Tactile Discrimination of Gaps by Slowly Adapting Afferents: Effects of Population Parameters and Anisotropy in the Fingerpad

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Wheat, Heather E. and Antony W. Goodwin. Tactile discrimination of gaps by slowly adapting afferents: effects of population parameters and anisotropy in the fingerpad. J Neurophysiol 84: 1430–1444, 2000. The aim of this study was to determine how acuity of the peripheral tactile system for gaps and to determine how stimulus orientation may impact on this. We quantified the ability of humans to discriminate small differences in gap width using a forced-choice task. Stimuli were presented passively to the distal fingerpad in a region where the skin ridges all run approximately in the same direction. Two standard gap widths were used (2 and 2.9 mm), and the comparison gap widths were larger than the standard gaps. With the gap axis parallel to the skin ridges, the average difference limen was approximately 0.2 mm for both standards. We examined the effect of stimulus orientation by asking subjects to discriminate between a smooth surface and a grating (ridge width, 1.5 mm; groove width, 0.75 mm). They were able to discriminate the two surfaces when the axis of the grooves was parallel to the skin ridges, but performance was below threshold in the orthogonal orientation. The underlying neural mechanisms were investigated using the gap stimuli to activate single slowly adapting type I mechanoreceptive afferents (SAIs) innervating the fingerpads of anesthetized monkeys. The edges of the gap produced response peaks, and the gap resulted in a trough in the receptive field profiles. The response magnitude at the peaks was greater, and at the troughs was smaller, for larger gap widths and also when the axis of the gap was parallel to the skin ridges than as compared with the orthogonal orientation. Simulated SAI population responses showed that response profiles were distorted by variation in afferent sensitivity and by neural noise. Using signal detection theory, based on a neural measure of the gaps computed over the active population, the acuity of the SAIs under realistic population conditions was compared with human performance. These analyses showed how parameters like afferent sensitivity, the pattern and density of innervation, and noise impact on performance and why their impact is different for the two stimulus orientations investigated. The greatest limitation was imposed by noise that is independent of response magnitude, and this effect was greater for stimuli oriented orthogonal to the skin ridges than for the parallel orientation.

INTRODUCTION

Gaps and edges are a feature of many of the objects we handle. Furthermore stimuli containing gaps and edges, particularly gratings, are used extensively for measuring tactile spatial acuity in both normal and clinical populations (Craig 1999; Sathian et al. 1997a; Van Boven and Johnson 1994b). In spite of their importance in these respects, however, we do not have a clear understanding of many of the issues that influence how the tactile system analyses these object features. A few studies have characterized single mechanoreceptive fiber responses to bars, edges, and gratings (Johansson et al. 1982; Phillips and Johnson 1981a; Vierck 1979), but many issues remain unclear. In particular, characterizing receptive field profiles for these stimuli has not given us a comprehensive explanation of how factors like fiber sensitivity and innervation density affect resolution. Moreover, previous studies do not allow us to determine the neural mechanisms underlying hyperacuity for this class of stimuli nor the extent to which neural population characteristics limit hyperacute performance of the type reported by Loomis (1979) and Morley et al. (1983), who found that subjects could discriminate a difference of 0.3 mm in the spatial interval between bars and a difference of 0.1 mm in grating period, respectively.

It is generally acknowledged that spatial acuity must be limited by the innervation density of the signaling afferent population (Craig 1999; Johnson and Phillips 1981; Van Boven and Johnson 1994a). Craig (1999) attempted to confirm the relationship between innervation density and spatial sensitivity by measuring grating orientation thresholds as a function of location on the finger. He found that thresholds were higher at a location 25 mm from the tip of the finger than at locations 5 or 15 mm from the tip and were considerably higher on the proximal phalanx. He concluded that spatial sensitivity is reduced at sites where innervation is less dense but found that “it was not possible to predict the threshold based on the density of innervation estimates.” Obviously other factors also play an important role in determining thresholds. For instance, skin mechanics, as well as innervation density, change with location on the finger.

