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HUMAN TACTILE DETECTION THRESHOLDS: MODIFICATION BY INPUTS FROM SPECIFIC TACTILE RECEPTOR CLASSES

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SUMMARY

1. Human detection thresholds for a vibratory stimulus applied to the volar surface of the index finger were examined under conditions where afferents from specific tactile receptor classes were simultaneously activated from the thenar eminence. The experiments were designed to test whether stimuli which have been shown previously to induce afferent inhibition of 'tactile' neurones in the cuneate nucleus of the cat could modify human subjective performance in a tactile detection task. Conditioning stimuli to the thenar eminence were usually of three forms; steady indentation to engage slowly adapting tactile receptors; 300 Hz vibration to engage Pacinian corpuscles; and 30 Hz vibration to engage the intradermal, rapidly adapting tactile receptors which are thought to be Meissner's corpuscles.

2. In ten subjects the mean detection threshold for a 30 Hz test stimulus in the absence of conditioning stimulation was $8\cdot6 \pm 1\cdot0$ μm (S.E.). Detection thresholds were increased substantially in the presence of a 300 Hz, 100 μm conditioning stimulus (mean increase $11\cdot1 \pm 2\cdot0$ μm), whereas minor or insignificant effects were seen with conditioning stimuli consisting of (*a*) 30 Hz, 100 μm (mean increase $1\cdot4 \pm 0\cdot8$ μm), (*b*) steady indentation, 1·5 mm in amplitude (mean increase $1\cdot3 \pm 0\cdot7$ μm) or (*c*) 300 Hz, 100 μm to the contralateral thenar eminence (mean increase $0\cdot4 \pm 0\cdot5$ μm).

3. The 300 Hz conditioning stimulus to the ipsilateral thenar eminence caused a marked increase in detection thresholds at all *test* stimulus frequencies over the range 10–450 Hz. The effects of the conditioning stimulation therefore operated on inputs from Pacinian corpuscles, which are responsible for vibration detection at 80–450 Hz, and on inputs from the intradermal, rapidly adapting receptors which are responsible for vibration detection at 10–80 Hz.

4. The band width of conditioning vibratory frequencies which was

effective at amplitudes of 100 μm in bringing about increases in detection threshold extended from 50–80 Hz to 300 Hz, the maximum tested.

5. Whereas amplitudes of 1–2 μm produced clear increases in detection thresholds with conditioning stimuli of 300 Hz, amplitudes of > 200 μm were needed at 30 Hz.

6. The observed elevations in detection threshold are consistent with an afferent-induced inhibitory action exerted at synaptic relays of the sensory pathway by tactile inputs arising exclusively or predominantly from Pacinian corpuscles.

INTRODUCTION

Perceptual consequences of the inhibition induced by afferent inputs at synaptic relays of the sensory pathways appear in a variety of sensory modalities. In vision, for example, it is believed that the zones known as Mach bands, at which perceived brightness is enhanced at borders of contrast arise from inhibitory interactions at the retinal synapses (Hartline, Wagner & Ratliff, 1956; Hartline, Ratliff & Miller, 1958; Ratliff, 1965). Afferent-induced inhibition is also believed to contribute to the perceptual illusion of 'funneling' in tactile sensation where the subject perceives only a single locus of stimulation from within an array of simultaneously presented stimuli at multiple points on the skin (von Békésy, 1958; Gardner & Spencer, 1972*a*, *b*). However, it is thought that the phenomenon of afferent inhibition within the somatosensory pathways normally aids in stimulus localization by limiting the lateral spread of excitation in the neural pathway (Mountcastle & Powell, 1959; Mountcastle, 1974). For individual central neurones it has been suggested that the afferent-induced inhibition could bring about a reduction in gain, defined as the ratio of the neurone output increment to the input increment, and an expansion of the input or stimulus range over which the neurone responds (Jänig, Schmidt & Zimmermann, 1968). Evidence for the reduction in gain but not for the expansion of input range was obtained in our earlier studies in the cat on slowly adapting neurones at the first relay level of the somatosensory pathways (Rowe & Carmody, 1970; Carmody & Rowe, 1974).

More recent studies on the afferent sources of inhibition operating on 'tactile' neurones within the cuneate nucleus of the cat indicated that Pacinian corpuscles were the dominant and perhaps exclusive source of afferent-induced inhibition (Bystrzycka, Nail & Rowe, 1977). These studies have now been extended to determine whether inputs from Pacinian corpuscles and other specific tactile receptor groups can modify human subjective performance in a tactile detection task in a way which is consistent with the differential capacities of these tactile receptors for inducing afferent inhibition. In these psychophysical experiments the subject's performance was compared in the presence and absence of stimuli which activated specific tactile receptor groups from an area of skin near the *test* site for the detection task. Precisely controlled and reproducible mechanical stimuli of the types used in our earlier cuneate studies (Bystrzycka *et al.* 1977) were used to selectively engage the different tactile receptor groups from the palmar surface of the hand. The results of these psychophysical experiments are consistent with observations in the earlier cuneate experiments in the cat (Bystrzycka *et al.* 1977) and imply that Pacinian corpuscles are the dominant or exclusive source of afferent-induced inhibition in the tactile somatosensory pathways in man as well as in the cat.

METHODS

Experiments were performed on ten healthy young adults, five females and five males, all of whom were totally naive about the objectives of the experiments. They were seated comfortably with their right hand placed palm downwards on a perforated metal plate (Fig. 1). Two servo-controlled mechanical stimulators (Darian-Smith, Rowe & Sessle, 1968; Carmody & Rowe, 1974; Bystrzycka *et al.* 1977) were positioned beneath the plate with their shafts protruding through 1·5 cm diameter holes in the plate. The shafts ended in circular probes, 6 mm in diameter, which were used for stimulation of the volar surface of the index finger and the thenar eminence (Fig. 1). They were initially positioned by raising them to the point of contact with the skin. In five experiments the left hand was also placed over a similar metal plate. In these experiments one mechanical stimulator was positioned beneath the index finger of the right hand and the other beneath the thenar eminence of the left hand.

