THE NEURAL SIGNAL FOR SKIN INDENTATION DEPTH

I. Changing Indentations[1]

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Abstract

Psychophysical tests on human subjects showed that judgments of skin indentation depth made when the fingertip was indented at rates from 0.2 to 16 mm/sec were quite insensitive to changes in indentation velocity. Similar results were obtained on the forearm at indentation velocities of 0.4 to 16 mm/sec. Recordings were made from mechanoreceptors in the monkey's hand that were able to respond over the same range of velocities and at comparable depths to determine how skin indentation depth might be signaled (coded) at the receptor level and to examine the rate sensitivity of the possible depth codes. It was found that most of the receptors with foci under the stimulator were recruited relatively early during an indentation, especially at velocities of 1.6 mm/sec and higher, making it improbable that the full range of indentation depths is signaled by the "subsurface" recruitment of different receptors at different indentation depths. A subsurface recruitment code involving subcutaneous receptors is not likely since subjects could feel virtually none of the stimuli after skin anesthesia. Progressive recruitment with depth of receptors whose foci lie further and further away from the stimulator ("lateral" recruitment) was considered an unlikely depth code because changing the area of the stimulator had little effect on its perceived depth. Also, it was shown that subjects could sense the curvature of the indentation (the profile of the depth at right angles to the skin surface), which requires information about the depth of individual patches of skin beneath the stimulator. There is no obvious way that a lateral recruitment code can provide this information. Thus it is probable that the discharge rate of some or all of the receptors excited by the indentation is involved in indicating its depth. Both impulse frequency and receptor recruitment at any given depth increased as the velocity of the identation increased. The demonstrated reliability of information about skin indentation depth in humans indicates that the central neural circuitry responsible for judgments of skin indentation depth is able to compensate for the rate-sensitive receptor signals.

It is well established that the mechanoreceptors excited by skin indentation increase the frequency of their discharge when the skin is indented more rapidly (Burgess and Perl, 1973). It is not known, however, whether one perceives an indentation to be deeper when the skin is indented at a greater rate. This question is of interest because compensation of indentation depth sensations for changes in indentation rate would allow more accurate judgments of indentation depth to be made during changing stimulus conditions. This presumably would increase the utility of indentation depth information. Rate compensation of indentation depth sensations would also imply either that the rate-dependent signals from the mechanoreceptors are modified in some way by the central nervous system or that the peripheral code for skin indentation depth is not particularly rate sensitive. In this paper we examine some of the ways that mechanoreceptors might signal skin indentation depth and we report on psychophysical experiments which show that indentation depth judgments by human sub-

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jects are little influenced by changes in indentation rate over a considerable range.

Materials and Methods

Psychophysical studies

Effect of indentation velocity on depth judgments. Four subjects were used, ranging in age from 23 to 39 years. One was a physiologist who knew the nature of the experiment and had previously participated in psychophysical studies. The others had no knowledge of why the experiment was undertaken and had not been tested previously. Each subject received stimuli both on the dorsal surface of the forearm and, in a different set of experiments, on the palmar aspect of the middle or index finger over the terminal phalanx (fingertip). They were comfortably seated with the forearm or hand in a moulded support fixed to a table. The skin was indented with the same feedback-controlled electromagnetic device as was used for the receptor studies (see below). The skin of the forearm was displaced with a flat circular plastic disc 13 mm in diameter in most experiments, but sometimes a 3.5-mm diameter plastic disc was used. The 3.5-mm disc was used without exception on the fingertips. The stimulator was carefully advanced with a micromanipulator until the subject reported that the disc had just touched the skin. It was then advanced an additional 0.5 mm. The largest stimulator excursion used (2 mm) caused a nearly complete, although non-noxious, compression of the smallest subject's finger pulp. Some of the slower and deeper stimuli could cause a shift in the rest position of the skin, particularly in the case of the older subjects, and the initial indentation ensured that the stimulator would remain in contact with the skin during a series of tests.

The subjects could not see the tested area or the moving portions of the stimulator, and operation of the device was silent. The subjects' verbal reports and the occasional failure of some subjects to detect the slowest stimuli indicated that no extraneous cues about stimulus application or amplitude were available.

The stimuli employed were "triangular" in form, indenting the skin at constant velocities to a present level and then immediately retracting at the same rate. The task of the subjects was to compare the depth of two such triangular skin indentations. These two stimuli were given successively and together constituted a trial. The subjects were asked to indicate which member of the pair indented the skin more deeply, or to state that they were equal if no difference could be detected. The subjects knew that the stimuli had a triangular form and that in some trials the amplitudes would be the same. Before testing, they were informed that calling equal amplitude pairs different would not be counted as an error but that when pairs that were different were called equal this would be treated as a serious error, as would any mistake in which the values were reversed. During the tests, they were told after each trial whether they had made a correct judgment. This procedure improved the motivation of the subjects and encouraged them to report any difference that they could sense between the stimuli, however small.

The two stimuli in a trial were delivered 4 to 6 sec apart. Generally, eight trials were given to a single skin site, and these eight trials constituted a set. Trials within a set were separated by 15 to 30 sec, and after a set was completed subjects were encouraged to stand up and move about the room. The next set was not started until the subjects felt rested. It was found that repeated testing of the same forearm site could cause failure to detect the slower indentations, which were not far above threshold. Therefore, the stimulator was moved between sets from one site to another on the distal half of the right forearm. Shifting the stimulator to the left forearm was discontinued after it was found that slow indentations were less well perceived on the left arm. (All the subjects were right handed.) Slow stimuli were more readily detected and produced less fatigue on the fingertip than on the forearm; nevertheless, after each set the stimulator was shifted between the index and middle fingers of the right hand.

Stimulus pairs with various characteristics were delivered. Some were of equal amplitude, but most differed in amplitude by 0.25, 0.5, or 1 mm. Some pairs had members with equal indentation rates (Fig. 1*A*), and in others the rise times were equal (Fig. 1*B*). Pairs whose members differed in both velocity and rise time (Fig. 1, *C* and *D*) were used to test the degree to which the perception of skin indentation depth depended on velocity. The equal velocity and equal rise time pairs served as controls. The usual practice was to give equal velocity and equal rise time pairs in one series, and to give pairs with unequal velocities and rise times in another series. In the latter, there were always as many pairs where the deeper indentation was faster as pairs where the deeper indentation was slower, to prevent the subjects from using the velocity as a cue for depth judgments. The stimuli were randomized with regard to whether the deeper member of the pair came first. Each pair was delivered eight times to each subject, and the sequence of the pairs in a series was random within this constraint.

The triangular stimuli used in these experiments may be defined by three parameters, any one of which is
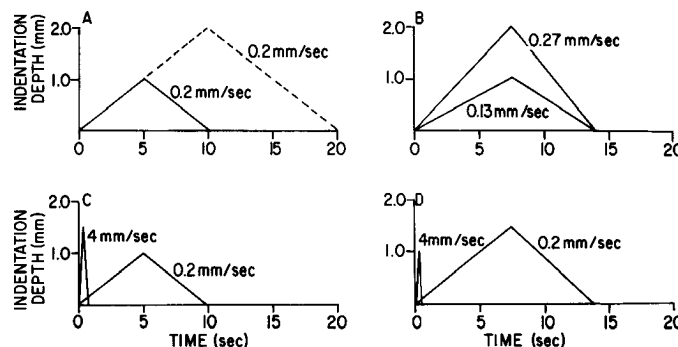
Figure 1. A shows an example of a pair of stimuli with equal velocities, and *B* shows a pair with equal rise times. Such equal velocity and equal rise time pairs served as controls. *C* and *D* illustrate pairs in which both the velocity and rise time differed. They were used to test the effect of velocity on judgments of indentation depth. Pair *C* has an amplitude ratio of 1.5 and a velocity ratio of 20. Pair *D* has an amplitude ratio of 1.5 and a velocity ratio of 1/20.

determined by the value of the other two. The three parameters are indentation amplitude, velocity, and rise time (time to peak). A stimulus pair can be described either as the difference in the magnitude of these parameters or as the ratio of their values. The amplitudes compared were 2 versus 1, 1.5 versus 1, 2 versus 1.5, 1.25 versus 1, and 2 versus 1.75 mm. Thus there were five amplitude ratios but only three amplitude differences. Examination of the subjects' responses to control (equal velocity and equal rise time) pairs (Fig. 2) suggested that amplitude ratio might have some influence on the performance of the subjects, and so the ratio was used. The rate combinations tested were chosen so that each velocity ratio corresponded to a unique velocity difference, and we have chosen to use velocity ratio as the other variable, in keeping with the use of amplitude ratio.