A number of models have contributed to our understanding of skin mechanics (Pawluk and Howe 1999; Phillips and Johnson 1981b; Srinivasan 1989; Srinivasan and Dandekar 1996). For the most part, however, studies of skin mechanics are based on models of homogeneous, isotropic, elastic, and, often, flat skin. But the skin is not flat; it curves in a nonuniform way on the fingerpad. Neither is the skin an isotropic structure (Lanir and Fung 1974), one component of this nonuniformity being the orientation of the skin ridges (Halata 1975). Current models do not take such nonuniformities into account. Furthermore it is not clear from the literature whether skin anisotropy is a significant factor affecting human discrimination perfor-
The stimuli were Delrin blocks with a groove (depth, 3 mm) milled into one face; this surface contacted the skin (Fig. 1A). The width of the groove, $\omega$, ranged from 2.0 to 3.29 mm; the smallest gap width used was well above the gap detection threshold of around 1 mm as measured by Johnson and Phillips (1981). The blocks were fixed to a hub attached to a gravity-operated, balanced beam stimulator [described previously, Goodwin et al. 1991] which lowered a selected block onto the fingerpad. Contact force was set by a counterbalance weight on the beam and calibrated to a resolution of 0.1 gram force (gf). A rotary damper controlled vertical motion of the beam so that the surface of the block contacted the skin at a contact velocity of about 20 mm/s. The beam was mounted on an x-y stage fitted with micrometers and dial indicators; this enabled stimuli to be positioned with a resolution of 0.01 mm.

In this study it is important to distinguish between the orientation of the stimulus with respect to the long axis of the finger and with respect to the direction of the skin ridges; these two directions do not always have the same relationship. We use the nomenclature “parallel” and “orthogonal” to refer to stimulus orientation relative to the skin ridges, that is, the axis of the gap (Fig. 1A) lies either parallel or orthogonal to the skin ridges. When referring to stimulus orientation with respect to the long axis of the finger, we use the terms “aligned” and “perpendicular,” that is, the axis of the gap is aligned with or perpendicular to the long axis of the finger. In the macaque fingerpad, the ridges all run in the same direction as the long axis of the finger so that the terms parallel and aligned are synonymous. Thus we always use the terms parallel and orthogonal when referring to the orientation of the stimulus on the monkey fingerpad. In humans, however, on much of the fingerpad the pattern is not consistent and therefore to avoid any ambiguity, the nomenclature aligned and perpendicular to the long axis of the finger is sometimes necessary.

**Human psychophysics**

GAP DISCRIMINATION. Six subjects (4 males, 2 females) ranging in age from 20 to 26 yr took part in these experiments. The subject was seated comfortably with forearm supinated, and the index finger of the dominant hand was secured in a plasticine finger mold to prevent lateral movement between stimulus and finger. A curtain prevented the subject from seeing either the stimulator or their finger. The finger was positioned so that the surface of the block, when it made contact with the skin, was tangential to the fingerpad and the line of force was normal to that plane; contact force was set at 55 gf (0.539 N). The stimulus was applied for 1 s to the distal fingerpad with the axis of the gap (Fig. 1A) perpendicular to the long axis of the finger.

A two-alternative forced-choice paradigm was used to measure the subject’s ability to discriminate small differences in gap width. Paired stimuli, the standard stimulus followed by a comparison stimulus, were presented with 1 shoulder located over the center of the receptive field (rfc) and then advanced, between trials, across the receptive field in increments of 0.2 mm until the other shoulder was located over the rfc (shaded profile). C: imprint of a monkey fingerpad indicating the finger coordinate system used.

**FIG. 1.** Gap stimulus and orientation conventions. A: the gap was presented with its axis either orthogonal or parallel to the skin ridges. The stimulus is invariant along the axis of the gap and is therefore defined by its profile in the direction at right angles to the gap axis, which incorporates the gap width $\omega$. B: in the neural recording experiments, the stimulus (open profile) was initially presented with 1 shoulder located over the center of the receptive field (rfc) and then advanced, between trials, across the receptive field in increments of 0.2 mm until the other shoulder was located over the rfc (shaded profile). C: imprint of a monkey fingerpad indicating the finger coordinate system used.
Body temperature was maintained at 37°C by a heat pad and insulating blankets. Antibiotic cover was provided throughout the experiment by intramuscular administration of amoxycillin (18 mg/kg) and at the end of the experiment by a single dose of procaine penicillin (60 mg/kg).

Single fibers were isolated by micro-dissection after exposing the median nerve, using aseptic surgical techniques, first in the upper arm and then in the lower arm. The process was repeated in the other arm making a total of four experiments for each monkey. Each experiment lasted a maximum of 18 h, and there was a rest period of at least 2 wk between each experiment. During this rest, period the monkeys were housed in large cages, together with or adjacent to other monkeys, with access to an outdoor exercise area. They were observed closely and regularly by trained personnel and were in good health with no evident signs of pain or distress. Buprenorphine hydrochloride (8 μg/kg) was available for pain relief but was judged unnecessary. At the end of the series, the monkeys were in prime condition and showed no signs of sensory or motor deficits; they were returned to a breeding colony.