Subjects were placed so that probe movements were not visible to them. They were also fitted with earphones, through which background music was played to ensure that they received no auditory cues associated with the vibratory test stimuli.

Tactile detection task

For the tactile detection task subjects were asked to indicate whether they could detect the presence of a sinusoidal vibration train, usually 30 Hz lasting for 1 sec, delivered to the distal pad of the index finger. This vibratory *test* stimulus, T in Fig. 1, was superimposed on a 4 sec duration step indentation of the skin of 670 μm amplitude. When the vibration train was presented it began 1·5 sec after the onset of the step, the latter providing the cue for the subject to concentrate on the detection task. All subjects were instructed to say '*Yes*' if they were reasonably sure that vibration was present and '*No*' if they could not detect it or were uncertain. They were also instructed to direct their attention to the text stimulus, whether this was delivered with the conditioning stimulus or delivered alone. Subjects were requested to make their decision during or immediately following the step indentation. The repetition rate of stimuli was one per 10 sec. A series of ten to twenty trials was initially given to familiarize each subject with the nature of the detection task.

The 30 Hz *test* vibration was delivered at four to ten different amplitudes in the range of 0–50 μm. Psychometric function curves (see Fig. 2) were constructed by plotting the number of '*Yes*' responses from ten stimulus deliveries at each amplitude of the test vibration, first when the *test* vibration was delivered alone (the *control* psychometric function curve), and secondly when it was accompanied by *conditioning* stimulation to the thenar eminence (the *conditioned* psychometric function curve). A random order was employed for presentation of *control* and *conditioned* stimuli. The detection threshold, read from the psychometric function curve was arbitrarily defined as the vibration amplitude at which the subject gave positive responses to 50 % of stimulus deliveries (Mountcastle, LaMotte & Carli, 1972; LaMotte and Mountcastle, 1975). The influence of conditioning stimulation on detection thresholds was evaluated by measuring the difference in detection threshold between the paired *control* and *conditioned* psychometric function curves. The mean change in μm was obtained for the group of subjects and a paired t test used to determine its significance. Conditioning stimuli to the thenar eminence (C in Fig. 1) lasted 4 sec and were coincident with the step indentation accompanying the *test* vibration. The choice of parameters for the conditioning stimulus was based both on the observations of Talbot *et al.* (1968) on the differential sensitivity of different tactile receptor groups to particular forms of mechanical stimulation, and on our recent observations on the susceptibility of cuneate neurones to inhibition induced by certain forms of controlled mechanical stimulation (Bystrzycka *et al.* 1977). The conditioning stimuli were usually of three forms; firstly, steady indentation at an amplitude of 1500 μm to engage slowly adapting tactile receptors from the thenar eminence; secondly, 30 Hz sinusoidal vibration at 100 μm amplitude to engage preferentially the dynamically sensitive tactile receptors located intradermally and which are believed to be Meissner's corpuscles (Talbot *et al.* 1968; Jänig, 1971); and

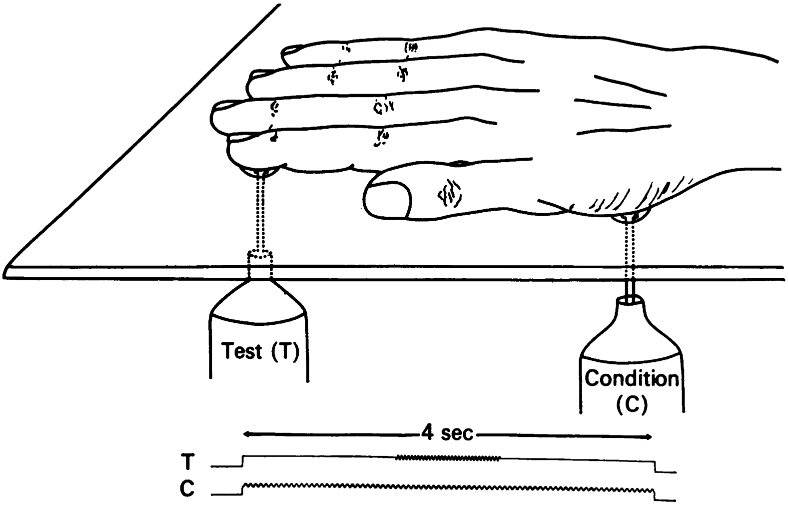

Fig. 1. Experimental arrangement. The subject's hand was placed palm downwards on a rigid metal plate. The shaft of each mechanical stimulator protruded through holes in the plate to permit delivery of *test* stimuli (T) to the index finger and *conditioning* stimuli (C) to the thenar eminence. The waveforms and timing of *test* and *conditioning* stimuli are shown in the lower traces. Both include a step indentation on which vibration was superimposed, in this case 30 Hz for the *test* stimulus and 20 Hz for the *conditioning* stimulus.

thirdly, 300 Hz sinusoidal vibration at 100 μm amplitude to engage Pacinian corpuscles (Hunt & McIntyre, 1960; Sato, 1961; Talbot *et al.* 1968). These tactile receptors which have been studied in detail in animals are also known to be present in the skin of human beings (Cauna, 1954, 1956; Cauna & Mannan, 1958; Miller, Ralston & Kasahara, 1958).