Three plots, each one a three-dimensional representation, were made of the subjects' performance (percentage of correct calls) as a function of amplitude ratio and velocity ratio, amplitude ratio and rise time ratio, or amplitude ratio and rise time difference. Visual examination of the resulting surfaces indicated that the surface with the fewest discontinuities resulted when the data were plotted as a function of amplitude ratio and velocity ratio.

Differences in the performances of the subjects on different pairs were evaluated by casting the data in a 2 × N table and using the χ^2 statistic. Comparison of the performances for a given pair to that expected if the subjects felt the two members of the pair as equal was made with the binomial distribution for $p = q = 1/2$. All statistical tests were double tailed, and a confidence level of 0.05 was chosen as the criterion for significance.

Effect of stimulator size on depth judgments. In another series, the effect of stimulator size on perceived depth was studied by giving individual triangular stimuli at 15-sec intervals to the fingertip and asking subjects to estimate numerically the depth of the indentation using whatever scale they wished. The stimuli were given in sets of eight. Each set consisted of two trials of each of the same four stimuli (1 mm amplitude, 0.4 mm/sec and 1.6 mm/sec; 2 mm amplitude, 0.4 and 1.6 mm/sec) given in a pseudorandom sequence. Six sets (48 stimuli in all) were given to each of four subjects. In half the sets the stimulator (which was a circular plastic disc) was 2 mm in diameter and in the other half it was 5 mm in diameter, sequenced pseudorandomly. All stimuli were given from an initial indentation of 0.5 mm. The stimulator was switched between the middle and index fingers between sets, and the subjects were allowed to rest. The effect of stimulator size on depth judgments was evaluated with the sign test, two tailed. A few preliminary trials were given before actual scaling began. The subjects knew nothing about the purpose of the experiment or the waveforms or stimulator sizes to be used, and they were told nothing about their performance until all tests were completed.

Judging the curvature of the indented area. Three stimulators 3.5 mm in diameter with tips of different curvature (Fig. 4) were used to determine whether subjects could distinguish the curvature of the indented area. Trials were carried out in which stimulator A was compared with stimulator B, stimulator B with C, and stimulator A with C. The stimuli to be compared were given successively to the fingertip, and the subjects were asked to state which of the two stimulators had the greater curvature. If they said they did not know, they were required to guess. In order to give the paired stimuli in close succession (3 to 5 sec apart), two moving coil drivers were used, each equipped with a stimulator of different curvature which was directed to a different portion of the fingertip. Care was taken to deliver the stimuli at right angles to the skin surface. The stimuli indented the skin at 1.6 mm/sec or 8 mm/sec to a depth of 1.5 mm from an initial position of no contact, held the skin steadily indented for 3 sec, and then retracted at the same rate to the initial position. Each pair (A versus B, B versus C, and A versus C) was delivered six times to each of 12 subjects in a pseudorandom sequence. Pairs (trials) were separated by 15 to 20 sec, and, after six trials had been given, the subjects were allowed to rest for 2 to 3 min. The next series of six trials was given to a different finger on the right hand (the index or middle finger), and all the subjects were right handed. The subjects were not told whether their judgments were correct until all tests had been completed, at which time they were also questioned about how they carried out the discrimination.

Anesthesia of forearm skin. Anesthesia of the skin of the forearm was carried out in two different ways. Three subjects had several milliliters of 1% Xylocaine with 1/200,000 adrenaline chloride injected into the subcutaneous space along a line across the front of the arm just distal to the elbow. This formed an obvious weal which was blanched due to vasoconstriction. Marked sensory loss developed over the next 15 to 20 min and extended 10 to 12 cm distal to the distal margin of the weal. This was probably due to cutaneous nerve block and not to diffusion of the anesthetic, because sensory loss was not detectable for more than 2 cm proximal to the proximal margin of the weal.

Two different subjects had a localized patch of skin anesthetized by cocaine iontophoresis. A circular plastic chamber 3 cm in diameter was sealed to the skin of the dorsal forearm with petroleum jelly and then filled with a solution of 2% cocaine in 80% alcohol to which one drop of 1/1000 adrenaline chloride was added. A silver wire was inserted into the fluid in such a way that it did not touch the skin and connected to the anode of a battery. The cathode was connected to a saline-soaked gauze pad on which the volar surface of the forearm rested. Currents corresponding to a density of about 0.1 mA/cm^2 were passed until movement of hairs within the area could no longer be felt (20 to 30 min). Sensitivity to superficial pinpricks disappeared before hair sensibility.

Measurements of skin thickness. This was done on both the forearm and the fingertip with a caliper designed to measure the thickness of an elevated fold of skin. A particular effort was made to make these measurements in a consistent fashion so that relative values would be reliable.

Electrophysiological studies

Adult monkeys (*Macaca mulatta*) were initially anesthetized with an intraperitoneal injection of pentobarbital which was supplemented sufficiently often via the

saphenous vein to prevent withdrawal reflexes. Arterial blood pressure was measured with a femoral cannula, and mean pressures were in excess of 80 mm Hg in all experiments. Rectal temperature was held between 37 and 38°C with external heat.

Recordings were made from single sensory fibers in the median nerve with micropipettes as previously described (Burgess and Perl, 1967). The micropipettes were inserted into the nerve just proximal to the wrist, and the search stimulus was delivered to the nerve just distal to the elbow. The hand and arm were stabilized by being embedded in modeling clay. Once a fiber was isolated, the glabrous skin of the hand was vigorously explored with a 4-mm diameter glass rod to locate the receptive field. A number of fibers could not be activated. If the receptive field was on the side of the hand or digitis, the fiber was not studied further. Receptive fields on the palmar aspect of the hand were examined with a 0.5-mm diameter stimulator (von Frey hair) to identify the receptive field focus, and this was marked with washable ink. In some cases the skin was gently squeezed with fine blunt forceps to test whether the endings were in the skin or located subcutaneously. The receptors were then stimulated with the same electromagnetic device used in the psychophysical studies. It produced a voltage proportional to its excursion, and this was recorded in parallel with the nerve impulses on a magnetic tape which was later analyzed with a computer. The moment of skin contact was determined by looking at the stimulating tip (a flat plastic disc 2 mm in diameter) through a dissecting microscope as the stimulator was slowly advanced by hand using a micromanipulator. After contact, the stimulator was lowered an additional 0.3 mm. Triangular indentations 1.3 mm in amplitude, with equal indentation and retraction rates, were used to stimulate the hand.

The receptors were classified on the basis of their adaptation rate to maintained 3-sec indentations of the skin (initial indentation rate 0.4 mm/sec, amplitude 1.3 mm). Receptors producing fewer than two impulses during the 3-sec steady displacement were classified as rapidly adapting (RA), those producing more than 10 impulses were called slowly adapting (SA), and those falling between these two categories were labeled intermediate (IA). Most studies have defined RA receptors as those that respond only as long as the stimulus is moving (e.g., Talbot et al., 1968; Knibestöl and Vallbo, 1980), with the remainder classified as SA. Accordingly, the IA receptors in our study can probably be assigned to the SA category of previous investigators (also see below). When the IA and SA receptors are combined, the percentages of RA and SA endings in our sample (RA = 108 (53%), SA = 97 (47%)) are similar to a median nerve sample collected by microelectrode recording from human subjects (RA = 186 (55%), SA = 154 (45%); Johansson and Vallbo, 1979). Note that for this comparison presumed Pacinian corpuscle endings have been included in the RA group, presumed muscle spindle endings have been included in the SA group, and "nail" units have been excluded from Johansson and Vallbo's sample since we did not include them in ours.