Single slowly adapting type I fibers (SAIs) were selectively chosen for study. These were classified by established response criteria (Talbot et al. 1968; Vallbo and Johansson 1984). The most sensitive spot in the receptive field of each fiber was located using calibrated von Frey filaments; this is subsequently referred to as the receptive field center. Only those fibers with receptive field centers close to the central, relatively flat region of the fingerpad were used. This ensured that any effects due to the curvature of the fingerpad or due to changes in skin mechanics close to the interphalangeal joint were minimized. Once the most sensitive spot had been identified, the fiber was immobilized in a customized mold with the most sensitive spot uppermost. The fiber was positioned so that when the stimulus made contact with the skin, the surface of the Delrin block was tangential to the fingerpad and the line of force was normal to that plane; contact force was set at 20 g (0.196 N). The contact force used in the neural recording experiments is roughly equivalent to that used in the human psychophysics experiments scaled to take account of the difference in size between human and monkey fingerpads (for rationale, see Goodwin et al. 1997).

Two stimulus gap widths were used for all fibers, 2.0 and 2.8 mm. For one fiber, responses were recorded for an additional six gap widths, 2.1, 2.2, 2.4, 2.9, 3.0, and 3.2 mm. Data were collected for all gap widths with the axis of the gap parallel to the ridges (in the macaque the skin ridges are also parallel to the long axis of the fingerpad). Responses were recorded from a total of 18 fibers; data were collected at both orientations for seven fibers, at the orthogonal orientation only for three fibers, and at the parallel orientation only for eight fibers. Whether the stimulus was presented in the orthogonal or parallel orientation, the protocol was the same. The stimulus was initially positioned so that one “shoulder” of the stimulus contacted the fingerpad with the edge of the gap located 2 mm from the receptive field center (Fig. 1B, open profile). The stimulus was applied for 1.5 s (a single trial), removed, advanced 0.2 mm, and then reapplied; the time between successive presentations was 3 s. This pattern of presentation was repeated until the opposite shoulder was positioned over the receptive field center (Fig. 1B, shaded profile). This whole sequence was repeated twice (n = 3 per gap width for each gap orientation and each fiber); n = 3 was deemed sufficient as we and others have shown that variation in the responses of peripheral fibers is low (Edin et al. 1995; Phillips and Johnson 1981a; Wheat et al. 1995). At the commencement of each traverse of the receptive field, a lead stimulus with the same time sequence, 1.5 s on, 3 s off, was presented to minimize differential interaction effects (the data from this trial were not included in the analyses with the result that for each trial analyzed, the inter-trial time period was constant). As the stimulus geometry was invariant in one direction, that is, the gap width was constant along the axis of the gap, the response profile could be described by one line through the center.
of the receptive field. The curvature of the fingerpad, both laterally and distally, and the distal interphalangeal joint limited the extent of the profile for a few fibers.

RESULTS

Human psychophysics

GAP DISCRIMINATION. Two series of gap discrimination experiments were conducted, each using a different standard stimulus, to determine the extent to which performance was dependent on the gap width of the standard stimulus. Figure 2A shows the mean performance across the six subjects. As the gap width of the comparison stimulus increased, the probability of correctly identifying it as different from the standard, \( p(R_d/S_d) \), increased and the likelihood of incorrect judgements, \( p(R_i/S_i) \), decreased. The \( d' \) values, plotted as data points in Fig. 2B, show that there is an approximately linear relationship between gap width and discrimination performance for both standards. Difference limens for each subject, calculated by linear regression of the \( d' \) values for each standard, are shown in Table 1; the difference limen corresponds to a \( d' \) value of 1.35 and is equivalent to the difference in gap width which could be discriminated with a probability of 75%. The mean difference limens were 0.19 and 0.22 mm for standards of 2.0 and 2.9 mm, respectively.

