. J. (1972). Responses of trigeminal ganglion and brain stem neurones in the cat to mechanical and thermal stimulation of the face. *Brain Res.* **42**, 367–384.

SCHMIDT, R. F., SENGES, J. & ZIMMERMANN, M. (1967). Presynaptic depolarization of cutaneous mechanoreceptor afferents after mechanical skin stimulation. *Expl Brain Res.* **3**, 234–247.

SCHMIDT, R. F., TRAUTWEIN, W. & ZIMMERMANN, M. (1966). Dorsal root potentials evoked by natural stimulation of cutaneous afferents. *Nature, Lond.* **212**, 522–523.

WALL, P. D. (1967). The lamina organization of dorsal horn and effects of descending impulses. *J. Physiol.* **188**, 403–423.

WERNER, G. & MOUNTCASTLE, V. B. (1965). Neural activity in mechanoreceptive cutaneous afferents: stimulus-response relations, Weber functions, and information transmission. *J. Neurophysiol.* **28**, 359–397.