

## TACTILE DISCRIMINATION OF TEXTURED SURFACES: PERIPHERAL NEURAL CODING IN THE MONKEY

By GRAHAM D. LAMB\*

*From the Sensory Processes Laboratory, Department of Physiology,  
University of Melbourne, Parkville, Victoria, Australia*

(Received 16 July 1982)

### SUMMARY

1. Recordings were made from single mechanoreceptive afferents in the median or ulnar nerve of the anaesthetized monkey while the appropriate digital pad was stimulated by a textured surface moving at a constant velocity tangentially across the skin. The surface was swept across the afferent's receptive field many times, each time having been displaced sideways (laterally) by a small amount.

2. The neural responses showed a temporal rhythm directly related to the period of the raised dots on the surface in the dimension parallel to the direction of movement. The responses also displayed direct dependence on the position of the dots and the period size in the lateral surface dimension. It was clear that only information from a *large number* of afferents could enable the discrimination of the textured surfaces examined.

3. For large-dot (2.0 mm period) surfaces, increases of up to 8% in the period of the dots, in either surface dimension, produced a roughly linear increase in the mean response rate of every rapidly adapting (r.a.) afferent. There was virtually no change in the response rate of any slowly adapting (s.a.) afferent when the period of the dots was increased by similar small amounts, and the pacinian afferents (p.c.) displayed a wide range of behaviour to such period changes.

4. In contrast, the mean response rate of p.c. afferents seemed most able of the three populations to transmit information about changes in the period in the case of small-dot (1.0 mm period) surfaces.

5. The adequacy of a number of neural codes in accounting for all the psychophysical discrimination reported in the preceding paper (Lamb, 1983) was examined. A strong case could be made for a code involving the total or mean number of impulses evoked (a rate code), based on the r.a. afferent responses for the large-dot surfaces and, less certainly, on the p.c. afferent responses for the small-dot surfaces.

### INTRODUCTION

The preceding paper (Lamb, 1983) described a series of psychophysical experiments in which human subjects were required to discriminate between two given textured surfaces differing only slightly in the spacing of their structural elements. If a subject performed at above chance levels when the surfaces were moved over his immobilized

\* Present Address: School of Physiology and Pharmacology, University of New South Wales, Kensington, New South Wales 2033, Australia.

finger (passive touch) then sufficient information to enable discrimination of the surfaces *must* have been contained in, and extracted from, the cutaneous neural response. That aspect of the neural response which transmits such 'behaviourally usable' information is called the 'neural code' (Uttal, 1969, 1973; Johnson, 1980*a, b*). This paper describes neural responses elicited by mechanoreceptors in the monkey digital pad when the same surfaces as were used in the preceding psychophysical study (Lamb, 1983) were moved tangentially over the monkey's finger.

The list of candidate neural codes for texture discrimination in the somatosensory system is very large. Earlier studies on thermal sensibility (Darian-Smith, Johnson, LaMotte, Shigenaga, Kenins & Champness, 1979*a*; Darian-Smith, Johnson, LaMotte, Kenins, Shigenaga & Vun, 1979*b*; Johnson, Darian-Smith, LaMotte, Johnson & Oldfield, 1979) had to consider only a relatively small number of candidate codes because the spatial and temporal characteristics of the stimuli were simple and because only one population of receptors was primarily activated by such stimuli. However, previous tactile studies have shown that all three mechanoreceptive populations in the monkey digital skin are activated by relative tangential movement between the skin and a surface (Darian-Smith & Oke, 1980; Darian-Smith, Davidson & Johnson, 1980; Johnson & Lamb, 1981). Moreover, it was found that pertinent information describing a textured surface might theoretically be coded by any of a number of aspects of the cutaneous response such as the mean response rate, the temporal sequence of the impulses, or the two-dimensional spatial arrangement of the activated receptor endings. It was nevertheless clear that, regardless of the particular neural code, only the responses of a *number of afferents* could signal sufficient information to permit discrimination of textures in which the structural detail varied in both planar surface dimensions. A single afferent could not provide unambiguous information about both surface dimensions.

Decision theory (Johnson, 1980*a, b*) enables calculation of the discriminative performance that would be theoretically possible if the nervous system based its judgements only on information about the stimulus contained in some particular aspect of the neural response, such as the mean response rate or the temporal spacing of the impulses. This technique was used in the investigation of the neural coding of thermal sensibility (Darian-Smith *et al.* 1979*a, b*; Johnson *et al.* 1979) and produced strong evidence that the nervous system coded the relevant information in the form of the *total response rate* (or a simple derivative) in a group of afferents (possibly between ten and one hundred). A rate (or intensive) code, even when it involves the integration of the responses of a number of afferents, is relatively simple, and this paper examines the adequacy of such a code in accounting for human texture discrimination (Lamb, 1983).

#### METHODS

Experiments were performed on anaesthetized macaque monkeys (three *M. nemestrina*, one *M. speciosa*) weighing between 4.0 and 10.0 kg. Anaesthesia was induced by intravenously administered pentobarbitone sodium (initial dose 30 mg/kg, followed by approx. 4 mg/kg every 30 min), and rectal temperature was maintained between 35 and 37 °C. Recordings were made in either the median or ulnar nerve; the fibre dissection and general procedures have been described previously (Darian-Smith, Johnson & Dykes, 1973; Darian-Smith & Oke, 1980). With one exception, only fibres innervating the distal phalangeal pads were used in this study. Mechanoreceptive units were

classified (Talbot, Darian-Smith, Kornhuber & Mountcastle, 1968) as being slowly adapting (s.a.), rapidly adapting (r.a. or q.a.), or pacinian (p.c.) afferents by using a 1.2 mm diameter punctate probe driven by a servo-controlled linear motor (Chubbuck, 1966); s.a. afferents were the only mechanoreceptors to respond for more than 1 sec to a steady indentation, and r.a. and p.c. afferents were distinguished from each other by their responses to punctate vibratory stimuli.

*Surfaces.* The plastic surface strips (320 mm × 17 mm) used consisted of regular arrays of raised dots (0.65 mm high); for one half of the strip the dots were arranged in a square array pattern A, and for the other half the dots were arranged in a (slightly modified) rectangular pattern B. The production technique was identical to that described by Lamb (1983). Two sizes of square array patterns (A surfaces) were produced: the period of the dots (centre-to-centre spacing) was either 1.0 or 2.0 mm, with the dot diameters being one third of the period. For both period sizes, two different series of modified (B) surfaces were produced in which the period of the dots in one of the two surface dimensions was made incrementally longer than in the corresponding A surface, by some constant amount. The first series had increases in the period in the dimension corresponding to the intended direction of movement (i.e. *along* the long axis of the strip) of approximately 1.0, 2.0, 3.0 and 5.0%. The second series had incremental increases in the period of 1.0, 3.0, 5.0 and 8.0% in the surface dimension perpendicular to, or *across*, the intended direction of movement (see Lamb, 1983). For each of the four combinations of period size (1.0 and 2.0 mm) and dimensional change (along and across), four strips were produced, each consisting of an A segment and one of the appropriate B segments detailed above. The four strips of each set were fixed side by side around the perimeter of one of four Perspex drums, in pseudo-random order.

*Pattern stimulation.* One of the above drums was mounted on the pattern stimulator (Darian-Smith *et al.* 1980; Johnson & Lamb, 1981) and rotated at a constant velocity, and when released by a solenoid the counterbalanced drum dropped down under gravity approximately 1 mm onto the immobilized monkey finger. The drum could be positioned so that any one of the four strips would contact the skin when the solenoid was released. The contact force was 40 g wt. and the circumferential velocities used were: 40, 73, 145 and 220 mm/sec. The force used here produced an average pressure of 1.0 g/mm<sup>2</sup>, which was in the range previously found optimal for human textural discrimination (Lamb, 1983). The solenoid was electronically controlled and could drop and lift the drum at any specified point in each revolution, thus enabling the tangential stimulation of the skin by any selected part of the surface strip. At any given velocity, the initial skin contact was always made at the same relative position along the square array section of the strip (A). The total contact time was varied with velocity so that *continuous* stimulation was produced by at least a 50 mm length of, first, the A section and then the B section of the strip; the total contact times per revolution were 3.0, 2.3, 1.4 and 1.0 sec at circumferential velocities of 40, 73, 145 and 220 mm/sec respectively.

The pattern stimulator enabled examination of the dependence of the neural response on the lateral dimension of the surface (the dimension perpendicular to the direction of movement) as it displaced the drum by 1/8 mm sideways (laterally) on every revolution (Darian-Smith *et al.* 1980). For each strip neural data was collected for 40 consecutive drum sweeps and thus neural responses were obtained with the surface in forty different lateral positions relative to the skin, the total lateral displacement of the surface being 5.0 mm.

The four strips on each drum were successively used for tangential stimulation in random order; the order of the various stimulation conditions (velocity, period size, dimensional change) was also random. Before the first recording every afferent was stimulated tangentially for 5 min to produce maximum comparability between subsequent recordings in the event of initial adaptation effects.