Although the difference limens were not significantly different for the two standards (Table 1), this \( t \)-test uses only one data point (at \( d' = 1.35 \)) for each of the six subjects. However it is clear in Fig. 2B that performance is better for the 2.0 mm standard at each of the gap width differences except the largest, where performance is equal for the two standards. When all 36 pairs of data points are considered (6 subjects \( \times \) 6 gap width differences \( \times \) 2 standards), two-tailed \( t \)-tests (Zar 1984) show that the regression lines in Fig. 2B do not differ significantly in slope \((P = 0.661) \) but differ significantly in elevation \((P = 0.005, \) mean difference is 0.208 \( d' \) units). Thus the performance of our subjects was significantly better for the 2.0 mm standard than for the 2.9 mm standard.

GRATING VERSUS SMOOTH SURFACE. In this series of experiments, we examined the effect of stimulus orientation on the subjects’ ability to discriminate between a smooth surface and a grating. Subjects were required to judge whether the grating (ridge width, 1.5 mm; groove width, 0.75 mm) was the first or second stimulus in a pair of stimuli presented passively to the distal fingerpad. Examination of the pattern of ridges in the region of skin making contact with the stimulus showed that here all the ridges ran in approximately the same direction. When the stimulus was presented with the groove axes oriented perpendicular to the long axis of the finger, the grooves ran approximately parallel to the skin ridges. Examination of the pattern of ridges in the area of skin making contact with the stimulus showed that here all the ridges ran in approximately the same direction. When the groove axes were aligned with the finger axis, the grooves were approximately orthogonal to the skin ridges.

Figure 2C shows that when the grating was presented with the axes of the grooves parallel to the skin ridges, discrimination performance was well above threshold \((d' = 1.35) \). When the grating was presented with the grooves orthogonal to the
response variability illustrated in Fig. 3 magnitude of the standard deviations demonstrates. The low width. Second, this was a consistent response feature as the increased both in width and depth with an increase in gap characterizing one trough in the response profile. This trough in the response profiles that increased in width and depth with increasing gap width and, for many fibers, the edges of the troughs in the response profiles. The response profiles of this fiber also illustrate a feature that was apparent for many fibers. As the width of the gap increased, the edges of the gap produced peaks in the response profiles, which corresponded to the position of the edges.

Neural responses

ORTHOGONAL ORIENTATION. To generate receptive field profiles, stimuli were presented for 1.5 s successively at 0.2-mm intervals along a line at right angles to the axis of the gap and passing through the center of the receptive field of single SAI fibers. As the stimulus was invariant in the direction in line with the axis of the gap (Fig. 1A), the receptive field was characterized by one profile in the direction at right angles to the axis of the gap. Figure 3A shows the responses of one SAI to gap widths of 2.0 and 2.8 mm presented with the axis of the gap orthogonal to the skin ridges. Responses are the mean number of impulses (±SD, n = 3) evoked in the first second of stimulus contact; this period corresponds to the time period used in our psychophysics experiments. Two important features are highlighted by this figure. First, the gap in the stimulus produced a modulation in response that is primarily characterized by a trough in the response profile. This trough increased both in width and depth with an increase in gap width. Second, this was a consistent response feature as the magnitude of the standard deviations demonstrates. The low response variability illustrated in Fig. 3A is typical of that observed for all fibers and is consistent with our previous observations (Wheat et al. 1995).

Two gap widths (2.0 and 2.8 mm) were characterized for all fibers. For one fiber, however, eight different gap widths were characterized: 2.0, 2.1, 2.2, 2.4, 2.8, 2.9, 3.0, and 3.2 mm. These spanned the range used in the psychophysics experiments. Mean responses (±SD, n = 6) to two of these stimuli, gap widths 2.8 and 3.2 mm, are illustrated in Fig. 3B. While the response profiles depicted in Fig. 3B were truncated due to the location of the receptive field center, they cover a sufficient region of the receptive field to see that the responses to these two gaps are clearly distinguishable, demonstrating that smaller changes in gap width also produced reliable changes in the width and depth of the troughs in the response profiles. The response profiles of this fiber also illustrate a feature that was apparent for many fibers. As the width of the gap increased, the edges of the gap produced peaks in the response profiles, which corresponded to the position of the edges.

