

Tactile stimulation: Psychophysical studies of receptor function*

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Psychometric functions for the detection of brief tactile pulses were determined at the fingertips and the dorsal forearm. Functions at both loci were shallower than those previously obtained for electrocutaneous pulses, demonstrating the different neural consequences of receptor and afferent nerve stimulation. Detection on the forearm was characterized by steeper slopes of psychometric functions and by lower rates of false alarms than on the fingertips, though absolute sensitivity was better at the latter site. An examination is made of explanations for the differential effects based on receptor type, receptor density, and static tremor.

Analogous psychophysical studies of each of our sensory modalities hold the promise of distinguishing between basic neural mechanisms common to all of them and modality-specific modes of stimulus transduction and analysis. Because of the prepotency of our auditory and visual channels, most such comparisons have involved these senses. However, the increased capacity for good stimulus control and specification has made careful psychophysical and neurophysiological investigation of the skin senses possible as well. Somesthesia is an important system for examination because one can present both mechanical and electrical stimuli whose physical characteristics and accompanying sensations are readily modifiable. Data presented here suggest that the ability to employ both types of stimulation makes possible the use of psychophysical techniques for studying the characteristics of receptors in the sensory transduction process.

Psychometric functions for electrical stimulation of the skin are characterized by their extreme steepness (Rollman, 1969a). The threshold for the detection of brief electrical pulses plus or minus about 15% spans the entire detection range. The measure adopted to compare the steepness of ogives obtained in different modalities was the ratio of the standard deviation to the mean of the psychometric function—the number of stimulus units required to increase the percentage detected from 50% to 84% (or to decrease it to 16%) divided by the threshold. This ratio, which is the reciprocal of Urban's h (Urban, 1908) and which has been called the coefficient of variation as well as the relative standard deviation, has a value of 0.08 for electrocutaneous stimulation (Rollman, 1969a), but for typical visual

functions, it ranges from 0.30 to 0.60, and for audition, the value is over 0.70.

Why are electrocutaneous functions so steep? Two major possibilities exist. First, the somatosensory system is appreciably more sensitive than other modalities to small changes in stimulating energy. Second, electrical stimulation has neural consequences that are very different from those following "natural" or "adequate" stimulation of a sensory system.

Earlier research (Rollman, 1969a, b) has suggested that electrical stimuli bypass the receptors and directly initiate an action potential in the sensory nerves. Similar suggestions have recently been made by Bujas and Pfaffmann (1971) and by Higgins, Tursky, and Schwartz (1971). In contrast, mechanical tactile pulses stimulate the cutaneous receptors, which produce generator potentials that evoke the nerve response. Thus, for tactile stimuli, the neural sequence begins at the receptor level, whereas electrical pulses bypass the receptors in exciting the afferent nerves.

Since the slopes of the visual and auditory functions suggest that psychometric functions are shallower when receptors are stimulated, the second hypothesis above would predict that tactile pulses will yield psychometric functions shallower than those reported for electrocutaneous stimulation, perhaps having slopes similar to those for visual or auditory presentations. This paper describes several experiments performed to determine the characteristics of psychometric functions for single mechanical pulses at several bodily loci.

EXPERIMENT I

Psychometric functions were obtained for brief tactile pulses presented to the right middle finger.

Method

Apparatus

Tactile stimuli were delivered to the O by a Goodmans V-47 vibrator fitted with a circular plastic contactor of 1-cm diam. A plastic surround with an o.d. of 2.6 cm and an i.d. of 1.2 cm was