Pubols and Pubols (1976) found that about 2% of the SA receptors in their median nerve sample from squirrel monkey responded only during the first 15 sec of a static displacement. Similar receptors, which they called "moderately slowly adapting," are prevalent in the raccoon median nerve (Pubols et al., 1971). Lindblom (1965) also found SA units in monkey glabrous skin with a discharge to static displacement that seldom lasted longer than 10 to 20 sec. It is likely that our IA receptors belong to this moderately slowly adapting population described by others.

Each receptor was tested with three repetitions of triangular stimuli with velocities of 0.2, 0.4, 1.6, 4.0, and 16.0 mm/sec. The indentation and retraction phases of the stimuli were divided into 10 bins each, and the number of impulses occurring in each bin was determined. Average input-output (stimulus-response) functions were generated by averaging the data, bin by bin, first over the three repetitions for each receptor and then over all receptors within a given class. The average impulse counts in each bin were divided by bin duration to convert them to frequency in impulses per second and were plotted versus indentation depth by centering each point over the corresponding bin (see Fig. 8). The resulting stimulus-response functions for individual receptors or receptor groups were used to measure receptor rate sensitivity and to determine response thresholds. Because no correction was made for peripheral conduction time, the peak frequency fell after the peak of the faster triangular stimuli and was thus averaged with the lower response that occurred during stimulus retraction. As a consequence, receptors' rate sensitivity is artifactually lowered; however, because this produces a conservative picture of the effects we are studying, we have not corrected for this shift.

Results

Psychophysical studies

Effect of indentation velocity on depth judgments

In these experiments the subjects had to judge the depth of triangular stimuli when they did not know in advance how deep any particular indentation would be. When questioned, all reported using a strategy in which they tracked the depth of the stimulator as it progressively indented the skin, registered the point at which it began to retract, and compared this with the other stimulus in the pair.

Fingertip stimulation. The results of the fingertip tests are shown in Figure 2A. Five amplitude ratios were studied: 2.00 (depths of 2 versus 1 mm), 1.50 (1.5 versus 1 mm), 1.33 (2 versus 1.5 mm), 1.25 (1.25 versus 1 mm), and 1.14 (2 versus 1.75 mm). Pairs of stimuli with equal velocities (speed ratio of 1) and pairs with equal rise times (*dotted line*) served as controls. Control indentation rates extended from 0.13 mm/sec to 21.3 mm/sec; the slowest indentation was readily perceived on the fingertip, but the fastest was near the upper limit of velocities that produced a clear sensation that the skin had been indented and then returned to its original position. At any particular amplitude ratio, there was no significant tendency for any one velocity or rise time to be better discriminated, and so equal velocity and equal rise time pairs with the same amplitude ratio have been
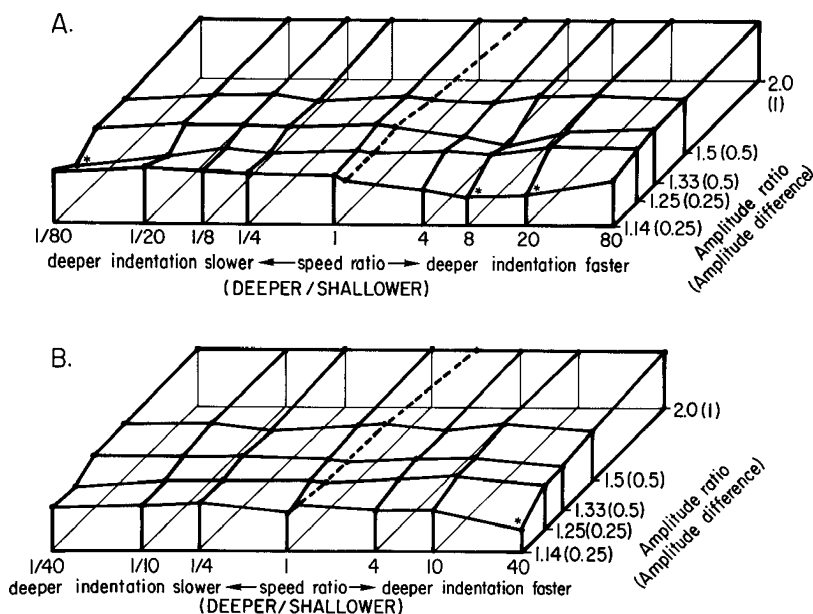
Figure 2. The height of the graphs indicates the percentage of correct depth judgments on the fingertip (*A*) and on the forearm (*B*) as a function of velocity (speed) and amplitude ratio. Corresponding amplitude differences (millimeters) are given in parentheses, and at a ratio of 2 the subjects were correct 100% of the time in both *A* and *B*. Equal velocity (speed ratio 1) and equal rise time pairs (*dotted line*) served as controls. Discriminations marked with an asterisk (*) were made significantly less well than control discriminations at the same amplitude ratio ($p < 0.01$) and did not differ significantly from chance ($p > 0.05$). The control trials were given to two of the four subjects. The equal rate and equal rise time data from these two subjects can be compared with the other values in the figure because, when responses to pairs which were presented to all the subjects were compared with the χ^2 statistic, the Wilcoxon test, and the sign test, all three indicated that there were no significant differences between the subjects. Equal velocity pairs indented and retracted at 0.2, 0.4, 4, and 16 mm/sec in *A* and 0.4, 0.8, 4, and 16 mm/sec in *B*. Equal rise time pairs indented in 7.5, 3.75, 0.375, and 0.094 sec in *A* and 3.75, 2, 0.375, and 0.094 sec in *B*. For a given amplitude ratio, there were no significant differences in responses to any of the control trials. Therefore, the results of equal velocity and equal rise time trials at each amplitude ratio have been combined for statistical tests, giving a total of 128 control trials at each amplitude ratio. However, differences in accuracy were found between different amplitude ratios. On the fingertip, control discriminations at amplitude ratios of 1.14 and 1.25 were made significantly less well than when the ratios were 1.33 or greater ($p < 0.01$). On the forearm, control discriminations at amplitude ratios of 1.25 and 1.33 were made significantly less well than at a ratio of 1.5 or greater ($p < 0.05$), and the control discrimination at a ratio of 1.14 was made significantly less well than all the others ($p < 0.05$). The only significant difference between forearm and fingertip controls was a failure to discriminate an amplitude ratio of 1.33 on the forearm as effectively as on the fingertip ($p < 0.01$). In all control discriminations the subjects were significantly more accurate than expected by chance. In all pairs other than the controls, the slower indentations had a velocity of 0.2 mm/sec on the fingertip and 0.4 mm/sec on the forearm, and 32 trials were given for each noncontrol point on the graphs.

combined. Also, at a given amplitude ratio there were no significant differences in performance between equal velocity and equal rise time pairs. However, control pairs with smaller amplitude ratios tended to be less well discriminated.

Figure 2*A* also illustrates the effect of velocity on perceived indentation depth. In three cases, when the difference in amplitudes was small, pairs which differed in both velocity and rise time were less accurately discriminated than the control pairs with the same amplitude ratio. With an amplitude ratio of 1.14 (i.e., 2 versus 1.75 mm) and velocity (speed) ratios of 8 and 20, the discriminations differed significantly from controls, the slower indentation being perceived as relatively deeper than it actually was (Fig. 2*A*). Significantly more difficulty was also experienced in discriminating 1.25 from 1

mm (amplitude ratio 1.25) when the deeper indentation was the slower pair member and the speed ratio was 1/80. More striking, though, is the fact that the other 37 pairs were about as accurately discriminated as their corresponding control pairs.

Perhaps the most sensitive way to test the effect of velocity on perceived indentation depth is to indent the skin with equal amplitude pairs that differ in rate. Figure 3*A* shows the results of such tests. With indentations of 1 mm, the depth of the slower indentation was perceived as similar to the faster indentation. With indentations of 2 mm, the slower indentation was more often called deeper, particularly at speed ratios of 8 and 20, where the differences reached statistical significance.

In summary, subjects did not misjudge the relative amplitudes of fingertip indentations which differed in velocity by almost two orders of magnitude unless the amplitude differences were small. Most of the errors occurred when the stimulator indented the skin deeply, and they were due to a slower stimulus feeling deeper than a faster one.