RESULTS

The psychometric function curves from which detection thresholds were obtained (Fig. 2) resembled closely those illustrated in earlier reports on cutaneous vibration thresholds (Mountcastle *et al.* 1972). The mean detection threshold for the 30 Hz *control*, or *test* stimulus to the index finger for the ten subjects was 8·6 ± 1·0 μm (S.E.) which was similar to values obtained in earlier studies on human and monkey subjects (Verrillo, Fraioli & Smith, 1969; Mountcastle *et al.* 1972). The mean for the five female subjects, 7·5 ± 1·2 μm (S.E.) was not significantly different ($P > 0{\cdot}2$) from the mean value obtained for the five males, 9·6 ± 1·4 μm (S.E.). The small subject-to-subject variation in absolute detection threshold was probably associated with differences in skin thickness and sensitivity, and variations in the decision criterion of individual subjects (Swets, 1964). This subject-to-subject variation in decision criteria is reflected in the 'false positives' registered by some subjects but not others at zero amplitude of the *test* vibration (see Fig. 2*B*).

Influence of conditioning stimulation on detection thresholds

The psychometric function curves of Fig. 2 were obtained in a female subject, aged 19 years. The continuous lines connecting filled circles in *A*, *B* and *C* represent *control* psychometric function curves and show the relation between the number of *yes* responses for the ten deliveries of the 30 Hz *test* vibration alone and the vibration amplitude. The horizontal interrupted lines represent the 50 % detection level at which thresholds were estimated. The broken lines connecting filled squares in *A*-*C* represent *conditioned* psychometric function curves obtained in the same series of trials as the associated *control* curves. For the control psychometric function curve in *A* the detection threshold, read from the abscissa, is approximately 8 μm. In the presence of a 300 Hz (100 μm) conditioning stimulus applied to the thenar eminence of the same hand the subject required larger amplitudes of the *test* vibration for detection, resulting in a shift to the right of the psychometric function curve. The detection threshold in this case was approximately 33·5 μm, a 294 % increase over the *control* value. In the same subject there was little or no change in the detection threshold in the presence of either a 30 Hz (100 μm) conditioning stimulus applied to the thenar eminence of the same hand (Fig. 2*B*) or a 300 Hz (100 μm) conditioning stimulus applied to the thenar eminence of the contralateral hand (Fig. 2*C*). In Fig. 3 the detection thresholds accompanying 30 and 300 Hz (100 μm) conditioning on the ipsilateral thenar eminence have been plotted for all cases in which studies were made at both frequencies. Values obtained for 30 and 300 Hz conditioning from the same series of trials in individual subjects are connected by a line. The mean change in detection threshold in the presence of a 30 Hz conditioning vibration was $1{\cdot}4 \pm 0{\cdot}8$ μm (S.E.) which was not significantly different from the *control* value ($P > 0{\cdot}1$). However, as all but one of the observations showed a small increase in threshold a non-parametric *sign test* based on whether the threshold change was above or below zero yielded a significant result ($P < 0{\cdot}02$). With the 300 Hz conditioning stimulation the detection threshold was elevated very significantly ($P < 0{\cdot}001$), the mean increase being $11{\cdot}1 \pm 2{\cdot}0$ μm (S.E.).

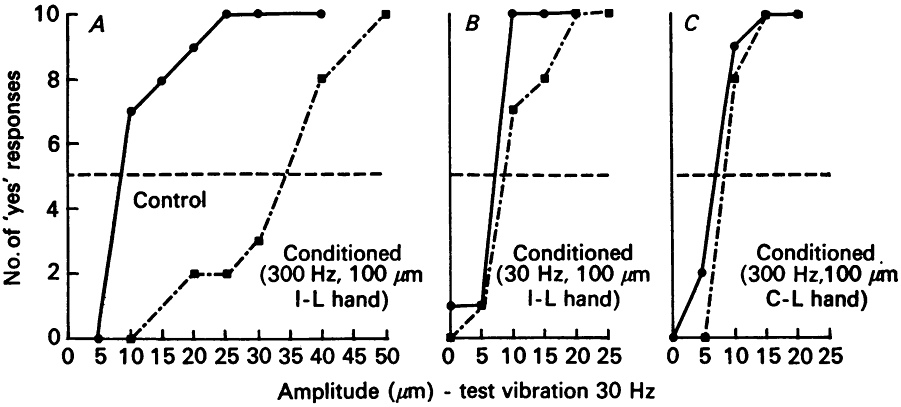

Fig. 2. Psychometric function curves relating the number of positive responses of the subject (female, aged 19 years) to the amplitude of the *test* vibration delivered to the index finger. Each point was based on 10 deliveries of the *test* stimulus. In *A*, *B* and *C* the continuous lines connecting filled circles are *control* psychometric curves. The interrupted lines connecting filled squares are psychometric function curves obtained when *conditioning* stimuli were applied to the thenar eminence. Detection thresholds were taken as the vibration amplitude at which the 50% detection level was reached (horizontal interrupted lines in *A*–*C*). In *A* and *B* the conditioning stimulus was applied to the ipsilateral (I–L) thenar eminence, while for *C* it was delivered to the contralateral (C–L) thenar eminence.

The absence of any clear effect on detection threshold of a 300 Hz (100 μm) *conditioning* stimulus to the contralateral hand for the individual subject in Fig. 2*C* was confirmed in five subjects, a mean increase of $0{\cdot}4 \pm 0{\cdot}5$ μm (S.E.) being obtained which was not significant ($P > 0{\cdot}4$). Observations in five subjects on the effects of a steady *conditioning* stimulus applied to the ipsilateral thenar eminence to engage slowly adapting tactile afferents, revealed no significant change ($P > 0{\cdot}3$) in detection thresholds (mean increase, 1·3 ± 0·7 μm, S.E.).