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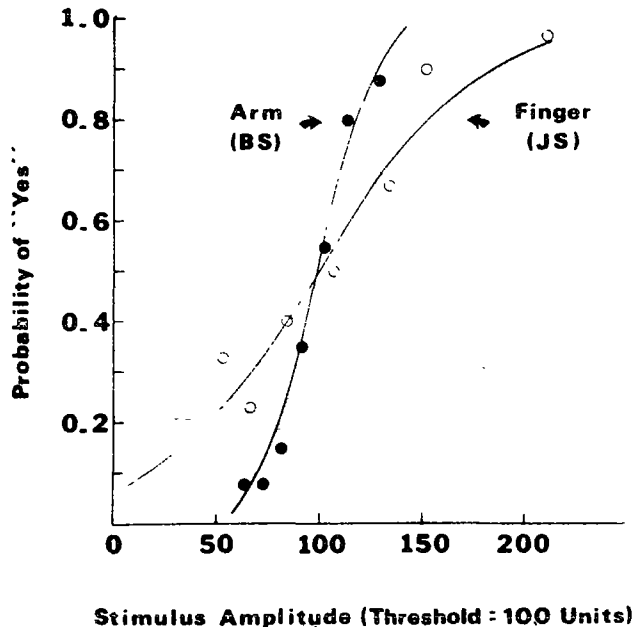


Fig. 1. Typical psychometric functions for tactile pulses at the fingertip and forearm. The threshold at the finger was 0.58 microns; at the forearm, it was 39.6 microns.

mounted on top of the vibrator, flush with the surface of the contactor, to provide a convenient rest for the fingertip and to control the pressure of the finger against the contactor.

A Tektronix Type 162 waveform generator triggered two Tektronix Type 161 pulse generators, whose outputs were fed to a 500-ohm mixer circuit. The combined signal, adjusted to provide a 3.0-msec (50% rise- and fall-points) pulse, was amplified by a Langevin Model 128-XJ amplifier and passed through a Hewlett-Packard Model 350 D attenuator to a transformer (United Transformer Corporation Model CVL-1) that matched the impedance of the Goodmans vibrator.

A switching system was employed to control a starting light, warning tones, and a light to indicate correct response when a forced-choice procedure was used. Stimulus interval was selected in the forced-choice sessions by a Gerbrands Model RP-1 ratio programmer, with holes on 16-mm leader tape punched to provide a random sequence of stimulus intervals. White noise was constantly delivered through a pair of earphones, with a 1,000-Hz signal superimposed during the warning interval.

Calibration

Initial calibration of the Goodmans vibrator was performed optically by applying a 100-Hz signal of known voltage across the device and observing the displacement of the contactor through a microscope under stroboscopic illumination. A filar micrometer eyepiece made it possible to measure peak-to-peak displacement for all values of input voltage.

An integral vibration detector (Sherrick, 1966) mounted on the Goodmans vibrator could also determine the amplitude of the sinusoid. This velocity-sensing system consisted of a 400-turn coil of 36-ga wire mounted on a Teflon spindle that was concentric with the contactor and served as the surround on which the O rested his finger. A ring magnet was placed inside the plastic contactor, and the induction effect created by its displacement produced a voltage proportional to its velocity. The voltage was amplified by a Ballantine Model 220 decade amplifier and connected to a MB Model M-3 vibration meter

which integrated the signal and displayed the waveform and voltage on a Tektronix oscilloscope. The coil output voltage was related to the voltage across the vibrator and a graph of displacement vs coil voltage was then plotted.

Once this relation was determined, measurements of waveform and displacement were made for single pulses. These were performed with the O's finger resting on the contactor and with the contactor placed on the dorsal forearm, since the amount of displacement was dependent on the pressure exerted against the tip.

Observers

The Os were three paid undergraduate males who were given extensive training in psychophysical tasks.

Procedure

The O rested his right arm on a padded table before him and placed his middle finger on the contactor and surround, which were mounted flush with the table top. His left hand pushed a button to initiate trials. Earphones were worn to provide a white masking noise, and a 1.2-sec tone was superimposed on the noise on each trial, with the stimulus occurring 600 msec after the tone onset.

A rapid estimation of threshold was obtained using the PEST procedure (Taylor & Creelman, 1967), and seven intensities were selected for presentation during the session: the estimated value and three larger and three smaller displacements. Generally, 2-dB steps of amplitude were used, though in some sessions the size between steps was 1 or 4 dB. An eighth setting of 100-dB attenuation was added to assess performance on trials when the displacement was negligible (about -50 dB SL). In most sessions, 40 trials were run at each level, for a total of 320 trials. Os served in five or six sessions.