Forearm stimulation. When the forearm was indented 1 mm with the 13-mm diameter disc at a rate of 0.2 mm/sec, the stimuli were sometimes not felt. Therefore, the slowest indentation used on the forearm was 0.26 mm/sec. Figure 2*B* shows the results of the forearm experiments. The forearm resembled the fingertip in that for a given amplitude ratio the accuracy of the control (equal rate or rise time) discriminations was not influenced by velocity or rise time within the range tested, and the data from these trials were combined as already described for the fingertip. Discrimination of the control pairs on the forearm was about the same as on the fingertip, although 2 versus 1.5 mm (amplitude ratio 1.33) was significantly less well discriminated on the forearm.

Figure 2*B* also shows the effect of indentation velocity on perceived indentation depth. Overall, the subjects' performance did not differ appreciably from control trials. Only 2.0 versus 1.75 mm (amplitude ratio 1.14) at a speed ratio of 40 was discriminated significantly less well than its corresponding control. When pairs with members of equal amplitude but different velocities were given (Fig. 3*B*), there was no clear evidence that slower indentations were perceived as relatively deeper than rapid indentations of the same amplitude. Equal amplitude pairs of 1 mm did show a rate effect in that faster indentations were perceived as relatively deeper at a speed ratio of 10.

To summarize, the perception of indentation depth on the forearm was generally well compensated for rate. At the shallow end of the range, there probably was some tendency for faster indentations to feel relatively deeper when the pairs were of equal amplitude, but this effect was too weak to interfere appreciably with the discrimination of 1- versus 1.25-mm indentations.

Effect of stimulator size on depth judgments

When the area of a fingertip stimulus was increased 625% (a disc with a diameter of 5 mm was exchanged for one with a diameter of 2 mm), there was a small but significant increase in the perceived depth of the inden-
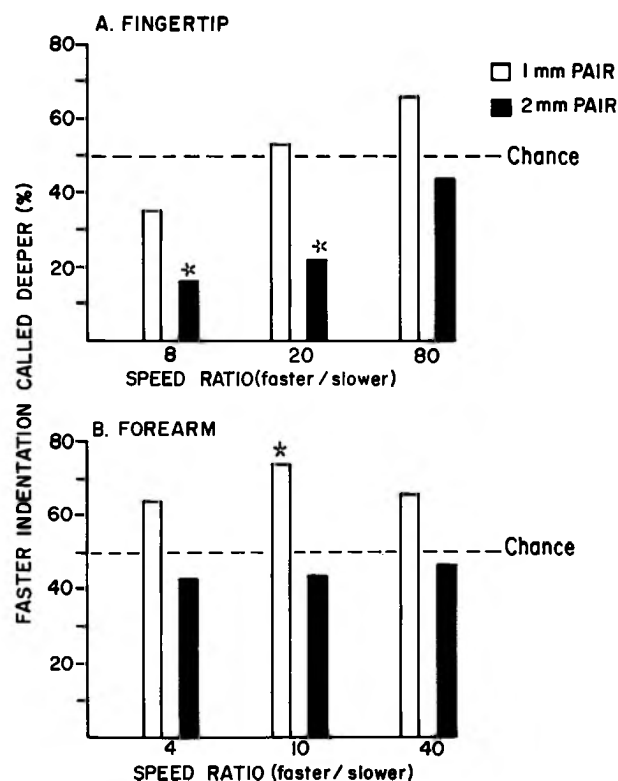
Figure 3. The subjects were given pairs of stimuli with equal amplitudes but different velocities. Data for the fingertip are shown in *A* and for the forearm in *B*. The height of the *bars* indicates the percentage of trials in which the faster indentation was called deeper at the velocity (speed) ratios shown on the abscissa. *Open bars* are for 1-mm indentations, and *solid bars* are for 2-mm indentations. In an occasional trial out of the 32 given, the indentations were called equal, and these responses have been omitted from the figure. *Bars* marked * show responses significantly different than expected if indentations had been felt as equal ($p < 0.01$). On both the fingertip and forearm, there was a consistent tendency for the slower 2-mm indentations to be called deeper than the faster 2-mm indentations. Conversely, there was, with one exception, a tendency for the faster 1-mm indentations to be called deeper than the slower 1-mm indentations. In both *A* and *B*, then, increasing the indentation depth from 1 to 2 mm caused a relative enhancement of the perceived depth of the slower stimuli.

tation. For triangular stimuli 1 and 2 mm in amplitude which indented the skin at 0.4 and 1.6 mm/sec, subjects increased their numerical scaling of depth by an average of 12% when the larger stimulator was used ($p < 0.01$).

Judging the curvature of the indented area

The stimulators shown in Figure 4 were used to determine whether subjects could distinguish stimulator curvature. When the skin was indented at 1.6 mm/sec (see "Materials and Methods"), A (the least curved) was correctly distinguished from C (the most curved) in 67 of 72 trials (93% correct), A was correctly distinguished from B in 57 of 72 trials (79% correct, $p < 0.01$), and B from C in 61 of 72 trials (85% correct). Four subjects were also tested at an indentation rate of 8 mm/sec with no significant change in performance.
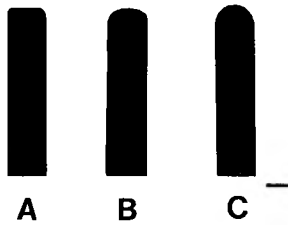
Figure 4. The three stimulators used to test the capacity of subjects to sense the curvature of the indented area are shown as silhouettes. The *horizontal bar* is equal to 2 mm.

Anesthesia of forearm skin

Two methods were used to anesthetize the skin of the dorsal forearm, cocainization and subcutaneous infusion of Xylocaine (see "Materials and Methods"). Tests of indentation sensitivity were made with the 13-mm diameter stimulator placed on forearm sites typically used for indentation studies (8 to 10 cm distal to the injection weal or directly over the cocainized area). None of the subjects could feel 2-mm indentations made at a rate of 4 mm/sec from the usual starting indentation of 0.5 mm. If the indentation velocity was increased to 8 to 16 mm/sec, the stimuli could be felt, but the sensations were localized deep to the skin.

Electrophysiological studies

The starting point for this portion of the study was to investigate whether skin indentation depth is signaled with a "recruitment" code or a "frequency" code. A recruitment code is one where the indentation produced by an object is signaled by which receptors in a population are active. A frequency, or interval, code is one where the level of activity in a population of receptors, rather than the depth at which they are recruited, provides the signal.

The electrophysiological studies were carried out on the monkey's hand because of its importance for tactile function. Also, by recording from the medain nerve, we had access to all the receptors on the palmar aspect of the first three digits, both cutaneous and deep. Fibers with receptive fields on the palm were also studied (see "Materials and Methods"), but more than half the sample came from the thumb, middle, and index fingers.

Although the microelectrode recording technique we used generates a sample biased in favor of large axons, small myelinated fibers can be recorded from with this method (Whitehorn et al., 1974). We recorded from 318 myelinated fibers, with conduction velocities ranging from 10 to 90 m/sec. Two hundred and five fibers responsive to non-noxious mechanical stimulation of the palmar surface of the hand and fingers were studied, and all conducted more rapidly than 35 m/sec (Fig. 5). Previous investigations of primate glabrous skin have likewise failed to demonstrate low threshold mechanoreceptors with slowly conducting myelinated fibers (Talbot et al., 1968; Darian-Smith et al., 1973; Georgopoulos, 1976). There were 108 rapidly adapting (RA), 84 slowly adapting (SA), and 13 intermediately adapting (IA) receptors in the sample (see "Materials and Methods"). Four of the RA receptors had marked vibratory sensitivity and wide receptive fields and were presumed to be Pacinian

corpuscles. Because these receptors are probably concerned with stimulus acceleration and vibratory sensations (Mountcastle et al., 1969; Burgess and Perl, 1973), they have not been included in the population analyzed below for indentation depth signaling. In addition, 19 RA receptors did not respond to the fastest triangular stimulus used (16 mm/sec) and so were not included in the analysis. Six SA receptors were analyzed separately because they were considered to be muscle spindles, since their receptive fields were located subcutaneously in the palm and they had resting activity.