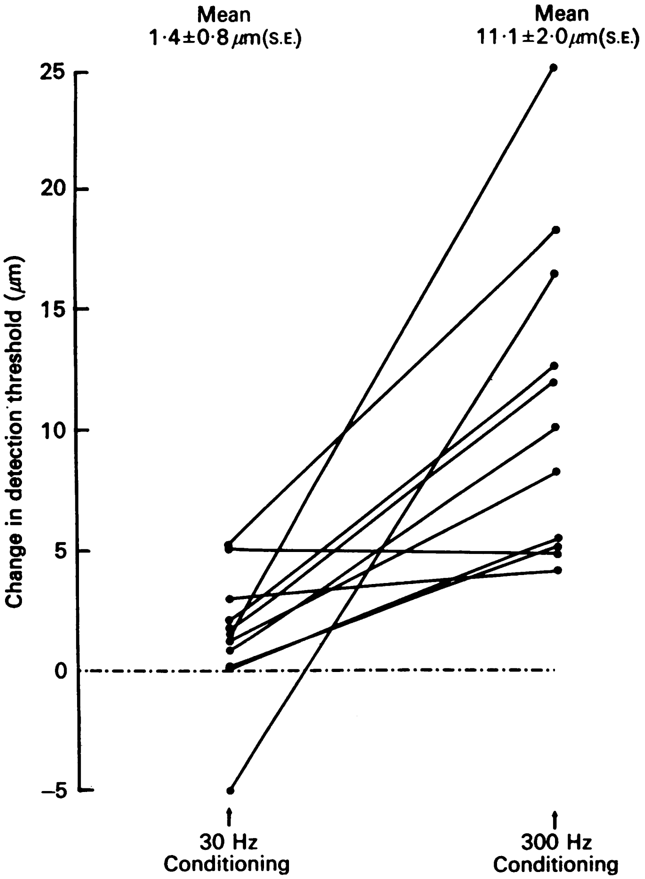

Fig. 3. Effect on detection threshold of 30 and 300 Hz conditioning stimulation at 100 μm amplitude. The change in detection threshold (μm) from the control values, represented by the horizontal interrupted line, is plotted on the ordinate. The lines connecting points at 30 and 300 Hz represent values obtained for one series of trials in 10 subjects. The results obtained in a separate series of trials for one subject have also been included.

Influence of conditioning stimulation on detection thresholds for 'test' stimuli of different frequencies

The neural information which accounts for the subjective ability to detect the 30 Hz *test* vibration delivered at low amplitudes to the glabrous skin comes from intradermal, rapidly adapting receptors (Talbot *et al.* 1968) which are believed to be Meissner's corpuscles (Talbot *et al.* 1968;

Jänig, 1971). Additional experiments were carried out to determine whether conditioning inputs could *also* modify subjective detection thresholds when the detection task depended on inputs from a different class of tactile receptor. For these experiments the *test* stimuli to the index finger were chosen at a number of different frequencies in the range 10–450 Hz, which covers most of the spectrum of human cutaneous vibratory sensibility. At high frequencies, 100-450 Hz, the perception of vibration depends upon neural inputs from the sub-cutaneous Pacinian corpuscles (Talbot *et al.* 1968).

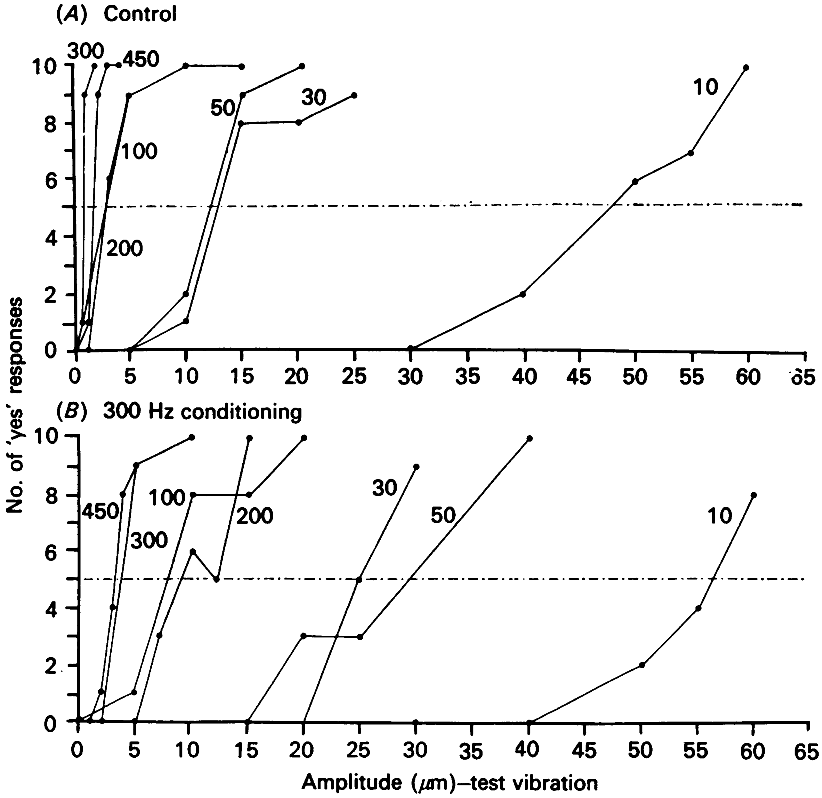

Fig. 4. Psychometric function curves relating the number of positive responses to the amplitude of the *test* vibration at a series of seven different frequencies indicated next to each curve. The *control* psychometric curves are plotted in *A* and those obtained in the presence of a 300 Hz conditioning stimulus plotted in *B*. The horizontal broken lines represent the 50 % detection level at which thresholds were estimated. Subject, male aged 20 years.