Two psychophysical procedures, the yes-no method and the two-alternative forced-choice method, were used to obtain psychometric functions. In the former, one of the eight stimulus values was presented during the warning interval and the O was instructed to indicate whether he detected a displacement. In the latter procedure, the stimulus followed, in a random sequence, one of two warning tones, and the O had to indicate during which interval he believed the tactile presentation had occurred. In the forced-choice sessions, Os received feedback concerning the correct interval.

RESULTS

Data from individual sessions for each O were analyzed separately. Psychometric functions were plotted for each session, and a typical function obtained on the fingers in a yes-no session is presented in Fig. 1. In this graph, the abscissa has been scaled so that the contactor displacement corresponding to a probability of 0.5 of the O's reporting "yes" to the stimulus (0.58 microns) is set equal to 100 units. The coefficient of variation for this example is 0.64 (see Table 1, JS-3) indicating that the stimulus would be detected with a probability of 0.84 (one standard deviation above the threshold) at about 164 units (0.95 microns).

All functions underwent probit analysis (Finney, 1947) on an IBM 7094 computer, using the UCLA biomedical program (BMD-03S). Each function was analyzed under two conditions: (1) when the abscissa was the actual displacement of the contactor tip, and (2) when the displacement was expressed in decibels re

Table 1
Results of Probit Analysis for Psychometric Functions for Finger, Yes-No Sessions

O	Session	Number of Trials	False Alarm Rate	Mean (Microns)	SD (Microns)	χ^2	SD/Mean
AD	1	217	.03	0.93	0.67	2.69	0.72
	2	320	.08	1.08	0.32	1.48	0.30
	3	200	.06	0.74	0.17	3.61	0.23
BS	1	320	.20	0.84	0.44	2.50	0.52
	2	320	.18	0.82	0.52	2.60	0.63
	3	240	.17	1.13	0.87	17.94*	0.77
JS	1	320	.10	0.57	0.46	2.74	0.81
	2	320	.21	0.69	0.51	2.60	0.74
	3	240	.27	0.58	0.37	3.24	0.64

*Significant χ^2 ($p \leq 10$)

0.001 V across the vibrator, rather than in linear terms. For each condition, the probit analysis obtained estimates of the mean and standard deviation of the underlying Gaussian function. Also obtained was a chi-square value for a test of goodness of fit of the data points to a cumulative normal function on probit coordinates. Table 1 presents these values for the three Os with no correction for false alarms when a yes-no decision was required. The data for the seven forced-choice sessions are not presented since the means, standard deviations, and coefficients of variation obtained for each O are essentially the same as those obtained in the yes-no sessions.

Because of the relatively small variation of stimulus amplitude required to span the detection range, there were no important differences in the characteristics of the psychometric functions obtained under the two transformations of the abscissa, linear or logarithmic. When a correction for false alarms was applied in the probit program, the functions for the fingertips became slightly steeper, but this questionable practice was not adopted. Some chi-square values for a test of goodness of fit to a cumulative normal function exceeded a conservative 0.10 level of significance, but little importance should be attached to this since it resulted from selecting several stimuli which were almost always detected or almost never detected and which therefore caused unduly high contributions to the value of chi square (Finney, 1947).

EXPERIMENT II

Psychometric functions were obtained for brief tactile pulses presented to the right dorsal forearm.

Method

Apparatus

A Goodmans V-47 vibrator identical to that used in Experiment I was mounted on a microphone boom stand and positioned over the O's right dorsal forearm about halfway between the wrist and the elbow. Small sandbags were placed on

the arm on each side of the vibrator to minimize arm movements, and weights on the boom were adjusted so that the pressure of the vibrator against the arm was 20 g. Stimulating equipment and calibration procedures were the same as in the first experiment.

Observers

The three Os from Experiment I also served in this experiment.

Procedure

With the exception of the site of stimulation, the procedure is like that in Experiment I. Two of the Os participated in four yes-no sessions; the third took part in three.