Recruitment coding

For skin indentation depth to be signaled by a recruitment code, two conditions need to be met: (1) the members of the receptor population that are active must change in a systematic way with indentation depth, and (2) the receptors recruited at different depths must be connected to different central neurons (depth must be topographically mapped within the central nervous system). We are concerned here only with the first of these requirements and will consider two possible ways in which a recruitment code could be set up at the receptor level. The first involves progressive recruitment with depth of afferent fibers whose receptive field foci lie beneath the stimulator. This will be referred to as depth signaling by "subsurface" recruitment. The second possible recruitment code for depth is one in which the recruitment of receptors whose receptive field foci lie progressively further and further away from the stimulator specifies the magnitude of the indentation. This
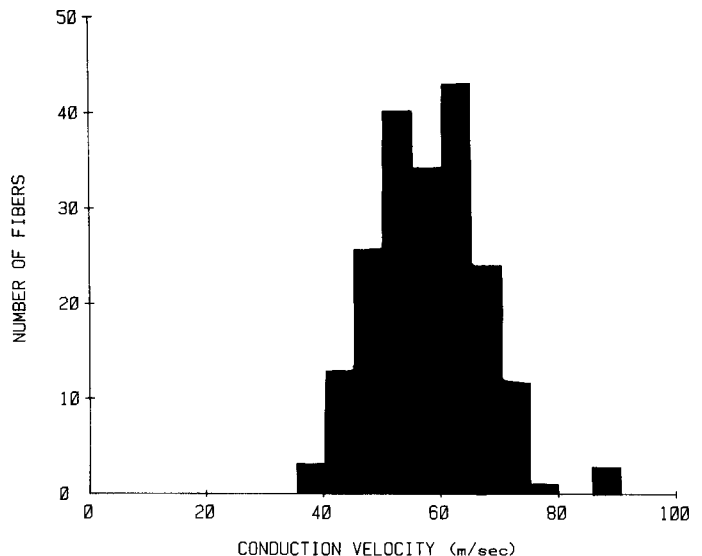

Figure 5. Histogram shows the conduction velocities of the 199 fibers activated by non-noxious mechanical stimulation of the palmar glabrous skin. Mechanoreceptive neurons whose receptive fields could not be reached by the mechanical stimulator have been excluded, but they had conduction velocities similar to those included in the sample. Other fibers conducting in this range could not be excited and may have been motor since the median is a mixed nerve. Eight percent of the total sample (N = 318) conducted below 30 m/sec, and several mechanically insensitive fibers conducting below 20 m/sec responded vigorously to cooling.

will be referred to as depth signaling by "lateral" recruitment.

Subsurface recruitment. To test the possibility that skin indentation depth might be signaled by progressive recruitment of receptors beneath the stimulator (subsurface recruitment), we centered the stimulator over the receptive field focus of each afferent fiber and determined the depth at which the discharge frequency exceeded 5% of the maximal frequency during the slowest indentation (in the range of 0.2 to 16 mm/sec) to which that receptor responded. These determinations were made from average input-output functions for each afferent fiber constructed as described under "Materials and Methods."

The lowest curve in Figure 6 shows the recruitment profile for the 118 receptors that responded to the slowest (0.2 mm/sec) triangle. All nonspindle SA receptors (78) and all the IA receptors (13) responded to this stimulus, as did 27 RA receptors; most were recruited during the first half of the indentation. The six presumed spindle receptors also responded at 0.2 mm/sec but were not included in Figure 6 and will be discussed separately below. Since rapidly adapting receptors have a range of velocity thresholds, the number of receptors in the responding population increased as the triangular stimuli became more rapid (Fig. 6). Also, as the velocity increased, the receptors were recruited earlier during the indentation; at velocities of 1.6 mm/sec and higher, more than 90% of the receptors were recruited during the first half of the indentation.

No receptors were excluded from Figure 6 because they were deeply located, other than six presumed spindles. The excluded spindles were also recruited during the first half of the indentation, even at 0.2 mm/sec.

Lateral recruitment. It is well known that the indentation thresholds of receptors increase as a stimulator is moved away from the focus of the receptive field (Armett and Hunsperger, 1961; Jänig, 1971; Tuckett et al., 1978), and such shifts were seen in the present study. Therefore, as stimulator depth increases, there will be a progressive recruitment of receptors at greater and greater distances from the stimulator (lateral recruitment). Lateral recruitment, like subsurface recruitment, is rate sensitive (Fig. 7), which is consistent with the earlier observation that receptors are more readily excited at a distance by rapid than by slow stimuli (Tuckett et al., 1978).

Frequency coding

If skin indentation depth is signaled by a frequency or interval code, the magnitude of the indentation is specified by the level of activity in some or all of the receptors
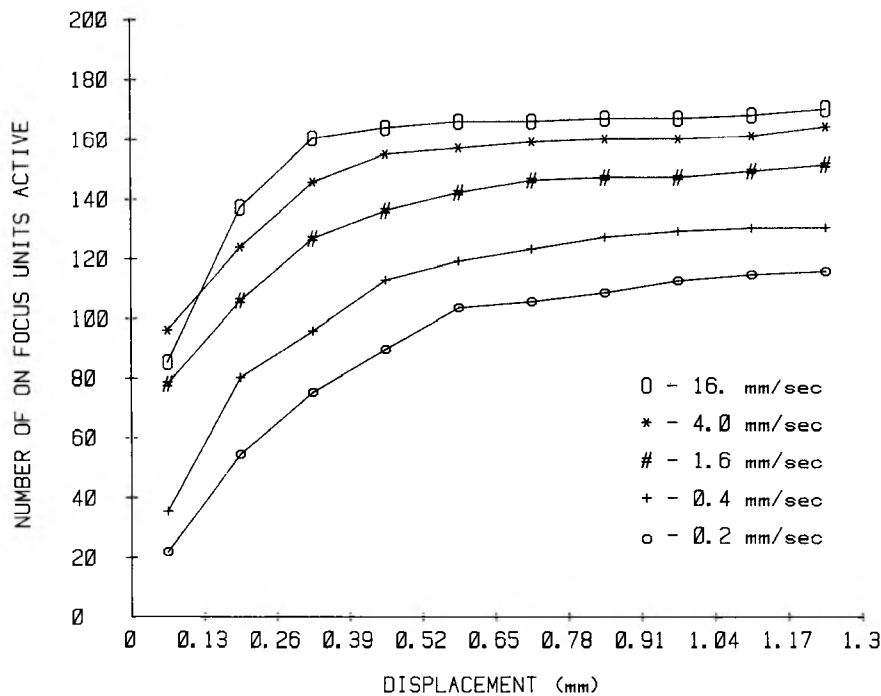
Figure 6. Receptor recruitment profiles are shown for skin indentation over the center of the receptive field at 0.2, 0.4, 1.6, 4, and 16 mm/sec. The total number of receptors recruited during an indentation increased as the indentation velocity increased because more RA receptors were recruited; the numbers range from 118 at 0.2 mm/sec to 176 at 16 mm/sec. The recruitment threshold for a given receptor was calculated as the bin (130-μm indentation increment) in which its discharge frequency exceeded 5% of the maximal frequency occurring during the slowest indentation ramp (in the range of 0.2 to 16 mm/sec) to which the receptor responded. The number of receptors whose thresholds had been exceeded by a given indentation increment has been indicated with a point placed at the center of the bin for that increment. Most of the receptors were recruited during the first half of the 0.2 mm/sec indentation, and this tendency became more pronounced at higher velocities.
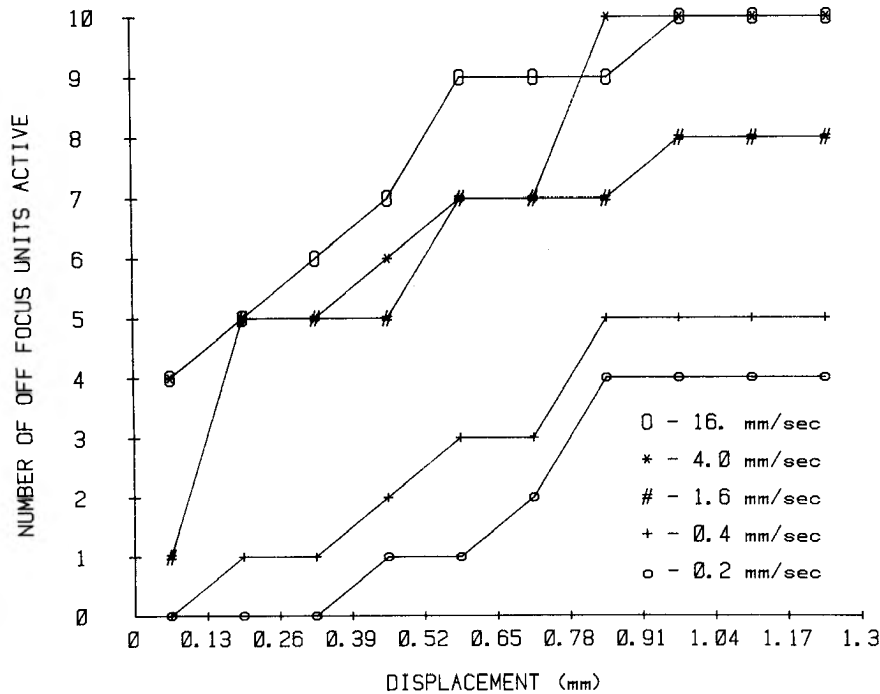
Figure 7. Receptor recruitment profiles are shown for 10 receptors (5 SA, 2 IA, and 3 RA) stimulated 1 to 2 mm from the focus of their receptive fields at indentation velocities of 0.2, 0.4, 1.6, 4, and 16 mm/sec. The data are presented as in Figure 6. All the receptors responded to the 0.2 mm/sec triangle when the stimulator was on focus.