Detection thresholds were examined in one subject at seven different frequencies of the *test* vibratory stimulus *with* and *without* conditioning stimulation. Fig. 4 illustrates for these seven frequencies the *control* psychometric function curves in *A* and the corresponding curves obtained in the presence of 300 Hz conditioning stimulation in *B*. For each of the seven *test* frequencies the paired psychometric function curves display a shift to the right in the presence of the 300 Hz conditioning stimulus. The detection thresholds taken from the *control* and *conditioned* curves are plotted in the lower half of Fig. 5 for these seven frequencies. In the upper

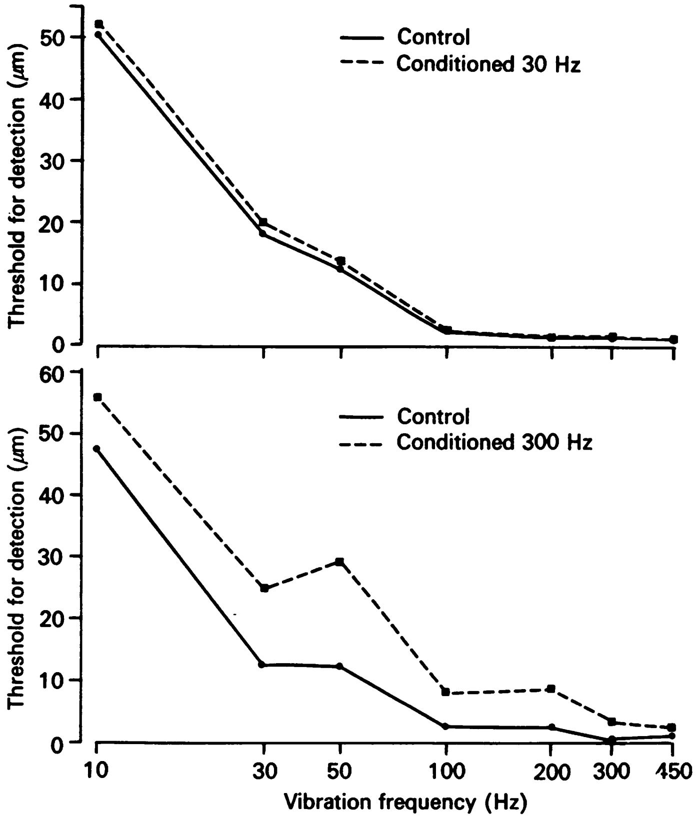

Fig. 5. 'Tuning curves' of detection thresholds at different frequencies of the *test* stimulus (abscissa) to the index finger. Individual points in the lower graph were obtained from the seven pairs of psychometric function curves of Fig. 4; those in the upper graph from corresponding *control* and *conditioned* psychometric function curves with 30 Hz conditioning. Lines connecting filled circles represent *control* tuning curves. Interrupted lines connecting filled squares represent curves for detection in the presence of the conditioning inputs. Conditioning vibration amplitude, 100 μm. Data for upper and lower graph from the same subject, male aged 20 years.

graph of Fig. 5 the *control* and *conditioned* detection thresholds are also plotted for the same subject when a 30 Hz conditioning stimulus was employed. Little or no change was associated with 30 Hz conditioning, while a consistent elevation in detection threshold is apparent at all *test* frequencies in the presence of 300 Hz conditioning. The largest absolute changes in threshold for this subject were seen at *test* frequencies of 30 and 50 Hz, considerably smaller absolute changes being seen for the higher *test* frequencies. However, as the thresholds at 300 Hz and 450 Hz are very low, e.g. 0·75 μm at 300 Hz, the changes at these frequencies represented large percentage increases.

Influence of different frequencies of conditioning vibratory stimuli on detection thresholds

In the preceding section it was shown that detection thresholds for all vibratory frequencies in the range 10–450 Hz were increased substantially in the presence of 300 Hz conditioning stimulation but not by 30 Hz conditioning vibration. The effect on detection thresholds of *conditioning* stimuli at a variety of frequencies was examined in order to establish the band width of frequencies which is able to modify subjective performance in the detection task. The results of this study are shown for three subjects in *A–C* of Fig. 6. In all cases the detection task involved a 30 Hz *test* stimulus. The change in detection threshold is plotted against the frequency of the *conditioning* stimulus (100 μm amplitude) to the thenar eminence. The height of the stippled area above and below the abscissae in *A–C* represents ± 1 S.D. unit expressed as a percentage of the mean for *control* detection thresholds in the absence of conditioning stimulation. For all three subjects the detection threshold in the presence of low frequency conditioning stimulation overlapped the scatter observed for control values of detection thresholds. However, detection thresholds were consistently increased in all three subjects at frequencies above 50–80 Hz, the maximum increase being observed at a conditioning frequency of 300 Hz in each case.

Effect on detection threshold of changes in amplitude of the conditioning vibratory stimulus

Conditioning stimulation at 300 Hz caused marked increases in detection thresholds at amplitudes as low as 1–2 μm (Fig. 7). For the subject whose results are plotted in Fig. 7 there was an irregular but marked increase in detection threshold as the amplitude of the 300 Hz *conditioning* vibratory stimulus was increased to 100 μm, the maximum amplitude tested. In the presence of the 30 Hz conditioning stimulus a small elevation in detection threshold was observed at amplitudes up to 200 μm, however, for the most part these values fell within one S.D. unit for the *control* detection threshold values indicated by the stippling above the