*Data recording and analysis.* The timing, storage and initial analysis of the synchronous stream of neural and surface position data have been described previously (Johnson & Lamb, 1981). Impulse (or spatial event) plots were produced to display the relative circumferential and lateral position of the surface upon occurrence of each action potential, for each set of 40 sweeps (drum revolutions). The circumferential positions of all surfaces were referred to the same arbitrary origin on the circumference of each drum.

All data was also displayed in the form of 'temporal profile' histograms (Fig. 7) which indicated the mean instantaneous response rate of the afferent (averaged over all 40 successive revolutions) at each circumferential position of the surface from initial contact to disengagement with the skin. The response rate was calculated as the weighted sum of the reciprocal of the time interval between successive action potentials, using 1.78 mm (i.e. 2.0°) bin widths.

Lateral-profile histograms (Fig. 6) were used to display the mean response rate in each of the 40 adjacent sweeps, over any selected circumferential range (usually 35 mm long). Adjacent bins in the histogram represented the mean response rate in the corresponding parts of successive revolutions, thus showing the responses when the surface was laterally repositioned with respect to the finger in 1/8 mm units, over a total of 5.0 mm.

*Temporal period analysis.* The presence of any periodicity in the neural response in the circumferential (temporal) dimension was examined by a computer which calculated the relative size and spacing of any periodic maxima and minima in the impulse plot data (Fig. 1). The calculations were made using the circumferential positions of every impulse evoked over a given circumferential range (50 mm long) on all 40 successive sweeps. A best-fit analysis was used to compute the cycle length (period) of the rhythmic groupings of impulses – such a value is presumably related to the period of the dots in the circumferential dimension of the stimulating surface. The ‘modulation fraction’ was used to quantify the relative size of the periodic minima in the neural responses (Fig. 1) and it indicates the fractional decrease in the impulse density at the minima relative to the maxima. A value of 0.0 indicates that there was no periodicity whatsoever in the circumferential (temporal) dimension of the neural response, and a value of 1.0 indicates that there were evenly spaced zones (times) in the response, of unspecified width, in which absolutely no impulses were elicited in any revolution by the surface.

*Mean rates.* The mean rate of response was determined for specified sections of the neural response by first calculating the average impulse frequency in each revolution over an integral number of periods in the circumferential dimension. The average of these individual revolution values was then calculated over that number of revolutions required to translate the surface by an integral number of periods in the lateral dimension. For example, for a 2.0 mm period square array surface the average was taken over 32 revolutions, during which the surface was moved laterally by 4.0 mm (exactly twice the centre-to-centre spacing of adjacent dots). Similarly for a surface in which the period had been increased by 3% in the ‘across’ dimension, (2.06 mm lateral period), 33 revolutions were used (4.125 mm).

## RESULTS

*Fibre sample.* Thirteen r.a., eight s.a. and seven p.c. afferents innervating the volar surface of the distal digital pads of macaque monkeys were studied with both punctate and tangential stimulation. In addition, one p.c. afferent innervating the palm was also investigated. For all digital afferents both punctate and tangential pattern stimulation were delivered as closely as possible to the zone of maximal sensitivity for each afferent, whereas for the palmar unit, punctate stimulation was similarly applied but the pattern stimulation was delivered to the distal pad of the middle finger. The response characteristics to punctate stimulation of all fibres formed representative samples of the ranges previously reported for each afferent population (Mountcastle, Talbot & Kornhuber, 1966; Talbot *et al.* 1968; Johnson, 1974). No units had spontaneous discharge, or responsiveness to stretching of the skin at points further than several millimetres away from the boundary of the receptive field defined by von Frey hairs.

*Pattern stimulation.* Fig. 1(A–F) displays segments of impulse plots obtained by stimulation of the three mechanoreceptor populations using the large (2.0 mm)-period square-array surface moving at 73 mm/sec across the skin. Examples of a relatively low and a relatively high mean response rate are shown in the Figure for all three populations, though these plots cannot be claimed to be totally representative of those recorded as the critical response parameters are not necessarily apparent or known. A number of features are immediately clear. First, fibres in all three populations responded vigorously to such moving stimuli, with mean rates ranging from 1.1 to 5.6 impulses/incident dot per revolution (Fig. 1 A and D respectively). Secondly, there was an obvious periodicity in the responses of all types of afferents, at least in the

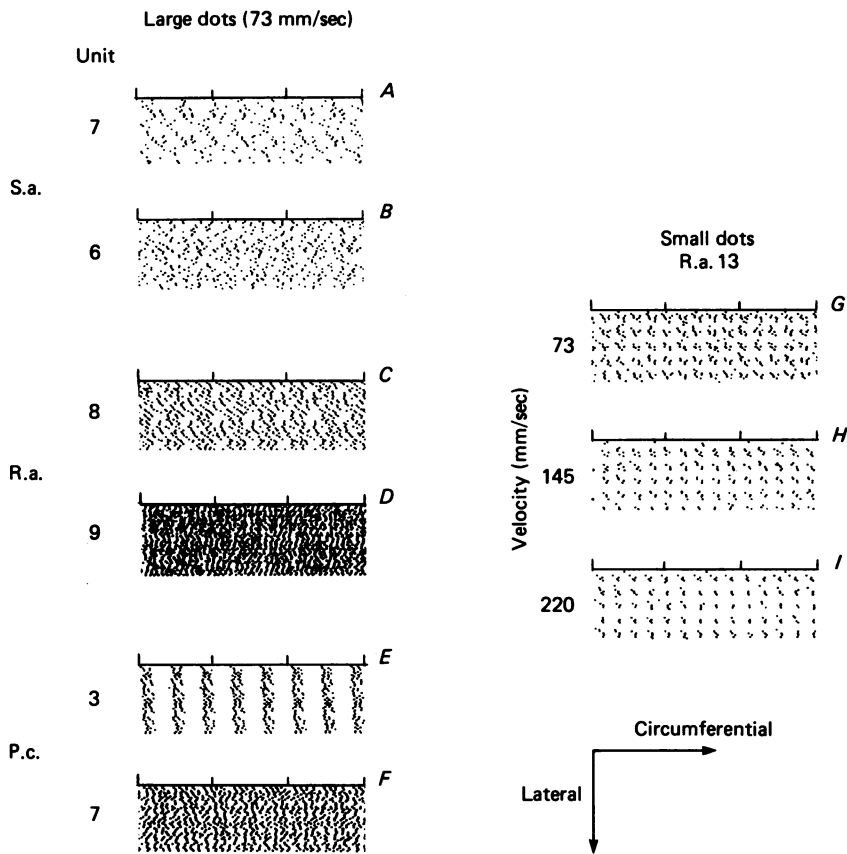


Fig. 1. Impulse plots for various afferents and velocities of surface movement. All plots show the response evoked by a 15 mm long circumferential segment of surface on 40 consecutive revolutions. Each point represents the occurrence of an action potential. *A-F* illustrate the responses produced by stimulation with a large-dot (i.e. 2.0 mm period) surface moving at 73 mm/sec. *G, H* and *I* display the response of an r.a. afferent to stimulation with a small-dot (i.e. 1.0 mm period) surface at different velocities; at all three velocities there is a clear periodicity in the response in both the circumferential (temporal) and lateral dimensions.

circumferential (temporal) dimension, that corresponded closely to the period of the incident surface dots (2.0 mm). Thirdly, the individual afferents responded in various fashions to the surfaces; some had very confined responses relative to the surface structure, and others responded over virtually the whole interval between adjacent dots.

These three features were invariably apparent in the responses of all afferents investigated with the large (2.0 mm)-period surfaces, at all speeds. However, many r.a. and s.a. afferents were relatively unresponsive to the small (1.0 mm)-period surfaces, regardless of the velocity, though in any fibre in which there was sufficient response (including all p.c. afferents) a basic temporal periodicity corresponding to the 1.0 mm spacing of the dots was always evident. The mean response rate to the small-dot surfaces was as low as 0.07 impulses/dot per revolution in some r.a. afferents and frequently dropped even lower at later times (e.g. 2.0 sec) in each sweep.

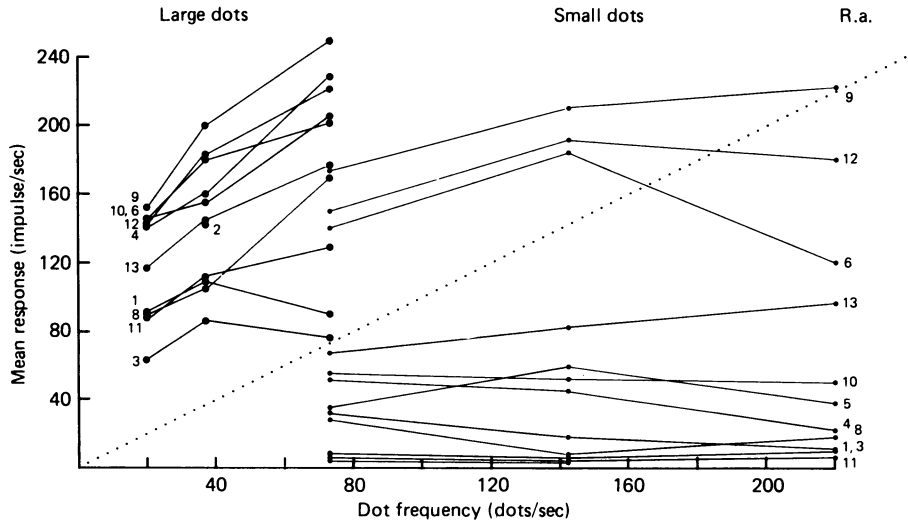


Fig. 2. Mean response rates to pattern stimulation of all r.a. afferents plotted against the frequency with which the lines of dots passed over the skin. The ordinate displays the mean response rates evoked by an approx. 40 mm long segment of surface, 0.5 sec after the initial contact with the skin on each revolution. The large filled circles indicate the response values for the large-dot surfaces (2.0 mm period) and the small filled circles do so for the small-dot surfaces (1.0 mm period). Continuous lines join points relating to the same unit, the unit number being shown with each. The dotted line indicates the response rate at which on average one impulse is generated by each line of dots passing over the skin on every revolution.