excited by the stimulator. Which receptors in the population are active is no longer important so long as they have equal access to the central circuitry that signals the depth of that particular patch of skin. Lateral or subsurface recruitment of additional receptors would simply add to the overall input in proportion to the strength of their connections to the depth circuit for that patch of skin. For frequency coding to operate, the discharge frequency of this receptor population or some measure derived from the frequency (e.g., the time integral of the frequency) must change in a systematic fashion with indentation depth. Both slowly and rapidly adapting receptors might contribute to such a frequency code.

Slowly adapting receptors. Figure 8 shows stimulus-response functions for the 78 nonspindle SA receptors in our sample, expressed as the response of an average receptor to displacing the skin at different velocities. Both the indentation and retraction phases of the triangular stimuli are shown. It can be seen that a frequency signal for depth is present at each velocity, in the sense that the frequency progressively increases with indentation. However, the actual frequency at a given depth is greatly dependent on the rate of indentation. For example, the discharge of the average SA receptor was about 40 impulses/sec at 1.3 mm when the indentation rate was 0.2 mm/sec. But this frequency had already been exceeded at a depth of only 0.65 mm when the rate of indentation was 1.6 mm/sec, and at the still smaller depth of 0.26 mm when the rate of indentation was 16 mm/sec. One way to estimate the rate error in depth coding is to compare depths at which a given impulse

frequency, such as 40 impulses/sec, occurs for different rates of indentation. In the example cited above, when the 0.2 mm/sec indentation rate is compared with 1.6 mm/sec the error is 0.65 mm; when compared with 16 mm/sec, the error is 1 mm.

We were concerned that some receptors in the SA group might have considerably less rate sensitivity, and hence a smaller error in depth coding, than the average shown in Figure 8. To identify the most tonic receptors in the population, we determined the mean frequency during the last 0.52 mm of indentation for each of the SA receptors at each velocity. The differences in these frequencies between 0.2 mm/sec and each higher velocity were then measured and added together. The eight receptors with the smallest total were considered to represent the most tonic 10% of the SA population. The average stimulus-response functions for these receptors (Fig. 9) are generally less steep, but they do not provide a more rate-independent signal of skin indentation depth than does the SA population as a whole.

Since under natural circumstances the stimulator would be off-focus for a number of receptors, eight SA endings were tested first with the stimulator on the focus and then with the stimulator moved laterally 1 to 2 mm so that the receptor was still excited but less vigorously. The off-focus stimulus-response functions were less steep, and the rate errors in depth coding were larger. Moving the stimulator back onto the focus restored the stimulus-response functions to their original form.

Rapidly adapting receptors. About one-third of the rapidly adapting receptors had stimulus-response func-
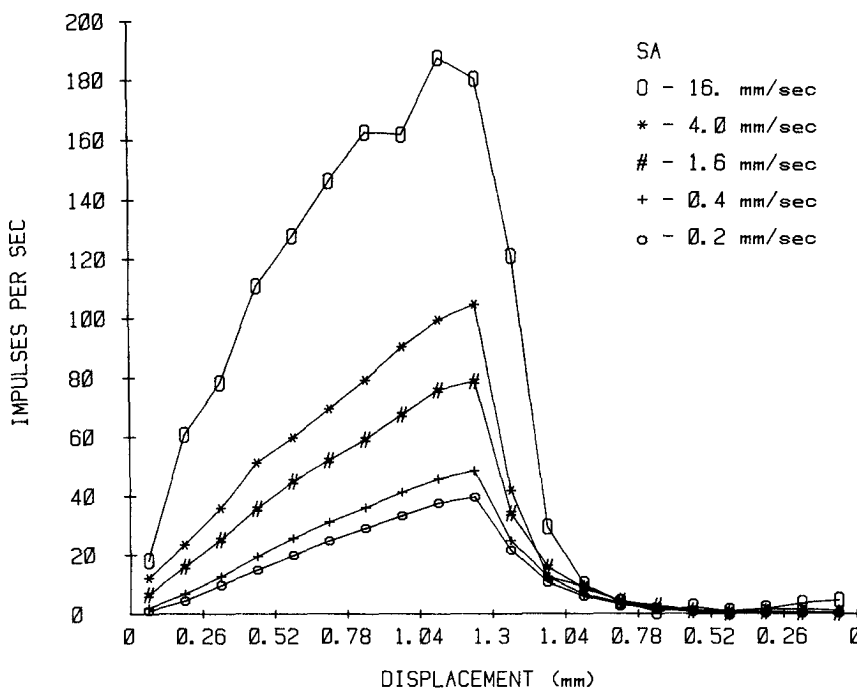
Figure 8. Frequency of discharge (*ordinate*) is shown as a function of skin indentation depth (*abscissa*) when the skin was indented with triangular stimuli having velocities of 0.2, 0.4, 1.6, 4, and 16 mm/sec. The average response for all 78 SA receptors is presented during both the indentation and retraction phases of the stimuli. To produce the average SA receptor response, the numbers of impulses occurring in a particular bin (130-μm indentation increment) for each receptor were added together and divided by the total number of receptors in the population and the bin duration. Points are plotted at the bin center. The discharge frequency at any particular depth increases progressively as the rate of indentation increases.
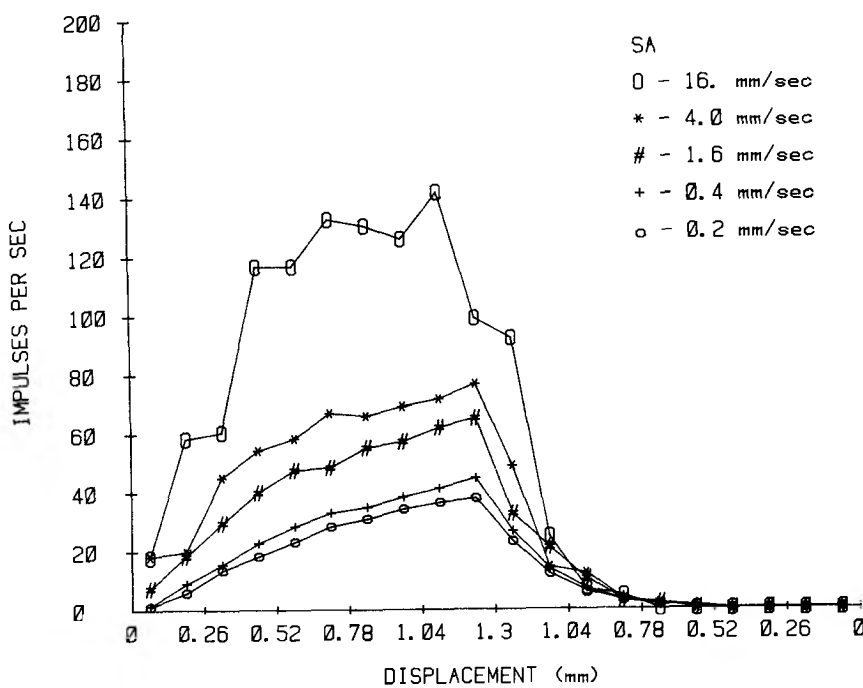

Figure 9. Frequency of discharge versus indentation depth is shown as in Figure 8 except that the most tonic 10% of the SA population is illustrated.

tions with negative slopes when they were excited by indentation ramps with near threshold velocities (Fig. 10A). Another one-third had stimulus-response functions with positive slopes (Fig. 10B), and the remaining third did not show either tendency with the slower stimuli but developed negative slopes at higher indentation velocities (Fig. 10C). All three groups had large depth-coding errors.