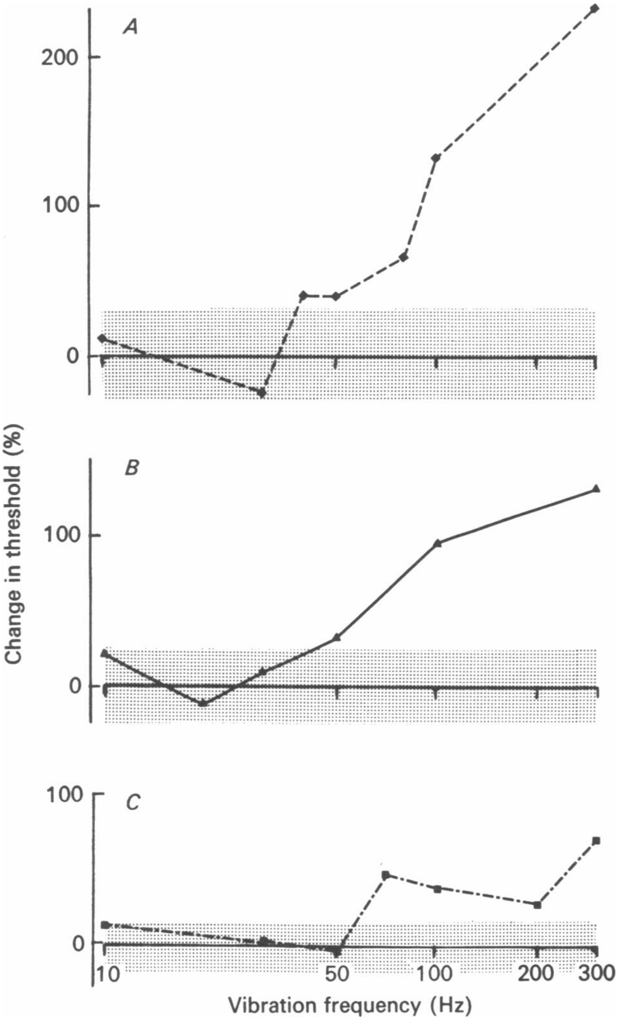

Fig. 6. Effect of different conditioning stimulus frequencies on thresholds for detection of a 30 Hz test stimulus for three different subjects, *A–C*. The percentage change in detection threshold from the control value, has been plotted (ordinate) for different frequencies of the conditioning stimulus (amplitude 100 μm) to the thenar eminence. The height of the stippled areas in *A–C* represents ± 1 S.D. unit expressed as a percentage of the mean value for the *control* detection threshold (six to seven observations for each subject). *A*, male subject, age 25 years; *B*, female subject, age 21 years; *C*, female subject, age 20 years.

abscissa in Fig. 7. At the higher amplitude of 500 μm the 30 Hz conditioning stimulus produced a greater increase in detection threshold. This was the only subject in which a systematic study of changes in conditioning stimulus amplitude was made at both 300 and 30 Hz. Two other subjects tested with a 300 Hz (5 μm) conditioning stimulus displayed a 107 and 21 % increase in threshold, while the 30 Hz (100 μm) conditioning stimulus produced 18 and 10 % increases respectively.

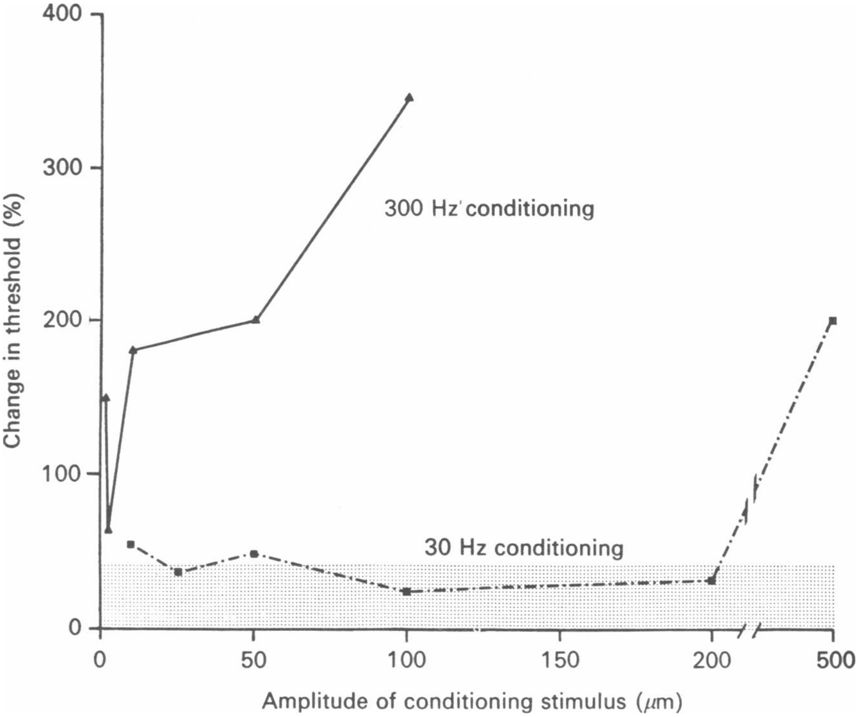

Fig. 7. Effect of different amplitudes of conditioning stimuli at 300 and 30 Hz on thresholds for detection of a 30 Hz *test* vibration to the thenar eminence. The stippled area above the abscissa represents 1 S.D. unit expressed as a percentage of the mean for the *control* detection thresholds (eighteen observations). Subject, female age 21 years.

DISCUSSION

Selection of the routine *test* stimulus for the detection task was guided by our earlier observations that among 'tactile' neurones of the cuneate nucleus, the class displaying the highest incidence of afferent-induced inhibition was that which derived its input from rapidly adapting receptors of the glabrous skin (Bystrzycka *et al.* 1977). These receptors and the cuneate neurones they supply are optimally sensitive to cutaneous vibration at frequencies of approximately 30 Hz (Talbot *et al.* 1968; Bystrzycka *et al.* 1977). The *control* detection thresholds obtained for the 30 Hz and other frequencies of the *test* stimulus were similar to those reported previously (Goff, 1967; Verrillo, 1962; Verrillo *et al.* 1969; Mountcastle *et al.* 1972).