The principle effect on any afferent of moving a surface at a higher velocity across the skin was to reduce the number of impulses elicited by each surface dot on each revolution; this is indicated in impulse plots in terms of a decreasing density of dots. Fig. 1*G, H* and *I* display this effect for an r.a. afferent responding to stimulation by a 1.0 mm square-array surface section (A). Furthermore, this unit clearly displayed the periodic structure of *both* dimensions of the surface, at all velocities. Despite the aforementioned decrease in the number of impulses/dot with increasing speed, the mean rate of response (impulses/sec) of all afferents almost invariably either was constant or increased with an increase in velocity.

*Mean response rates.* Fig. 2 shows the mean response rates for the thirteen r.a. afferents studied. The ordinate gives the instantaneous response rate and the abscissa indicates the frequency with which the lines of dots on each surface passed over the skin. The very low discharge rate in some r.a. afferents produced by stimulation with the small dots is immediately apparent. It is also clear that increased velocity evoked more impulses in some afferents and made little difference in others. Similar plots were produced for both the s.a. and p.c. afferents and Fig. 3 illustrates the mean responses of the three populations.

*Correlation of responses to punctate and pattern stimulation.* The mean response rate for each of the three afferent populations, to pattern stimulation with both small- and large-dot surfaces (at 73 mm/sec) was correlated with measures of the 'sensitivity' derived in the punctate stimulation studies. Standard measures of 'sensitivity' to punctate stimuli were used (Talbot *et al.* 1968; Johnson, 1974); these were the minimum amplitude of vibration producing one impulse on every cycle at 40 Hz for

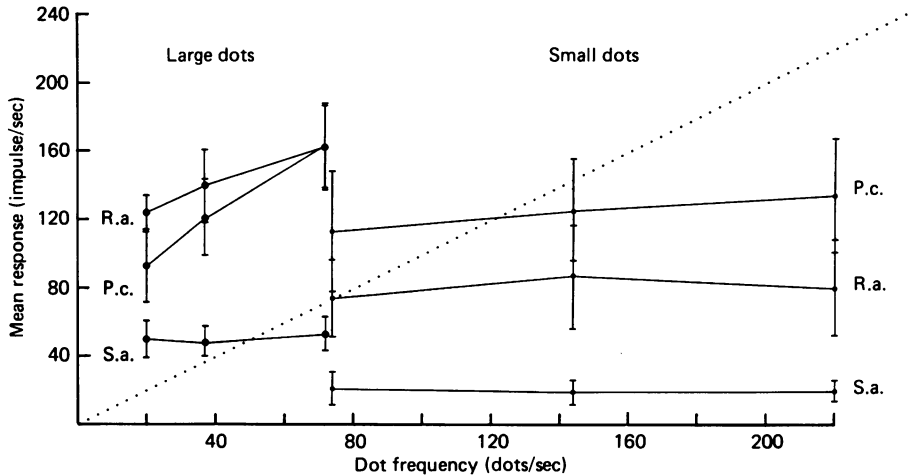


Fig. 3. Mean of the mean response rates for all ten r.a., seven s.a. and six p.c. afferents for which complete data was obtained (see also legend of Fig. 2). The error bars indicate one s.e. of the mean.

the r.a. afferents and at 250 Hz for the p.c. afferents, and the number of impulses evoked in 1 sec by the 1000  $\mu\text{m}$  step indentation was used for the s.a. afferents. None of the linear regression coefficients obtained were significant at the 0.05 level, and hence there was no evidence for the existence of any linear correlation between the punctate and pattern stimulation response measures.

#### *Periodicity in the response to pattern stimulation*

The apparent periodicity in the neural responses to pattern stimulation was investigated quantitatively in both the circumferential and lateral dimensions.

*Periodicity in circumferential dimension.* Segments of the neural responses to every surface were analysed to quantify (a), the degree of temporal periodicity (modulation fraction) and (b), the period length in the circumferential dimension of each response – such periodicity presumably arises from the successive rows of dots on each surface striking the skin. Fig. 4 compares changes in the period of the stimulating surface with the observed changes in the temporal period of the neural data. If the neural periodicity was exactly determined by the circumferential period of the dots, the measured points should fall along a 45° line in *A*, *B* and *C*, and along the abscissa in *D* (as there was no difference between the circumferential periods of any of the surfaces of the ‘across’ series). Clearly, the data strongly supports this.

Similarly, for all other stimulation conditions and receptor classes, a change in the circumferential period of the dots invariably produced an identical change in the temporal period of the neural responses.

*Modulation fractions.* All the modulation fractions found for the large-dot surfaces were invariably greater than 0.5 for all three afferent populations. In other words, all the responses showed a clear temporal periodicity in which the density of impulses at the ‘minima’ of each cycle (Fig. 1) was less than half that at the points of maximal response. (A value of 1.0 would indicate regular zones in which no impulses were produced.)

Fig. 5 shows the modulation fractions of all the digital afferents plotted against

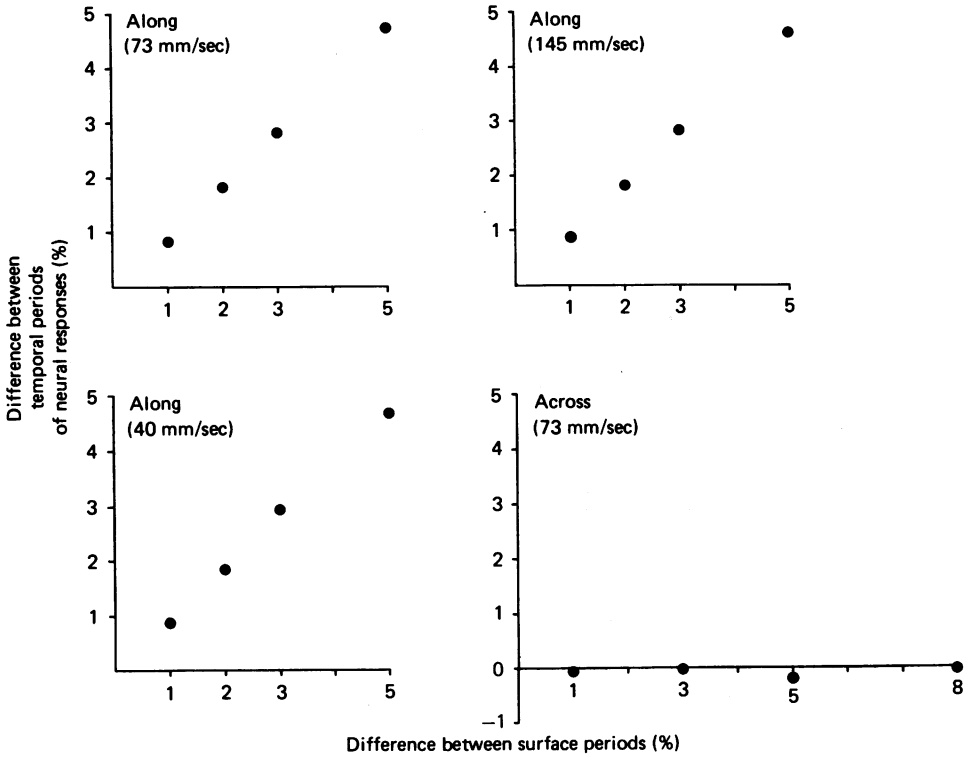


Fig. 4. Evidence that the circumferential period of the stimulating surface precisely determined the temporal periodicity of the neural responses (Fig. 1). Stimulation was produced with surface strips which each consisted of both an A and a B segment. The abscissa of each graph shows the percentage difference between the periods of the A and B segments of each surface. Note: for the 'across' surface series (*D*) the abscissa shows the difference in the *lateral* period – the *circumferential* periods of the A and B surfaces were identical. The ordinate of each graph illustrates the percentage difference between the temporal periods of the neural responses produced by the appropriate A and B segments. Each point shows the mean difference found for the responses of ten r.a. afferents; the largest s.e. of the mean was 0.2% and most were far smaller. The velocity of surface movement and the dimension in which the A and B surfaces differed (along or across) are shown in each panel.

their mean rate of response, for pattern stimulation with a large dot surface moving at 73 mm/sec. Three different symbols are used to show the data for the three mechanoreceptive populations. It is clear that, though there are differences in the mean values for each population, there is considerable overlap of the modulation fractions for each. Moreover, a linear regression analysis ( $n = 23$ ,  $r = 0.71$ ) indicated that there was a significant inverse correlation ( $P < 0.01$ ) between the mean response rate and the modulation fraction. The inverse relationship found indicated that, in general, very responsive afferents produced impulses over the whole of each dot 'cycle' whereas less responsive afferents only produced impulses when each row of dots was in a particular position relative to the receptor terminal.