Results

All functions underwent probit analysis under the same conditions as those of Experiment I. A typical psychometric function for stimulation of the arm is plotted in Fig. 1 along with the function for the finger, so that the steepness of the two curves can be compared. For this curve, threshold was 39.6 microns and the coefficient of variation was 0.22 (Table 2, BS-3). Table 2 presents the values of the important parameters determined from the probit analysis; all curves were obtained in sessions where the O was required to say "yes" or "no" after each trial.

DISCUSSION

In order to have a common basis for comparing steepness of psychometric functions, the linear displacements were adjusted so that the threshold value (probability of a yes response to a signal equaled 0.50 in yes-no sessions; probability of a correct response in the two-alternative procedure equaled 0.75) was set at 100 stimulus units. The actual threshold on the fingertip for a pulse of this duration and a contactor of this size was about 1 micron, while on the arm, median threshold was about 36 microns.

If the electrocutaneous ogive (Rollman, 1969a) were plotted in Fig. 1 along with the tactile ones, it would

Table 2
Results of Probit Analysis for Psychometric Functions for Forearm, Yes-No Sessions

O	Session	Number of Trials	False Alarm Rate	Mean (Microns)	SD (Microns)	χ^2	SD/Mean
AD	1	320	0.03	41.49	10.97	26.29*	0.26
	2	320	0	35.72	9.13	5.70	0.26
	3	320	0.03	31.40	6.34	7.04	0.20
	4	320	0	34.11	7.05	2.53	0.21
BS	1	320	0	43.76	16.20	59.37*	0.37
	2	320	0	46.20	10.70	1.95	0.23
	3	320	0	39.63	8.56	2.31	0.22
	4	320	0	55.60	13.39	6.81	0.24
JS	1	320	0.10	17.89	8.36	4.65	0.47
	2	320	0.35	10.83	11.35	10.39*	1.05
	3	320	0.08	29.27	7.84	2.23	0.27

*Significant χ^2 ($p \leq .10$)

extend from about 85 to 115 units. The tactile stimuli, at both loci, yield shallower functions. The median value of the ratio of standard deviation to threshold in yes-no sessions, which was 0.08 for electrical pulses on the arm, is 0.26 for tactile pulses there and 0.64 for tactile pulses on the fingertip. Both of the values for mechanical stimulation are in the same range as the ratios for visual flashes, and the second of the explanations presented in the introduction seems to gain support. That is, the somatosensory system *per se* does not demonstrate extraordinary sensitivity to small changes in stimulus intensity. When so-called "adequate" stimulation is employed, the steepness of psychometric functions for vision, audition, and touch are of the same order of magnitude. But when electrical stimuli are presented to cutaneous nerve fibers, the properties of the neural tissue excited are such that the fibers are more responsive than receptors to small changes in stimulus level. This would indicate that the role of the receptors in the transduction process is not only to summate energy over time and space, but also to perform a compressing transformation of the stimulating energy so that a relatively larger increase in intensity is necessary to produce a discriminable increase in peripheral or central neural responsiveness. While this limits the discrimination of changes in stimulus intensity, it serves to increase greatly the system's dynamic range. Such mechanisms do not operate only at threshold. Studies of magnitude estimation for tactile (Stevens, 1961, 1968; Verrillo, Fraioli, & Smith, 1969) and electrical (Rosner & Goff, 1967; Sternbach & Tursky, 1964; Stevens, 1961) stimuli have demonstrated that the power functions have a much steeper rise when electrocutaneous presentations are made. Also, Hawkes (1961) has found that the DL for electrical intensity is considerably smaller than that reported for mechanical stimulation of the skin (Craig, 1972).