The observed elevation of detection thresholds in the presence of conditioning stimulation may be associated with a number of possible actions of the conditioning stimulus. These include mechanical interference with the *test* stimulus as a result of travelling waves from the conditioning site, distraction of the subject with loss of attention to the *test* stimulus and sensory inhibition at synaptic relay sites in the sensory pathways of the brain. Considerable dispersion normally occurs for travelling waves of disturbance set up in the skin by a vibrating probe, although the extent of spread is profoundly affected by factors such as the mechanical impedance of the tissues in the region of the stimulus site, the surface area of contact and the frequency of the applied vibration (von Gierke, Oestreicher, Franke, Parrack & von Wittern, 1952; von Békésy, 1955, 1967; Moore, 1970). In the present study we have sought to minimize the spread of mechanical disturbances by applying the vibratory probes to the skin through 1·5 cm diameter holes in a rigid metal plate. The plate not only supported the hand but prevented the spread of surface waves beyond the free surround which was circumscribed by the perimeter of the hole (Verrillo, 1962).

The elevation in detection thresholds accompanying conditioning stimulation could be attributed to an impairment in the subject's ability to attend to the *test* stimulus. However, it seems improbable that this explanation can account for the results as the marked increases in detection threshold were obtained only with quite specific forms of conditioning stimuli, and then only from quite specific locations. Steady indentation and low frequency vibration produce minor or insignificant increases in threshold, whereas 300 Hz conditioning vibration produced very significant elevations in detection threshold. The 300 Hz stimulus might be more distracting than 30 Hz at the same amplitude, as equal subjective magnitude estimates for the two frequencies require the amplitude of the 30 Hz vibration to be 15–20 times that at 300 Hz (Verrillo *et al.* 1969). However, it seems unlikely that the marked increases in detection threshold with 300 Hz were due simply to distraction as the increases were obtained only with ipsilateral stimulation. No significant effect was seen from the contralateral stimulus site. Nevertheless, a general but slight distraction effect may be exerted by all forms of conditioning stimuli as the minor changes in threshold which accompanied both steady indentation and 30 Hz (100 μm) conditioning to the ipsilateral hand and 300 Hz conditioning to the contralateral hand were almost always in the direction of an increase in threshold rather than a decrease.

In many respects the modifications in detection threshold accompanying 300 Hz conditioning are consistent with a central inhibitory action induced by afferent inputs. First, the location-specificity of the effect is consistent with the 'surround' organization of areas which can give rise to afferent-induced inhibition within the relay nuclei of the tactile somatosensory pathways (Mountcastle & Powell, 1959; Gordon & Paine, 1960; Perl, Whitlock & Gentry, 1962; McComas, 1963; Gordon & Jukes, 1964; Darian-Smith, 1965; Darian-Smith & Yokota, 1966; Andersen, Etholm & Gordon, 1970; Gordon, 1973; Carmody & Rowe, 1974; Bystrzycka *et al.* 1977).

Secondly, the afferent-induced inhibition observed within the first relay of the somatosensory pathway is known to reduce the responsiveness of neurones over the entire range of stimulus intensities to which they respond (Rowe & Carmody, 1970; Carmody & Rowe, 1974; Bystrzycka *et al.* 1977). Thus, the elevation in subjective detection thresholds accompanying conditioning inputs is consistent with these inputs causing inhibition of central neurones at threshold and near-threshold levels of response.

Thirdly, there was a striking correspondence between the conditioning stimulus forms which caused an elevation in tactile detection thresholds in the present psychophysical experiments and those which gave rise to afferent-induced inhibition of different 'tactile' neurone types of the cuneate nucleus in the cat (Bystrzycka *et al.* 1977). In both studies we employed identical mechanical stimulators and stimulus controls. Neither steady indentation (1·5 mm amplitude) nor low frequency sinusoidal vibration at amplitudes of 50–100 μm induced afferent inhibition of cuneate neurones or caused significant elevation in tactile detection thresholds. In contrast, high frequency vibration, > 80–100 Hz, induced powerful inhibition of cuneate neurones (see Figs. 3 and 4, Bystrzycka *et al.* 1977) and in the psychophysical studies produced marked elevations in tactile detection thresholds. In *both* the neural and the psychophysical studies the effects of the 300 Hz conditioning stimulus were apparent at amplitudes as low as 1–5 μm. For the 30 Hz conditioning stimulus, significant inhibition and threshold elevation was only seen when the amplitude exceeded 100–200 μm.

The elevation in detection thresholds occurred over the whole range of frequencies (10–450 Hz) used in the detection task. Over this range the ability to detect cutaneous vibration depends on inputs from two classes of tactile receptors (Verrillo, 1968; Talbot *et al.* 1968). Pacinian corpuscles are responsible for detection at the high frequencies (80–450

Hz), whereas a class of rapidly adapting, intradermal tactile receptors, thought to be Meissner's corpuscles, is responsible for detection at low frequencies, 10–80 Hz (Talbot *et al.* 1968; Jänig, 1971). The present results therefore indicate that the actions of the 300 Hz conditioning stimuli which bring about an elevation in detection threshold operate on inputs from both of the tactile receptor classes involved in the present detection tasks. Again, this is consistent with the earlier neural data which demonstrated that the inhibitory actions of the 300 Hz conditioning stimulus operated on all classes of 'tactile' neurone tested in the cuneate nucleus (Bystrzycka *et al.* 1977).