*Lateral-profile histograms.* The periodicity in the neural responses in the dimension perpendicular to the direction of movement was investigated by plotting lateral-profile histograms which displayed the mean response over any specified circumferential



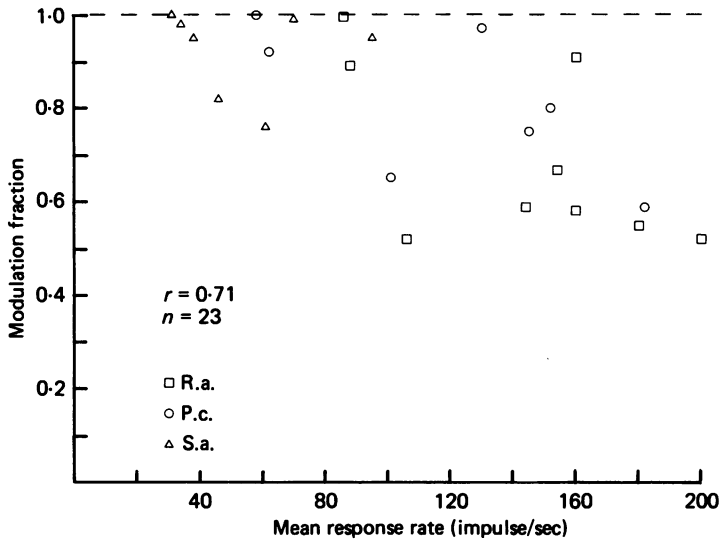


Fig. 5. Modulation fraction *versus* mean response rate for all mechanoreceptive afferents, when stimulated by large-dot surfaces moving at 73 mm/sec. The modulation fraction expresses the relative impulse densities of any periodic minima in the impulse plots – a value of 0.0 indicates that there was a completely uniform distribution of impulses, and a value of 1.0 indicates that there were periodic zones in which no impulses whatsoever were generated on any revolution. A linear regression analysis of the twenty-three points produced a significant regression coefficient ( $r = 0.71$ ,  $P < 0.01$ ).

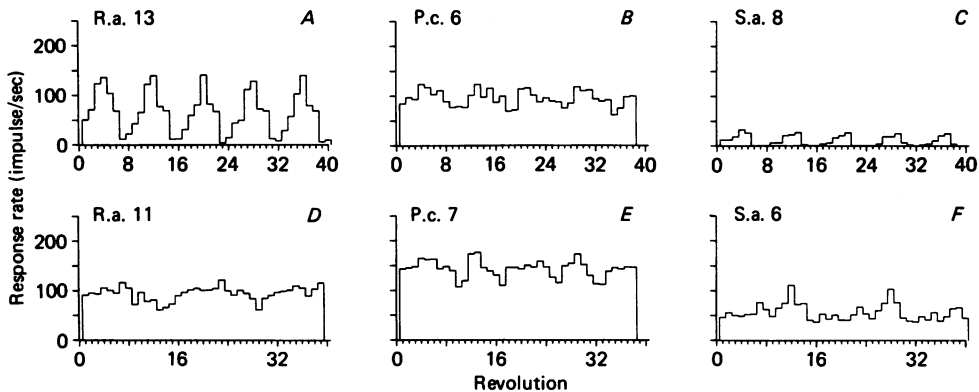


Fig. 6. Lateral-profile histograms for r.a., s.a. and p.c. afferents when stimulated by a 1.0 mm period surface (A, B and C) or a 2.0 mm period surface (D, E and F), moving at 73 mm/sec. The ordinate of each graph shows the mean response rate in the interval between 0.5 and 1.0 sec after contact on the revolution indicated by the abscissa. The surface was moved laterally by 1/8 mm on every revolution, producing a clear periodicity in the lateral profiles every 8 or 16 revolutions, for the 1.0 and 2.0 mm period surfaces respectively.

section for each of the 40 revolutions. Fig. 6 displays such histograms for the large-dot (2.0 mm period) and small-dot (1.0 mm period) surfaces for the impulses evoked by the square-array segment (A) of each strip. These histograms are not totally representative of all the data but do display the general trends. The histograms clearly show the responses are directly related to the position of the dots in the

lateral-surface dimension; the lateral translation of each surface at 1/8 mm per revolution produced a rhythmic change in the neural response with a period of 8 revolutions for the 1.0 mm surfaces and 16 revolutions for the 2.0 mm surfaces. All units at all velocities displayed such lateral periodicity. It is not, however, possible to rank the receptor populations in terms of their abilities to transmit information about the lateral periodic structure of the impinging surface, as the critical response features are not known and each population displayed a wide range of responses. The periodicity discussed above does not imply that there is only one 'peak' in the discharge every period (8 or 16 revolutions); some afferents, particularly p.c.s (e.g. Fig. 6E) exhibited two peaks in their mean response when a surface was displaced laterally by one period (e.g. 16 revolutions for a 2.0 mm period surface). This behaviour might be the result of there being two or more critical points in each surface period which elicited vigorous responses (e.g. the two edges of each dot), or of there being two or more points on the skin which each dot vigorously stimulated (e.g. two adjacent skin ridges). The lateral-profile histograms also show that the *average* response was constant across the 40 bins (revolutions) in every case. As the bins (left to right) represent the responses at progressively later times relative to the initial contact (4.4 sec/bin at a circumferential speed of 73 mm/sec), it is quite clear that the responsiveness of each afferent hardly altered over the entire time of surface contact. A similar result was found at every velocity, and at the lowest velocity this involved a total contact time of 5½ min. Thus, adaptation across successive revolutions was never a problem in comparing results. Moreover, adaptation had virtually no effect in comparisons between successive trials with different surfaces, or indeed even over a time scale more than 5 hr.

#### *Changes in response rate with small period changes*

To examine the effect of small changes in the period on the response of each afferent, temporal profile histograms were produced. The histograms in Fig. 7 illustrate the responses of an r.a. and a p.c. afferent when stimulated by a set of four A/B surface strips (large-dot 'along' surfaces). The numbers inside the histograms represent the increase in period of the surface producing the response, a zero indicating the A surface. The initial 'transient' peak in the response rate was primarily dependent on the distance the drum dropped onto the skin in each trial, and consequently was not analysed. The transient peak was followed by a period of slow 'adaptation'; many afferents, particularly the p.c.s, often displayed no adaptation at all, there being virtually a constant discharge rate. Afferents which displayed adaptation for any one surface also did so in a nearly identical manner for all surfaces in which the same stimulation conditions were used.

Comparison of the profiles in Fig. 7 makes it clear that the discharge rate of both the r.a. and p.c. afferents increased in a graded manner with the increased dot periods. All ten r.a. afferents which were stimulated with the large-dot surfaces showed a similar increase in their response rate with any increase in the period of the dots in *both* the 'along' and 'across' dimensions, at all velocities investigated. However, in general, the p.c. afferents did not display a uniform relationship between response rate and period increments; one unit even displayed an inverse relationship.

*Quantification of response increments and adaptation rates.* The mean response rates