Two other features of the tactile curves merit attention. The slopes of the psychometric functions obtained at the two loci differ: the functions on the arm

show steeper slopes than those on the fingertips. The differences in slope are reflected in the different values for SD/mean, 0.26 for the arm and 0.64 for the fingers. Comparisons are affected, however, by the values of the threshold. On the arm, SD is about 9 microns, while at the fingertips it is about 0.5 microns. Thus, in absolute terms, the fingers are appreciably more sensitive, whereas in relative terms the smaller change in amplitude is on the arm. Since psychophysical theory has traditionally emphasized the relative change in magnitude required to produce a given effect (Urban's *h*, the Weber fraction, Thurstone's judgment scaling model), this convention has been adopted here, though the absolute values should be noted as well. If a decibel scale is used to describe stimulator displacement, the change required to alter detection probability from 0.50 to 0.84 is only 2 dB on the arm but 4.3 dB on the fingers. The latter value is relevant to Craig's (1972) study of difference thresholds for single mechanical taps on the fingertips. He found that the DL for pulses at 28 and 35 dB SL was about 1.5 dB but that the DL increased to 2.5 dB as sensation level was reduced to 14 dB SL. These data suggest that DL should continue to increase as threshold is approached.

In addition to the differences in slope, there were striking differences in the false alarm rates at the two sites. When the stimulator was on the arm and catch trials were inserted during yes-no sessions, Os almost never reported detecting a stimulus when none was there. When the contactor was on the fingertips, however, the median false alarm rate rose to 17%. Thus, steep psychometric functions on the arm were accompanied by a low rate of false positives. The differences in performance at the two sites have implications for a signal detection theory analysis of the somatosensory system which will be discussed in a subsequent paper (Rollman, in preparation). The shallower slope on the fingers is not an artifact of the probit analysis due to a high rate of "yes" responses at smaller displacement, since the forced-choice procedure

yielded similar values for mean and SD.

If false alarms are instances of physical or sensory noise passing a subjective criterion, the results of these experiments indicate that the frequency of such occurrences varies with bodily locus. There are several possible reasons for this dependence of false alarm rate on site of stimulation. Perhaps the greater density of receptors at the fingertips results in a greater probability of spontaneous neural responses at that site and therefore a greater confusion between internal noise and the consequences of low-intensity stimulation.

The difference may also relate to the types of receptors that innervate the two regions. The glabrous fingertips include Meissner's and Pacinian corpuscles and Merkel's disks, whereas the hairy forearm possesses deep-lying Pacinian corpuscles and various receptors associated with the mouth and shaft of the hair follicles (Iggo, 1968; Merzenich, 1968; Verrillo, 1968). Both sites have free nerve endings as well. Which receptors were activated by the pulse used in this study? The stimulus resembled the positive half-cycle of a 125-Hz sinusoid, with a rise time from baseline to peak of about 2 msec. Given the median thresholds at the two sites, the rate of skin displacement was 0.5 mm/sec on the finger and 18 mm/sec on the arm. The finger stimulus probably engaged a small group of Pacinian corpuscles and perhaps some Meissner's corpuscles (Lindblom, 1966; Talbot, Darian-Smith, Kornhuber, & Mountcastle, 1968), but it is unlikely that Merkel's disks were included. On the arm, the stimulus was sufficiently intense to engage Pacinian corpuscles and also some of the receptors associated with the hair follicles.

The recent findings of Harrington and Merzenich (1970) suggest that the Pacinian corpuscle is unlikely to play an important role in signaling the magnitude of cutaneous pressure on hairy skin. Slowly adapting afferents arising from skin layers closer to the surface are the fibers probably involved in responding to large displacements of hairy tissue, and Mountcastle, Talbot, and Kornhuber (1966) suggest that the slowly adapting fibers signal intensity on glabrous surfaces as well. However, Mountcastle et al described the quickly adapting fibers (such as those from the Meissner and Pacinian corpuscles) as "movement detectors," and perhaps these afferents are sufficient to provide the neural information used in making the decisions required in this study, since it was the presence or absence of a signal, rather than its magnitude, which Os were required to judge. Thus, the relative contributions of the rapidly adapting and slowly adapting fibers in such a task are not firmly established.