The close parallels between the conditioning stimulus forms which were effective in inducing inhibition of cuneate neurones and elevations in tactile detection threshold strongly suggests that the behavioural effects are mediated by inhibitory actions at central relays of the tactile sensory pathways. A similar conclusion was reached by Wall and Cronly-Dillon (1960) who observed an elevation in subjective thresholds for detecting 'warmth' and 'pain' in the presence of a vibratory conditioning stimulus of 60 Hz at an amplitude of 3/16 in. At the time of their study the differential sensitivity of different classes of tactile receptors to sinusoidal vibration had not been demonstrated. Frequencies around 60 Hz represent the switch-over region from the activation of intradermal, rapidly adapting receptors to the activation of Pacinian corpuscles (Talbot *et al.* 1968). Undoubtedly, the amplitudes used at 60 Hz by Wall & Cronly-Dillon, approximately 4 mm, will activate both Pacinian and the intradermal, rapidly adapting tactile receptors. In the present study we have chosen stimulus parameters which will selectively or preferentially activate *particular* tactile receptor groups in order to examine their separate capacities for producing alterations in subjective detection performance, and to determine whether this paralleled their capacity for inducing inhibition of 'tactile' neurones within the cuneate nucleus (Bystrzycka *et al.* 1977). The results indicate that only those stimuli which activate Pacinian corpuscles produce significant elevations in detection thresholds in the present detection task. Although Pacinian corpuscles are optimally sensitive to cutaneous vibration at approximately 300 Hz they may be activated at low frequencies, for example 30 Hz, if high amplitudes are used. Consequently, the clear elevation in detection threshold observed with 30 Hz conditioning at 500 μm amplitude (Fig. 7) need not be attributed to inputs from intradermal, rapidly adapting tactile receptors as some Pacinian corpuscles will be activated under these conditions (Talbot *et al.* 1968). The parallels between the present psychophysical data and our earlier cuneate results suggest that the dominant or exclusive source of afferent-induced inhibition in the tactile sensory pathways of *both* man and cat is from Pacinian corpuscles. Fig. 8 summarizes in simple, schematic form for a sensory relay such as the cuneate the organization of afferent-induced inhibition which has been inferred from our neural and psychophysical data. It depicts the three major classes of tactile afferent from the glabrous skin (Brown & Iggo, 1967; Burgess, Petit & Warner, 1968; Burgess & Perl, 1973), the stimuli which will selectively engage them, the Pacinian afferents as the source of the inhibition, and, the distribution of the inhibition on the different classes of tactile neurones.

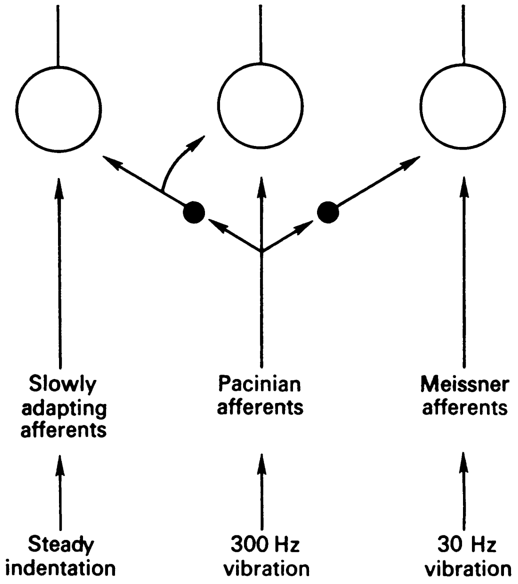

Fig. 8. Scheme showing source of afferent-induced inhibition at a sensory relay nucleus based on prior neural data on the cuneate nucleus (Bystrzycka *et al.* 1977) and the present psychophysical observations. Three classes of myelinated tactile afferent fibres activated from the glabrous skin are represented along with stimulus forms which may be used to selectively engage them. The open circles represent secondary relay neurones and the filled circles inhibitory interneurones mediating the afferent-induced inhibition.

The significance of afferent-induced inhibition which is brought about by Pacinian inputs may relate to the fact that the Pacinian corpuscles are particularly responsive to rapidly changing mechanical stimuli. Consequently, when abrupt changes occur in the patterns of tactile stimulation the Pacinian inputs will initiate an inhibitory suppression of other channels for tactile inflow, thereby ensuring that information about the abruptly changing aspects of tactile inputs is given priority of access to higher centres. Earlier behavioural observations of von Békésy (1955) tend to support this notion. He found that when the edge of a wire frame was lowered abruptly on to the skin the resulting sensation was more localized than with slower rates of application. He concluded that inhibiion was strong for stimuli of rapid onset producing a great amount of 'funneling'. These actions of inhibition in the tactile sensory pathways are perhaps analogous to the Mach band effects in vision where perceived brightness is accentuated at regions of abrupt change in contrast (Hartline *et al.* 1956; 1958; Ratliff, 1965).

One of the aims in seeking correlations between the synaptic interactions observed in our earlier cuneate studies and subjective sensory performance is to specify those neural mechanisms underlying the subjective performance. Although the involvement of the dorsal column–lemniscal pathway in transmitting information about passively received tactile stimuli has been seriously questioned (Wall, 1970) the correlations reported above are quite consistent with the notion that the cuneate nucleus serves as a relay for sensory information underlying subjective performance in the tactile detection task under study. Of course, our data do not preclude similar neural interactions at parallel ascending relays in the spino-thalamic pathway or the spino-cervico-thalamic pathway. However, no evidence has been found for Pacinian inputs activating spino-thalamic neurones (Willis, Maunz, Foreman & Coulter, 1975) or spino-cervical tract cells (Brown, 1968). Nor does the spino-cervical tract show the surround pattern of inhibition observed for the dorsal column–medial lemniscal system (Brown, 1973).

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