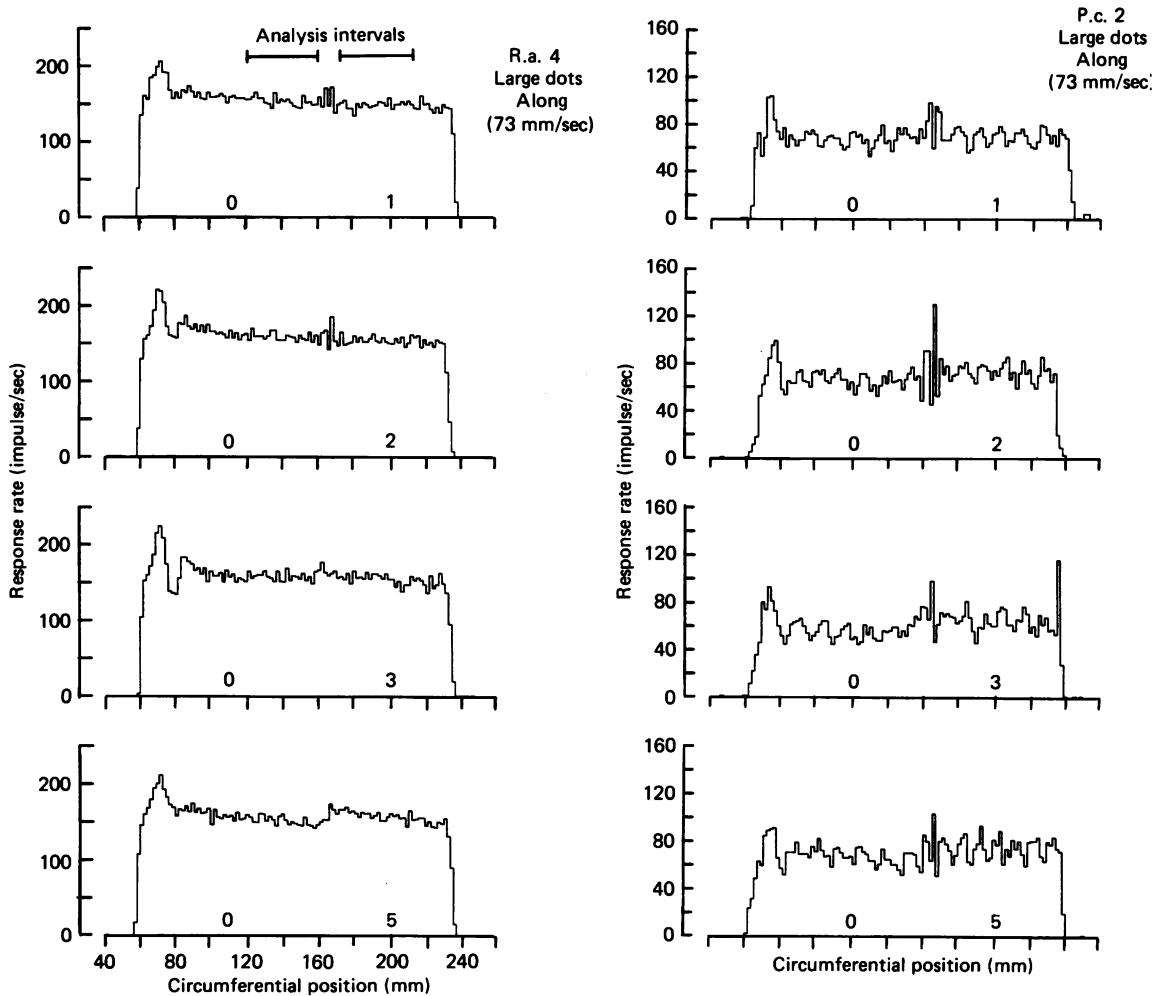


Fig. 7. Temporal profiles for an r.a. afferent and a p.c. afferent stimulated with four large-dot surface strips at 73 mm/sec. The ordinates indicate the instantaneous response rate, averaged over 40 consecutive revolutions, from initial contact until the surface was lifted from the skin. The numbers on the profiles indicate whether the response was produced by the square array segment (A) of the surface (signified by 0) or the modified segment (B) of the surface (1, 2, 3 or 5% increase in the period in the circumferential dimension). The join between the two surface segments on each strip occurred at a circumferential position of 165 mm in all the graphs. The approximate circumferential intervals used in the calculation of the mean response rates for the A and B surface segments are indicated in the top left panel. Much of fine structure visible in the histograms is the result of interaction between the bin width (1.8 mm) and the temporal periodicity (2.0 mm).

evoked by both A and B sections of each surface were evaluated over segments (approx.) 40 mm long (see Fig. 7), and the difference between the two values was calculated. Such rate differences were calculated for the responses to all four A/B strips of each set, and plotted as in Fig. 8 (left-hand panel). A linear regression analysis was used to estimate the intercept with the ordinate (i.e. 0% difference); such

a value indicates the mean adaptation in the afferent's response rate over an interval of approximately 0.7 sec (the time taken for the surface to move between the mid-points of the two analysis segments). This procedure was used to analyse data from every afferent and the mean of such adaptation rates for the three mechanoreceptor populations (for the large dot surfaces moving at 73 mm/sec) were 15.0, 7.2 and 0.4 impulses/sec. sec for the r.a., s.a. and p.c. populations respectively.

If the A and B surfaces had been presented separately rather than continuously the adaptation effect would not have influenced the difference between the mean response rates to the two surfaces. Consequently the adaptation of each afferent was

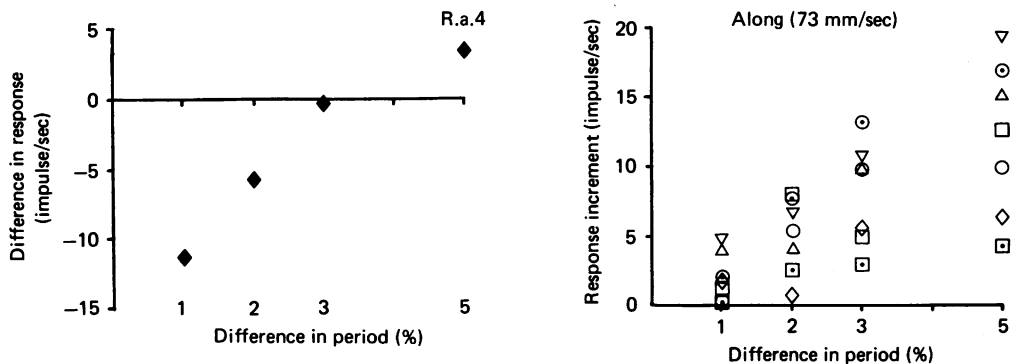


Fig. 8. Left panel, difference in the mean response rates evoked by the A and B segments of each strip for the r.a. data displayed in Fig. 7. The abscissa represents the percentage difference in the period of the A and B segments on each surface strip. A positive value of the ordinate indicates that the modified segment (B) elicited a greater response rate than did the corresponding standard (A) segment. Right panel, increment in response rate produced by an increase in the period of the large-dot (2.0 mm period) surfaces for all seven r.a. afferents for which complete data was obtained. The A and B surfaces differed in period in the circumferential dimension (i.e. 'along' series), and the velocity of movement was 73 mm/sec.

compensated for when calculating the incremental change in the response rate produced by a small change in dot period (i.e. the period difference between the A and B surfaces).

Fig. 8 (right-hand panel) shows the response increments calculated for seven r.a. afferents stimulated with the large-dot (2.0 mm period) surfaces at 73 mm/sec. The gradient of the line of best fit for data for each r.a. afferent separately was invariably positive, for this and all other conditions. The mean of this data is shown in Fig. 9, together with the corresponding data for the other three conditions of velocity and dimensional change. The responses of the other three r.a. afferents, for which incomplete data were collected, were in no way differentiable from the data displayed (e.g. gradients of 0.9, 1.0 and 2.1 impulse per 1% period change at 73 mm/sec for the 'along' surfaces) and such data was only omitted to enable quantitative comparisons between the four stimulating conditions. The gradient of the mean r.a. data is shown in each plot. Fig. 9 also shows the mean data for the seven s.a. afferents for which complete data was obtained. Linear regression analysis showed that the period change

produced a significant effect ( $P < 0.01$ ) in all four conditions for the r.a. data, but only with the 'across' surfaces for the s.a. data.

The response increments seen with the p.c. afferents were very different from those of the r.a. and s.a. afferents in that they displayed marked heterogeneity. Fig. 10 illustrates all the incremental response data obtained with p.c. afferents and large-dot stimuli. One p.c. afferent displayed an inverse relationship between response rate and

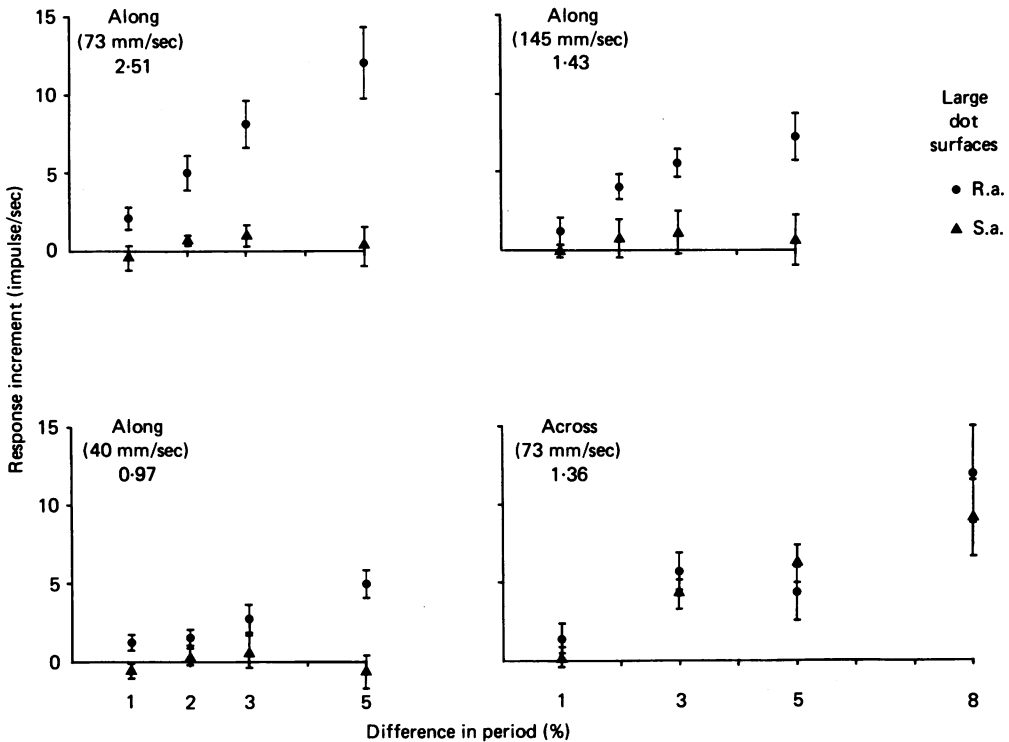


Fig. 9. Mean values ( $\pm 1$  s.e. of the mean) of the response increments produced by an increase in the period of the dots; all data relates to the seven r.a. and seven s.a. afferents for which complete data was obtained when stimulated by the large-dot surfaces. The velocity of surface movement and the dimension in which the period was changed are shown. A linear regression analysis was used to calculate the gradient of the line of best-fit of the r.a. data; the gradient is shown in each panel.

period difference for the one stimulation condition examined with the large-dot stimuli before the unit was 'lost'; the same unit displayed a similar behaviour with the one small-dot stimulation condition examined (Fig. 11). The other p.c. afferents variously displayed response rate increments with increasing, constant, decreasing or irregular behaviour when plotted against the period change.