Almost all the receptors that were intermediate in adaptation (the IA group) had stimulus-response functions with positive slopes (Fig. 11) that were steeper than the corresponding RA group (Fig. 10B) but less steep

than the SA receptors (Fig. 8). They also had large depth-coding errors.

Discussion

Apart from some threshold determinations (Renfrew and Melville, 1960; Smaje and McLellan, 1981), ours appear to be the only psychophysical experiments in which subjects have been asked to judge the indentation *depth* of a cutaneous stimulus. Previous work has focused on the relationship between the force of a cutaneous stimulus and its perceived intensity (see Sherrington, 1900) and more recently on the relationship between
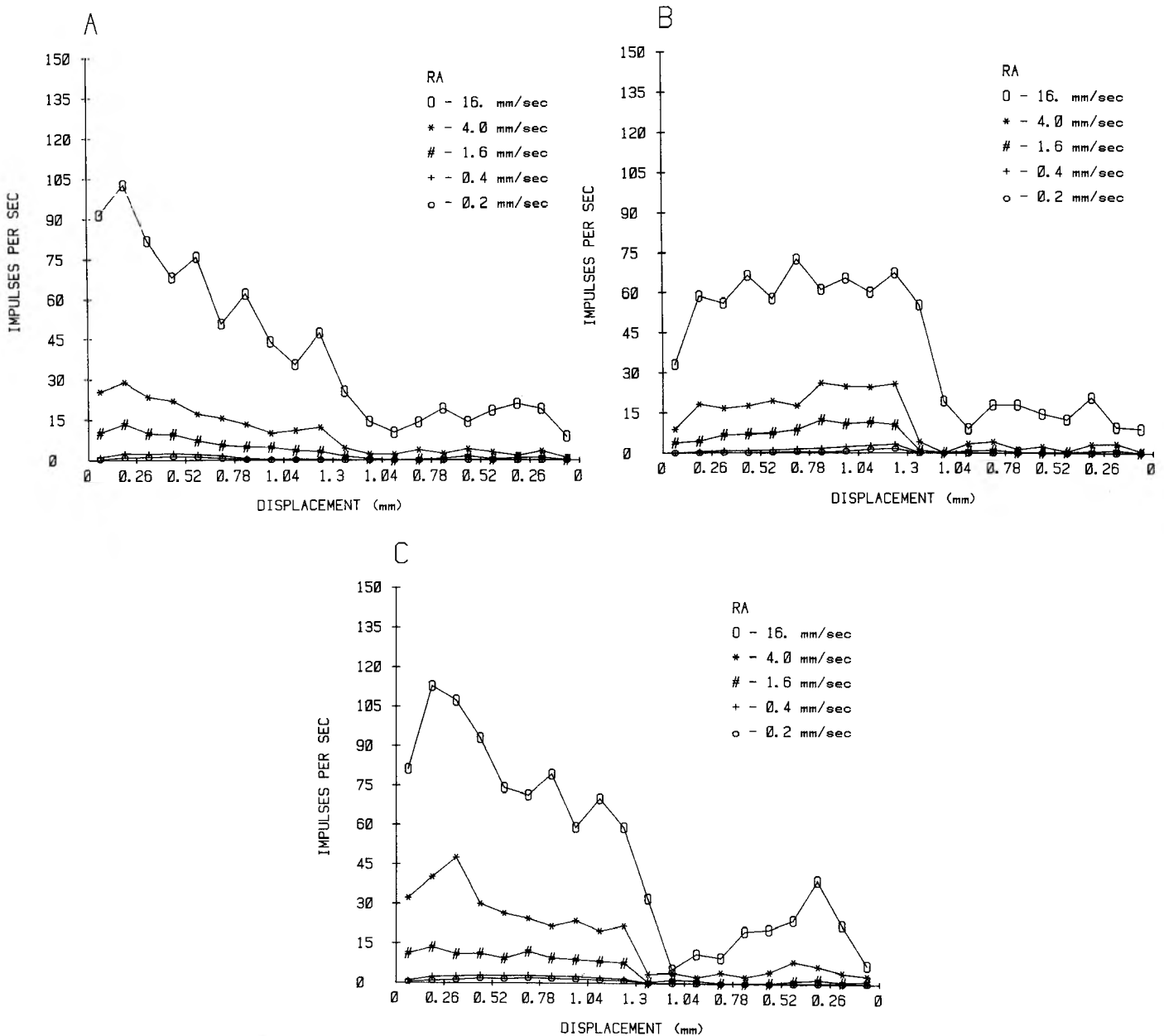

Figure 10. Average frequency of discharge versus indentation depth is shown for RA receptors, presented as in Figure 8. *A* shows receptors with negatively sloping stimulus-response functions, *B* shows receptors with positive slopes, and *C* shows receptors that did not demonstrate either tendency when stimulated near their velocity thresholds. The numbers of receptors responding increased as the rate and magnitude of the indentation increased (see Fig. 6). The averages shown here are for all the receptors in each population, nonresponding receptors contributing 0 impulses per bin. The numbers of receptors activated were 7, 10, 16, 25, and 30 in *A*; 10, 13, 23, 25, and 27 in *B*; and 10, 15, 24, 26, and 28 in *C*.
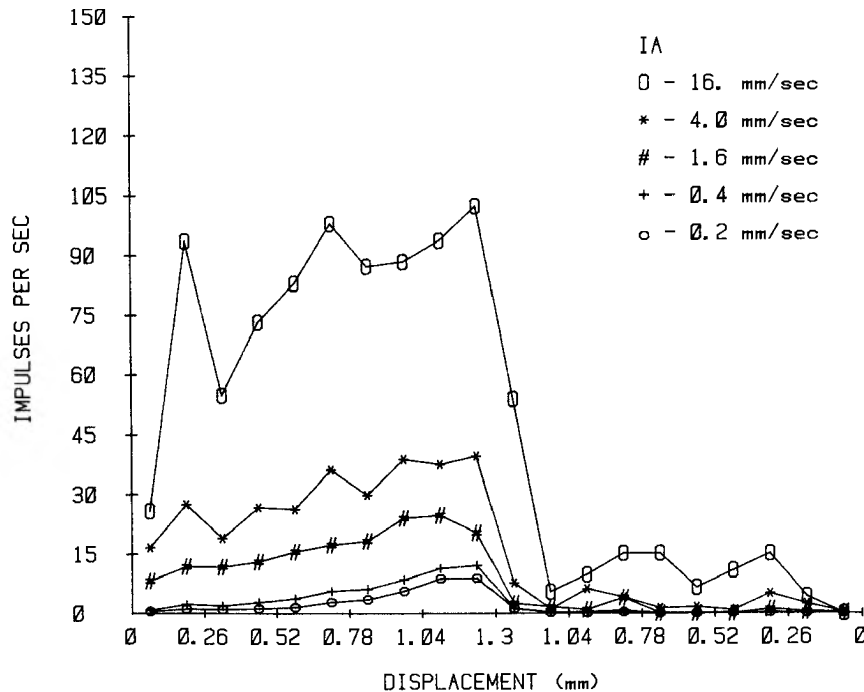
Figure 11. Discharge frequency versus indentation depth is shown for the 13 IA receptors, averaged as in Figure 8 for the same triangular stimuli.

skin indentation depth and perceived intensity (Harrington and Merzenich, 1970; Knibestöl and Vallbo, 1980). Our subjects were asked not which of the two stimuli they received was more intense but which indented the skin more deeply. They had no difficulty with this task and reported that they were accustomed to making indentation depth discriminations in daily life. Skin displacements of the magnitudes we have used on the fingertips commonly occur when objects are grasped, and indentation sensations are particularly salient when the object is small or has edges. Further evidence that we were testing a well practiced sensory function comes from the fact that the subjects did not show any improvement in their performance over time, even though they were told after each trial whether they were correct in their judgments.