Spontaneous neural activity is generally not present in Pacinian afferents (Mountcastle, 1966), but the fibers from some slowly adapting receptors show continual spontaneous discharge (Iggo, 1966; Merzenich, 1968). Thus, the "noisy" slowly adapting fibers could lead to confusion between the effects of stimulation and ongoing background activity. However, the results of

electrophysiological studies have suggested that the proportion of fibers showing spontaneous activity is higher on hairy than on glabrous skin (Iggo, 1966; Mountcastle, 1966). If these impressions are confirmed in more detailed investigations, the rate of false alarms at the two loci is not simply a function of the proportion of fibers spontaneously active. The much denser innervation at the fingers, however, could result in a higher absolute number of fibers showing some activity than on the forearm.

It seems most likely, however, that the difference in rate of false positives to the pulses can be ascribed to the exquisite sensitivity of the fingertips coupled with differences in the mechanical impedance of the tissue at the two sites. The small tremors of the limbs and body probably move the skin slightly with respect to the contactor surface. On the insensitive arm, this produces a negligible effect, but the neural consequences for fingertip receptors may be considerable. In fact, considering the small absolute and differential sensitivities on the fingers, it is extraordinary that the false alarm rate was so low.

Differences in receptor type, density, and the consequences of static tremor could explain the varying steepness of psychometric functions as well. With respect to the nature of the receptors and their sensory fibers, the results of studies by Mountcastle, Talbot, and Kornhuber (1966) and Harrington and Merzenich (1970) are relevant. Mountcastle et al studied the number of neural impulses obtained from myelinated slowly adapting axons following various amounts of indentation on the glabrous skin of the monkey's hand. Harrington and Merzenich performed a similar study on the hairy skin of the monkey forearm, and they also examined psychophysical power functions obtained with human Ss from magnitude estimation experiments on the two kinds of skin. Both electrophysiological and psychophysical studies demonstrate a larger exponent on the glabrous skin (about 0.9) than on the hairy skin (0.4). These values are for functions describing the relation of nerve impulses or magnitude estimations to a large range of skin displacement. Examination of just those points for small displacements on their linear graphs, however, shows that the increase in responses or estimates grows much faster on the hairy skin than on the glabrous. Thus, for example, a doubling of displacement from that required to produce a single spike on the arm produces about an 18-fold increase in neural responses; a similar change on the hand yields at best only a 2- or 3-fold rise. The differences in exponent reported above occur because the rate of change slows down considerably on the arm as displacements increase, whereas there is no departure from linearity on the hand.

The instability of the skin-contactor coupling could also account for differences in slope of psychometric functions. The ogives have an underlying normal distribution representing variability in the physical

stimulation and/or in the neural responsiveness of the somatosensory system. If the small tremors cause movements of the finger resting on the contactor, then the actual displacement of the skin will show some variation from trial to trial and the resulting psychometric function will be shallower than it would be in the absence of such movement. Craig (1972) has shown that an externally produced background noise on the fingertips interfered with the ability to discriminate small increments in displacement, with DL increasing as a function of background vibration level. Given the great sensitivity of the fingertips, the monotonic ordering of detections with increasing displacement (in steps of about 0.1 to 0.2 microns) shows that individual tremors, if they affected the skin indentation, were exceedingly small.

A third possible source for the effect of locus or skin type on steepness of psychometric functions is the difference in density of innervation at the fingertips and the arm. Békésy (1967) reported results which suggest that density of innervation is inversely related to sensitivity to small stimulus changes. He found that the size of the difference limen (in decibels) for a 150-Hz vibrating stimulus on the arm increased as the stimulus excited larger numbers of receptors. This would lead to the prediction that relative sensitivity to stimulus increments or decrements would be worse on the fingertips than on the arm, as was reported in this study.

Thus, the results of Harrington and Merzenich's work on two skin sites involving different classes of receptors and Békésy's experiments on a single site involving different numbers of the same receptor type suggest the results that were, in fact, obtained. An extension of Békésy's experiment, involving several sizes of contactors for single mechanical pulses on glabrous and hairy skin, may help delineate the role of involuntary tremors, receptor type, and receptor density.

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