*Response increments with small-dot surfaces.* When the responses of the twelve r.a. afferents to small-dot stimuli at 73 mm/sec were considered six gave insufficient and inconsistent responses to enable examination of the incremental changes: the response rates were all less or far less than 35 impulses/sec (Fig. 2) initially and often dropped considerably lower during the time course of each sweep of the surface. For

one further unit only an insufficient amount of data was obtained. Of the remaining five afferents only two produced an increase in response with increased period for the 'along' series of surfaces, whereas all five did so for the 'across' series. Hence, of the eleven fibres examined with the small-dot surfaces (excluding the unit with insufficient data) only two showed a similar behaviour to that found in all ten r.a. fibres quantified with the large-dot surfaces. The magnitude of the response increment seen in those two cases was of a similar order to that calculated for the large-dot stimuli.

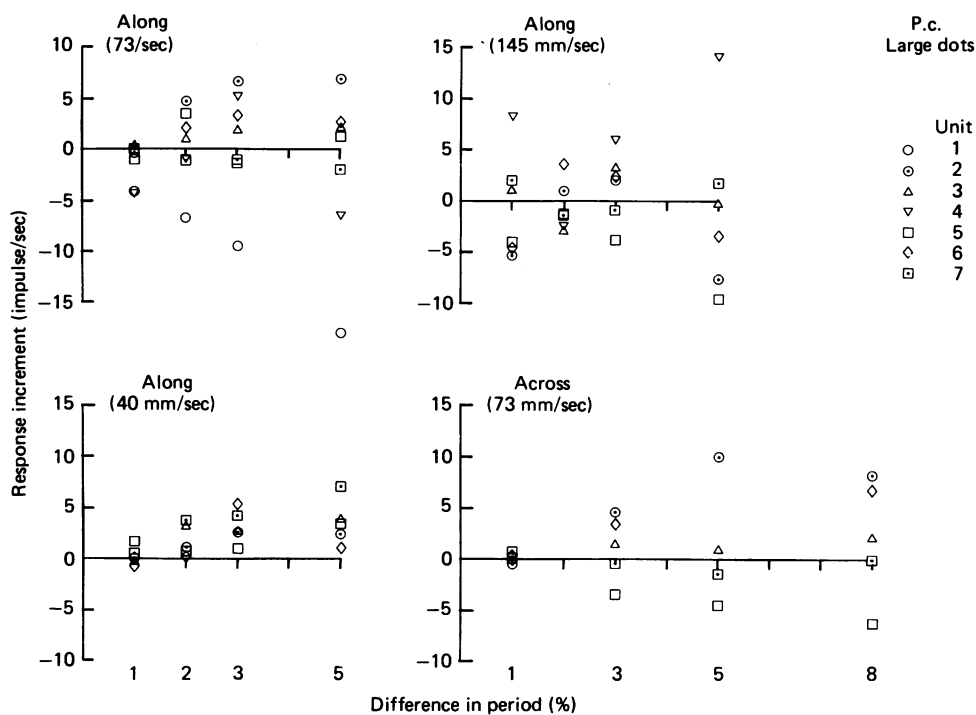


Fig. 10. Increment in response rate produced by an increase in the period of the large-dot (2.0 mm period) surfaces for all seven digital p.c. afferents. The velocity of surface movement, and the dimension in which the period was increased, are indicated.

Response increment data for virtually all r.a. afferents could not be calculated for the two fastest speeds (145 and 220 mm/sec) with the small-dot surfaces because of irregularities in the responses to the modified surfaces (which followed the surface join); marked adaptation or poor skin/surface contact was evident in the responses just following the join, and this prevented meaningful quantitative comparisons with the response rate evoked by the preceding standard surface. This phenomenon was never encountered with the large-dot surfaces.

Fig. 11 shows all response increment data for the p.c. afferents which were (a), examined at least partially (some units were 'lost' before complete investigation), and (b), not detrimentally affected by the presence of the join. Some of the p.c. units, particularly those with low discharge rates, did provide information about the response increments at the higher speeds in spite of the surface join. Over all four

stimulation conditions with the small-dot surfaces, all p.c. afferents investigated (a), gave sufficient responses to be quantifiable (though some response rates were very low, they were maintained throughout contact) and (b), displayed an increase in response rate for any increase in the period (except for one case of a reciprocal relationship). This is in marked contrast to the r.a.s. stimulated with the small-dot surfaces.

Of the eight s.a. afferents stimulated with small-dot surfaces, six gave too little

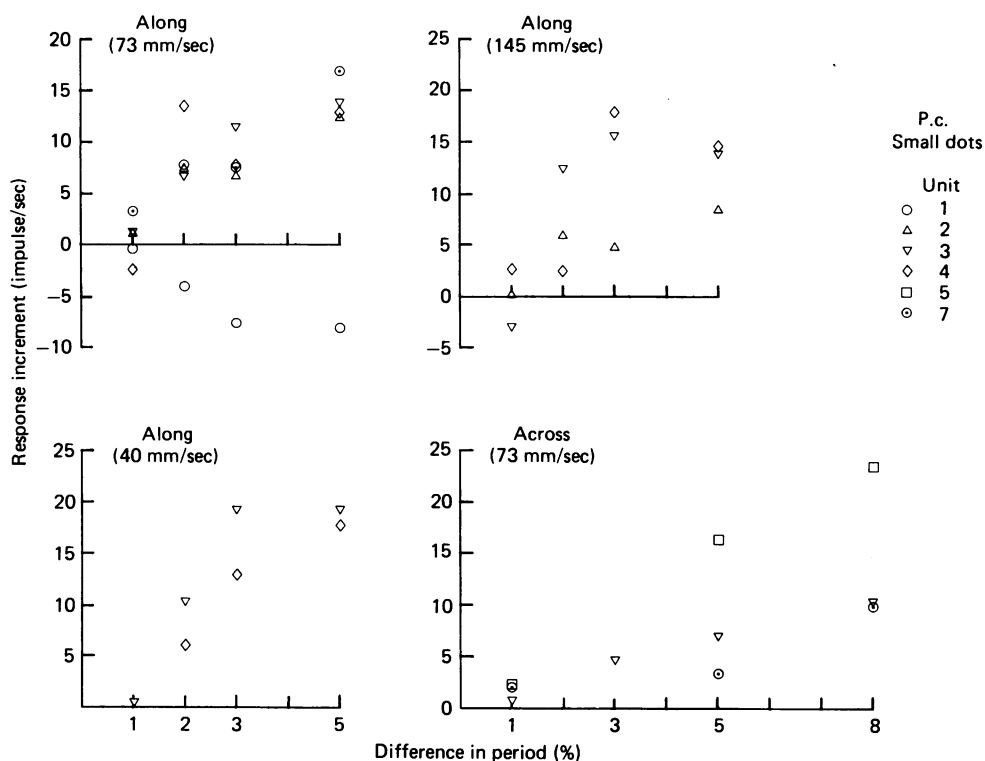


Fig. 11. Increment in response rate produced by an increase in the period of the small-dot (1.0 mm period) surfaces for all p.c. afferents for which appropriate data was obtained. The velocity of surface movement and the dimension in which the period was increased are indicated.

response to allow comparisons of the standard and modified surfaces (< 20 impulses/sec initially), and the other two afferents displayed no uniform changes in response rate (as was the case with the large-dot surfaces).

#### *Palmar p.c. afferent*

The response of one p.c. afferent which innervated the palmar skin (hyperthena eminence) was recorded when pattern stimulation was applied to the distal digital pad of the middle finger. The 'receptive field' of the unit was so large that such stimulation elicited response rates of the order of 70 impulses/sec. This afferent gave a variable response to stimulation, in terms of its mean rate, at various time intervals

(a), within each revolution; (b), over successive revolutions. This afferent was the only one in which such variability was seen which almost certainly indicates that it was the result of the large distance between the stimulation and innervation sites. Nevertheless, lateral-profile histograms clearly demonstrated that, despite the remote stimulation, the palmar p.c. afferent was affected by the *lateral* position of the surface on the fingertip in a similar manner to all other afferents.