The principal finding in the psychophysical portion of this study is that the perceived depth of a skin indentation is not greatly altered by changes in the velocity with which the skin is indented. The fact that cutaneous indentation sensations are largely independent of velocity allows a more accurate judgment of indentation depth than would be possible otherwise. However, the adequacy of this rate compensation varies with stimulus conditions, failing most strikingly when a stimulus is sufficiently slow and shallow that it is not felt at all. On the dorsal surface of the forearm a 7-mm diameter stimulator which indents the skin 1 mm at 0.2 mm/sec is not reliably sensed (Horch et al., 1975). On the fingertip, which is presumably more densely innervated, similar failures do not occur until the velocity falls below 0.005 mm/sec (1-mm displacement, 3.5-mm diameter stimulator; K. W. Horch, R. P. Tuckett, and P. R. Burgess, unpublished observations). In addition, slow stimuli were felt less well on the forearm if the diameter of the stimulator was

reduced from 13 mm to 3.5 mm or if the skin was partially anesthetized by cocaine iontophoresis (K. W. Horch, R. P. Tuckett, and P. R. Burgess, unpublished observations). These findings are consistent with the idea that slow stimuli need to generate a certain level of activity to be able to activate the neural circuitry responsible for judgments of skin indentation depth.

In an effort to understand how cutaneous mechanoreceptors might signal skin indentation depth, we recorded responses from receptors in the monkey hand to stimuli appropriately scaled from the human psychophysical studies. The evidence is good that similar mechanoreceptors are present in monkey and man (Knibestöl, 1973, 1975; Johansson and Vallbo, 1979), and at least some aspects of tactile sensibility are similar for both (Mountcastle et al., 1972). Our arguments do not depend on the overall numbers of fibers or the relative abundance of different receptor types in the two species.

Two different recruitment codes were considered as possible candidates for signaling skin indentation depth: a lateral recruitment code and a subsurface recruitment code. Although lateral recruitment could potentially operate over the full depth range, it is doubtful that a simple code of this sort is employed to signal skin indentation depth because a 625% increase in stimulator area was found to produce only a 12% increase in perceived depth. Moreover, to judge the curvature of an indented area (see "Results") requires the assessment of the depths of small regions of skin within the indented area, and a lateral recruitment mechanism cannot provide this information.

In evaluating the likelihood of a subsurface recruitment code with receptor recording, it is particularly important that the search stimulus by which the receptors are initially identified (see "Materials and Meth-

ods") reveals all the receptors, including those in a deeper tissue, that can be excited by indentations comparable to those used in the psychophysical experiments. Electrical stimulation of the median nerve (which contains all the afferent fibers, both cutaneous and deep, that supply the palmar aspect of the first three digits) combined with brisk mechanical search stimulation of the skin met this criterion, as evidenced by the fact that 19 receptors isolated by the search stimuli did not respond to the mechanical driver. This does not mean that there are not receptors in the deep tissues of the hand able to respond to mechanical stimuli still stronger than any we employed and which might contribute to "deep pressure" sensibility (Head and Sherrin, 1905). The existence of deeply referred "pressure" sensations elicited by forceful skin deformation after cutaneous nerve interruption indicates that subsurface recruitment coding can occur. Evidence that subcutaneous receptors are not important for the discriminations carried out by our subjects was obtained by anesthetizing the skin of the forearm. Both cocaine iontophoresis and Xylocaine block of cutaneous nerve[5] gave a similar result in which subjects' ability to detect the stimuli was virtually eliminated. We were unable to anesthetize the skin of the fingertips selectively because digital nerve block interrupts all receptor input and iontophoretically applied cocaine does not penetrate the heavy cuticle well. However, the five subjects whose forearm skin was anesthetized were spare and they had skin of greater thickness over their fingertips than on the dorsal forearm, as measured with a caliper (see "Materials and Methods"). Hence, it is unlikely that propagation of mechanical stimuli to the subcutaneous receptors of the fingertip would be greater than on the forearm in these subjects. Additional support for the idea that subcutaneous receptors are not important for the discriminations we tested comes from the observation that although the four subjects we studied most extensively differed widely in subcutaneous fat (the thickness of an elevated fold of skin ranged from 2 to 7 mm), there were no significant differences in their ability to judge skin indentation depth. Soft tissues such as subcutaneous fat decrease the propagation of mechanical stimuli to subcutaneous receptors (see Merzenich, 1968, for a comprehensive review).

Returning to the evidence from receptor studies concerning subsurface recruitment coding of skin indentation depth, the endings in the monkey hand excited under our stimulus conditions were recruited relatively early as the skin indentation depth increased. As reported in the psychophysical portion of this study, human subjects can distinguish 1.75-mm from 2-mm fingertip indentations nearly as well as they can distinguish 1- from 1.25-mm indentations throughout the velocity range from 0.2 to 16 mm/sec. Since almost all the receptors were recruited by 1.5 mm, subsurface recruitment apparently could not code the deeper portions of the range. The argument that the receptors were nearly all recruited by 1.5 mm assumes that a 1.3-mm indentation on the monkey hand is equiv-

alent to a 2-mm indentation in humans and that the criteria for recruitment are adequate (Fig. 6). The appearance of appreciable activity at depths less than 0.65 mm in the frequency versus displacement records of Figures 8 to 11 also supports early recruitment. No receptors able to respond to the largest and most rapid excursion used to activate the mechanical driver were excluded from these records because they were deeply located, except for six presumed spindles in the palm which were also recruited early. Note that the stimulator started from a rest indentation of 0.3 mm on the monkey hand and 0.5 mm in the human studies. Had the initial contact been shallower, the range of subsurface recruitment might have been more extensive. Nevertheless, it appears that a subsurface recruitment mechanism is not available on the fingertip over much of the range where accurate depth judgments can be made.

Thus it seems likely that depth is signaled, at least in part, by a frequency or interval code. The magnitude of the frequency change could then code the size of the excursion (depth) at any point, and the relative frequency across the displaced skin (frequency gradient) could code the curvature (depth gradient) of the indentation. However, the frequency signal is influenced by the rate of skin indentation (Tapper, 1965; Iggo and Muir, 1969; Chambers et al., 1972; Knibestöl, 1975; Pubols and Pubols, 1976). For example, extrapolating from the stimulus-response functions of the SA receptors in Figure 8, a 1-mm indentation at 1.6 mm/sec would feel as deep as a 2-mm indentation at 0.2 mm/sec. Rate-dependent errors of this magnitude were not made by our human subjects. In fact, rate compensation was sufficiently good that a deep indentation delivered at 16 mm/sec felt little if any deeper than one of the same depth given at 0.2 mm/sec (Fig. 3A), although the peak discharge frequency produced by the 16 mm/sec stimulus was almost 5 times greater than that produced by the 0.2 mm/sec stimulus (Fig. 8). Therefore, if a frequency code is used, this rate sensitivity must be compensated for in some fashion by the central neural circuitry responsible for judgments of skin indentation depth. One way that this could be done is by an integration (in the mathematical sense) of the receptor discharge within the central nervous system. The depth at which a receptor is recruited is likewise influenced by the rate of the indentation (Figs. 6 and 7), so, if lateral or subsurface recruitment is used to signal skin indentation depth, these signals would also have to be rate compensated.

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[5] Cutaneous nerves may give off some fibers to deeper tissues but almost all of these have thresholds suggestive of a nociceptive function (Chang et al., 1978).

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