#### DISCUSSION

*Neural coding of texture discrimination.* This discussion considers the adequacy of various neural codes in accounting for all the psychophysical data on texture discrimination described in the preceding paper (Lamb, 1983). The neural coding underlying texture discrimination might be based on the responses of the afferents of any or all of the three separate mechanoreceptor populations of the glabrous skin. However, though the relative importance of each of the three populations is not known, most of the following comments on the various candidate codes are applicable regardless of the particular population(s) involved. It is initially assumed that the *same* neural code transmitted the relevant information needed for texture discrimination in all the experiments described in the preceding psychophysical study. Indeed, it will be shown that a single code (a rate code) can account for all the psychophysical data. However, it is not intended to imply that only the rate of response of certain mechanoreceptors transmits any information about the stimulating surface; clearly in the preceding psychophysical experiments subjects extracted more information about the surfaces than was quantified by the *discrimination* task, for example they almost certainly could feel that all the surfaces consisted of discrete raised dots, and probably obtained at least a rough estimate of the spacing of those dots.

The neural recordings detailed in this paper showed that the responses of all the mechanoreceptive afferents were affected by, and directly related to, the spacing of the structural elements in *both* the circumferential and lateral dimensions of the stimulating surface. As the receptor responses were influenced by the lateral position of any surface, in one sweep no single afferent could transmit unambiguous information about both dimensions of the stimulating surface. Hence, only by using information from the responses of a *number of afferents* could a subject tactually discriminate the surfaces used in these experiments. Furthermore, the corresponding receptor endings of those afferents must be distributed in the skin such that, as a group, they signal information about at least one entire period of the lateral surface structure. Johnson & Lamb (1981) showed that, at least for the r.a. and s.a. populations, a tangentially moving surface elicits the greatest response from an afferent when a dot on that surface passes very closely over the site of innervation of the afferent (as inferred from punctate studies). Consequently, when a surface passes once across the skin the mechanoreceptive afferents will display a whole range of relative response rates (i.e. peaks or troughs, etc., in their respective lateral profiles; Fig. 6), each being determined by the relative lateral position of the corresponding receptor ending in the skin.

*Candidate neural codes.* A number of candidate codes involve temporal aspects of



the response. One of these could be called a 'modulation' code as it might signal information in terms of the temporal (i.e. circumferential) periodicity which is clearly visible in the response of every afferent (Fig. 1). However, examination of Fig. 4 clearly shows that such a candidate code could not provide information for distinguishing surfaces which differed only in the lateral spacing of their dots (the 'across' surface series). Furthermore, such a code could not explain the exquisite discriminative performance seen in the active-touch experiments, even for the 'along' surfaces unless the subject could *obtain* precise information about the velocity profile and then *use* it to interpret the constantly varying cutaneous responses.

Another candidate temporal code is one in which the pertinent information is signalled by the length of the interspike intervals. Clearly in the case where each surface dot elicits exactly one impulse in every afferent this code is exactly the same as a modulation code. Nevertheless, many afferents produce more than one impulse per stimulus dot, and the behaviour of the response increment data (Fig. 9) indicates that the spacing of the surface dots indeed *must*, in some way, be reflected in the interspike intervals of at least the r.a. afferents. However, the interspike intervals in a group of afferents (a), must vary (as does the response rate) according to the relative lateral position of the stimulating surface structure, and (b), will differ between afferents according to their responsiveness. In psychophysical experiments in which the surfaces can contact the skin in any relative lateral position, even ignoring conduction velocity variations, extraction of precise information from the interspike intervals of a (by necessity) large number of afferents can only be described as 'extremely complex processing'. Furthermore, as the interspike intervals are affected by the velocity of the surface movement, the use of such a code seems even more unlikely in the active-touch discriminations because of the irregular velocity profiles involved (Lamb, 1983).

Another population code which might be postulated to account for the discrimination is a 'spatial' code in which surfaces are differentiated by the relative two-dimensional positions of the receptor endings they activate or in which they produce some particular response; for example, the presence of a surface dot immediately over a receptor ending might cause an increased response rate in that receptor's afferent. However, in a true 'spatial' code information contained in the temporal variations of the response is *not* used. Consequently it is difficult to see how such a code could account for discrimination of the 'along' surfaces as the key spatial parameters would only be apparent if the central nervous system could take 'snapshots' of the neural image because each surface dot will at some time stimulate all the receptors in its path. Consideration of this problem led Uttal (1973) to state '... a spatial snapshot, in which the temporal aspects are fixed at a specific moment, also usually obscures key variables. The spatio-temporal pattern may be no more divisible in psychobiology than it is in quantum or astronomical physics.'

The possibility that the nervous system might utilize a spatio-temporal code, a code involving the integration of information from *both* the spatial and temporal aspects of the total neural response, was referred to by Johnson & Lamb (1981). The use of such a code will not be considered here other than to say that, for these fine discriminations, its successful employment would require: (a), an ability to extract and use precise information about the velocity profile; (b), 'knowledge' of the exact

positions of all relevant receptor endings (though this might be achieved by an accurate topographic projection to the 'site' of processing); (c), an ability to identify the period of the modulation in both the temporal and lateral dimensions and (d), a method of knowing and compensating for the conduction delay of every afferent.

*Rate code.* It is clear that the summing or averaging, over many afferents, of information in the form of the mean response rate is a relatively 'simple' task, as it requires no knowledge of (a), the velocity of movement, (b), the relative positions of the receptors endings and (c), the conduction velocities of the individual afferents. Furthermore, it does not even require any constancy or regularity in the relative surface movement so long as two successive contacts involve roughly similar movements (see Lamb, 1983).

Inspection of Figs. 8 and 9 (large-dot data) makes it clear that the r.a. afferents, both individually and in terms of their mean, show incremental changes in their mean response rate with changes in the dot period which are known to be detectable psychophysically. This behaviour is evident at *all* three velocities for the 'along' surfaces *and* for the 'across' surfaces. Moreover, the functions in all four cases can be adequately described as linear, thus suggesting that the response rate might be responsible for information transmission, as in all the corresponding psychophysical experiments (Lamb, 1983) a linear relationship was always seen between the performance measurement ( $d'$ ) and the period difference. Thus, these data suggest that the discriminative performance is dependent on the peripheral afferent sensitivities as hypothesized by Mountcastle (1967). However, direct comparison of the gradients of the neural and psychophysical functions is not possible unless some assumption is made about the relative loss of information in more central parts of the nervous system for the various stimulation conditions (or mean response rates) (Johnson, 1980*b*).

*Peripheral and central noise and the discriminable stimulus increment.* In order to use decision theory (Johnson, 1980*a, b*) to relate, in absolute terms, the neural and psychophysical data, it is necessary to have a measure of the variability of neural events. The total variability or noise is a function of both the peripheral and central noise.

The facts that (a), the response of each afferent depends on the lateral surface structure, and (b), the surface contacted the skin randomly with respect to its lateral structure in the psychophysical experiments, imply that the total response from only a relatively large number of r.a. afferents dispersed evenly in the fingertip, would not be adversely affected by the consequent fluctuations in the responses of individual afferents. Such a large number of r.a. afferents will indeed be activated by each surface contact: the contact area (53–98 mm<sup>2</sup>) and the afferent innervation density (150 r.a.s/cm<sup>2</sup>; Johansson & Vallbo, 1979; Darian-Smith & Kenins, 1980) imply that between 80 and 160 r.a. fibres would respond to each stimulus. However, it must be expected that the randomness of the relative lateral position of the surface will produce variability in the mean or total rate of response of the afferents. The magnitude of such 'positional' peripheral variability is difficult to estimate but is almost certainly very small as another psychophysical study (Morley, Goodwin & Darian-Smith, 1982) found almost identical performance (difference limen = 3% difference) to that found in this study when subjects were required to discriminate

grating surfaces, for which there would clearly have been no 'positional' variability at all due to the invariance of the surface structure in the lateral dimension.

A second source of peripheral noise could arise from 'temporal' variability of the response of each afferent – that is, the variability in successive responses with identical stimulation conditions. Because of the lateral surface structure it was difficult to separate which response differences in successive revolutions were due to (a), 'temporal' variability, and (b), changes in the surface position. Two different methods of analysis suggested an upper limit of 1.0 impulse/sec for the standard deviation of the 'temporal' variability. This value is appreciably higher than that suggested by the results of an earlier study on the responses of r.a. afferents to stimulation with grating surfaces (Darian-Smith & Oke, 1980).

Decision theory (Johnson, 1980*a*) can be used to estimate the discriminable stimulus increment (d.s.i.), that is the predicted performance level, assuming that the mean response rate of the r.a. afferents signalled the pertinent information and that the total variance ( $\sigma_s^2$ ) was dependent only on the peripheral 'temporal' variance:

$$\text{d.s.i.} = 1.35\sigma_s / \left( \text{mean} \frac{\Delta R}{\Delta S} \right),$$

where  $\text{mean } \Delta R/\Delta S$  = the mean response increment of the r.a. fibres produced by a period increment  $\Delta S$  (i.e. the gradients shown in Fig. 9).

In this calculation the responses of all afferents are equally weighted, paired-comparison strategy is assumed, and the constant, 1.35, is used in order to relate the neural data with the psychophysical design used (SSSM design of Johnson, 1980*a*). If the standard deviation of the variability ( $\sigma_s$ ) is 1.0 impulse/sec, d.s.i. values indicate *predicted* discriminable period changes of 1.4, 0.5, and 0.9 % for the large-dot 'along' surfaces at 40, 73 and 145 mm/sec respectively, and 1.0 % for the 'across' surfaces at 73 mm/sec. All these values are below the *measured* performance levels ( $\Delta S(d' = 1.35) = 2.0, 1.9, 3.0$  and  $4.1$  %), indicating that the mean r.a. response rate in the peripheral nerve *does* indeed contain sufficient information to account for the discrimination of the large-dot surfaces, if the assumption of low 'positional' variability is correct. Furthermore, both 'optimal' discrimination strategy (Johnson, 1980*a*) or lower 'temporal' variability (as suggested by the results of Darian-Smith & Oke (1980)) would produce even smaller d.s.i. values. Thus, the principle source of the variance in the neural processing appears to be of central origin.

Regardless of hypotheses about the source and behaviour of any noise in the neural responses, it is possible to calculate the incremental change in mean response rate produced by that difference in the period which was detected psychophysically at the 75 % correct level. Such a value might be termed the 'discriminable rate increment', and it had values of 1.9, 4.8, 4.3 and 5.6 impulses/sec, for the four stimulation conditions with the large-dot surfaces. It might thus be hypothesized that the data is reflecting a fundamental constancy in the value of the response-rate increment (4–5 impulses/sec) which is detectable by the discrimination processes. A similar hypothesis was advanced by Werner & Mountcastle (1965) who examined the responses of hairy skin slowly-adapting mechanoreceptors to step indentations. They found that over a 1.0 sec interval the stimulus increments ( $\Delta S$ ) which elicited response

increments ( $\Delta R$ ) of 5 impulses/response were described by a Weber function ( $\Delta S/S$ ) very similar to that established in psychophysical experiments.

*Small-dot surfaces.* Despite the small amount of data, the most likely neural code underlying the discrimination of the small-dot (1.0 mm period) surfaces is also a rate code, though perhaps involving the p.c. afferents rather than the r.a. afferents (Figs. 3 and 11). Such a situation would bear striking parallels with vibratory frequency detection and discrimination using a punctate probe (Talbot *et al.* 1968; Mountcastle, *et al.* 1969; LaMotte & Mountcastle, 1975).

*The perception of roughness.* LaMotte (1977) compared human subjective magnitude estimates of 'roughness' with the neural recordings of the mechanoreceptor responses in monkeys when various fabrics were moved sinusoidally back and forth over the skin. The neurophysiological results of LaMotte's study bear a striking resemblance to those described here: the response rates of the r.a. afferents were directly related to the inter-fibre period of the fabrics, whereas the responses of the s.a. afferents were virtually independent of spacing of the fibres. Furthermore, LaMotte found that the human sensation of 'roughness' increased with increased inter-fibre periods of the fabrics. This latter finding is totally consistent with that of Lederman & Taylor (1972) who showed that the subjective 'roughness' of a grating surface increased with an increased gap width. Finally it should be noted that all surfaces which were described as 'rougher' than another surface in the preceding psychophysical paper (Lamb, 1983) invariably elicited a greater response in the r.a. afferents. When all these results are considered together they offer strong support for LaMotte's hypothesis that the sensation of roughness is directly dependent on the response rates of the r.a. afferents. Experiments involving cutaneous anaesthesia would be of great help in identifying any role that the p.c. afferents might play.

Professor I. Darian-Smith and Dr K. O. Johnson made useful comments on this work, for which I am grateful. Mr Barrie Johnson and Mr Jim Pringle built and maintained the stimulator, and Miss Heather Jessel prepared the manuscript.

#### REFERENCES

- CHUBBUCK, J. G. (1966). Small motion biological stimulator. *Appl. Phys. Tech. Digest*, Baltimore, U.S.A., May-June, 19-23.
- DARIAN-SMITH, I., DAVIDSON, I. & JOHNSON, K. O. (1980). Peripheral neural representation of spatial dimensions of a textured surface moving across the monkey's finger pad. *J. Physiol.* **309**, 135-146.
- DARIAN-SMITH, I., JOHNSON, K. O. & DYKES, R. (1973). 'Cold' fiber population innervating palmar and digital skin of the monkey: responses to cooling pulses. *J. Neurophysiol.* **36**, 325-346.
- DARIAN-SMITH, I., JOHNSON, K. O., LAMOTTE, C., KENINS, P., SHIGENAGA, Y. & VUN, C. M. (1979*b*). Coding of incremental changes in skin temperature by single warm fibers in the monkey. *J. Neurophysiol.* **42**, 1316-1331.
- DARIAN-SMITH, I., JOHNSON, K. O., LAMOTTE, C., SHIGENAGA, Y., KENINS, P. & CHAMPNESS, P. (1979*a*). 'Warm' fibers innervating palmar and digital skin of the monkey: responses to thermal stimuli. *J. Neurophysiol.* **42**, 1297-1315.
- DARIAN-SMITH, I. & KENINS, P. (1980). Innervation density of mechanoreceptive fibres supplying glabrous skin of the monkey's index finger. *J. Physiol.* **309**, 147-155.
- DARIAN-SMITH, I. & OKE, L. E. (1980). Peripheral neural representation of the spatial frequency of a grating moving across the monkey's finger pad. *J. Physiol.* **309**, 117-133.

- JOHANSSON, R. S. & VALLBO, A. B. (1979). Tactile sensibility in the human hand: relative and absolute densities of the four types of mechanoreceptive units in the glabrous skin. *J. Physiol.* **286**, 283–300.
- JOHNSON, K. O. (1974). Reconstruction of population response to a vibratory stimulus in Q.A. mechanoreceptive afferent fiber population innervating glabrous skin of the monkey. *J. Neurophysiol.* **37**, 48–72.
- JOHNSON, K. O. (1980*a*). Sensory discrimination: decision process. *J. Neurophysiol.* **43**, 1771–1792.
- JOHNSON, K. O. (1980*b*). Sensory discrimination: neural processes preceding discrimination decision. *J. Neurophysiol.* **43**, 1793–1815.
- JOHNSON, K. O., DARIAN-SMITH, I., LAMOTTE, C., JOHNSON, B. & OLDFIELD, S. (1979). Coding of incremental changes in skin temperature by a population of warm fibers in the monkey: correlation with intensity discrimination in man. *J. Neurophysiol.* **42**, 1332–1353.
- JOHNSON, K. O. & LAMB, G. D. (1981). Neural mechanisms of spatial tactile discrimination: neural patterns evoked by braille-like dot patterns in the monkey. *J. Physiol.* **310**, 117–144.
- LAMB, G. D. (1983). Tactile discrimination of textured surfaces: psychophysical performance measurements in humans. *J. Physiol.* **338**, 551–565.
- LAMOTTE, R. H. (1977). Psychophysical and neurophysiological studies of tactile sensibility. In *Clothing Comfort: Interaction of Thermal Ventilation, Construction and Assessment Factors*, ed. HOLLIES, R. S. & GOLDMAN, R. F., pp. 83–105. Michigan: Ann Arbor Science Publ.
- LAMOTTE, R. H. & MOUNTCASTLE, V. B. (1975). Capacities of humans and monkeys to discriminate between vibratory stimuli of different frequency and amplitude: a correlation between neural events and psychophysical measurements. *J. Neurophysiol.* **38**, 539–559.
- LEDERMAN, S. J. & TAYLOR, M. M. (1972). Fingertip force, surface geometry, and the perception of roughness by active touch. *Percept. Psychophys.* **12**, 401–408.
- MORLEY, J. W., GOODWIN, A. W. & DARIAN-SMITH, I. (1982). Tactile discrimination of gratings. *Exp. Brain Res.* (in the Press).
- MOUNTCASTLE, V. B. (1967). The problem of sensing and the neural coding of sensory events. In *The Neurosciences: An Intensive Study Program*, ed. SCHMITT, F. O., QUARTON, G. & MELNUCHUK, T., pp. 393–407. New York: Rockefeller Univ. Press.
- 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.
- MOUNTCASTLE, V. B., TALBOT, W. H., SAKATA, H. & HYVARINEN, J. (1969). Cortical neuronal mechanisms in flutter-vibration studied in unanaesthetized monkeys. Neuronal periodicity and frequency discrimination. *J. Neurophysiol.* **32**, 452–484.
- TALBOT, W. H., DARIAN-SMITH, I., KORNHUBER, H. H. & MOUNTCASTLE, V. B. (1968). The sense of flutter vibration: comparison of the human capacity with response patterns of mechanoreceptive afferents from the monkey hand. *J. Neurophysiol.* **31**, 301–334.
- UTTAL, W. R. (1969). Emerging principles of sensory coding. *Perspect. Biol. Med.* **12**, 344–368.
- UTTAL, W. R. (1973). *The Psychobiology of Sensory Coding*, pp. 379. New York: Harper & Row.
- 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.