Sensitivity varied between fibers in the sample. To reveal the underlying response characteristics common to all fibers in the pool, we normalized the responses of each fiber. This was done by dividing the responses of each fiber by the average response of the fiber over 10 data points spanning the center of the receptive field and incorporating the response trough and one peak; this region corresponded across all fibers. The normalizing factors had a Gaussian distribution with a coefficient of variation of 0.36, which is consistent with our previous studies (Goodwin et al. 1995; Wheat et al. 1995). When the normalized responses were pooled, it was clear that all fibers in the sample responded similarly to the stimuli. This is exemplified in Fig. 3C, which shows mean normalized responses (±SE) of 10 SAI fibers to stimuli presented with the gap axis oriented orthogonal to the skin ridges. The stimulus gap resulted in a trough in the response profiles that increased in width and depth with increasing gap width and, for many fibers, the edges of the gaps produced peaks in the response functions. This latter feature was more apparent for the wider gap with this stimulus orientation.
Mathematical characterization of response profiles

Receptive field profiles, characterized in terms of the position of the stimulus along a line at right angles to the axis of the gap, were similar for all fibers in the sample, differing only by a multiplicative constant which reflected the difference in sensitivity between fibers. The response profiles could be described by a difference of Gaussians of the form \( r = a + be^{-cu^2} - de^{-fu^2} \) where \( u \) represents the coordinate at right angles to the gap axis and the constants \( a, b, c, d, \) and \( f \) were determined by the gap width and orientation with respect to the skin ridges. For each gap width and orientation, the preceding function was fitted to the pooled normalized data by nonlinear regression. Table 3 lists values for the constants for the two gap widths for both stimulus orientations, and also the \( R^2 \) values as a measure of the goodness-of-fit of the functions. The \( R^2 \) values confirm the suitability of the fitted functions for both gap widths and for both orientations. The correspondence between the data and fitted functions is further illustrated in Fig. 5, which shows mean normalized responses and corresponding functions for both gap widths presented orthogonal to the skin ridges.

Describing our data in mathematical terms allows us to address a number of questions that relate to the behavior of populations of SAIs and to determine how specific population parameters impact on the representations described in the preceding text. There are several critical parameters that will distort the spatial representation of the stimulus in the population response: the variation in sensitivity between fibers within a population, the density and geometry of the sampling population, and random variation in the responses of individual afferents.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parallel</th>
<th>Orthogonal</th>
</tr>
</thead>
<tbody>
<tr>
<td>( a )</td>
<td>0.724</td>
<td>0.724</td>
</tr>
<tr>
<td>( b )</td>
<td>0.753</td>
<td>2.090</td>
</tr>
<tr>
<td>( c )</td>
<td>0.261</td>
<td>0.299</td>
</tr>
<tr>
<td>( d )</td>
<td>1.049</td>
<td>2.364</td>
</tr>
<tr>
<td>( f )</td>
<td>5.001</td>
<td>2.149</td>
</tr>
<tr>
<td>( R^2 )</td>
<td>0.510</td>
<td>0.596</td>
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</table>

Nonlinear regression was used to fit the function to the pooled normalized responses \( r \) for gap widths 2 and 2.8 mm aligned parallel and orthogonal to the skin ridges (\( P < 0.001 \) for all constants; parallel, \( n = 290 \); orthogonal, \( n = 183 \)).
located with its receptive field center at position \((r_{ij}, y_{ij})\) in a matrix. When the axis of the gap is parallel to the skin ridges, \(u = x\) and \(k = i\), and when it is orthogonal, \(u = y\) and \(k = j\). Response is measured as the number of impulses occurring in the first second of response (imp/s) as this was the time period used in the analysis of our experimental data from monkeys and humans. The sensitivity \(s_{ij}\) of each fiber in the matrix varies randomly from fiber to fiber with a distribution derived from our current and previous experimental data (the distribution is Gaussian with a coefficient of variation of 0.387). Changing the gap width or orientation of the stimulus changes the values of the constants \(a, b, c, d,\) and \(f\). In the simulation, we used the values in Table 3 for gap widths of 2.0 and 2.8 mm, and for gap widths in between, the constants were determined by linear interpolation. Figure 6A shows a simulated response profile for an ideal population of fibers with uniform sensitivity and a high innervation density (4 mm\(^{-2}\) with a uniform fiber spacing of 0.5 mm); the stimulus had a gap width of 2.8 mm and was presented with the gap axis orthogonal to the skin ridges.

**Variation in fiber sensitivity**

The ideal response profiles simulated by the model and exemplified in Fig. 6A reproduce the essential features of the stimulus. When fiber sensitivity across the population is varied to resemble that of a real population of SAI fibers, however, the ideal population response profile is severely distorted even in the absence of response noise and the location of the gap is no longer evident. This is illustrated in the bottom three panels in Fig. 6B, which shows the responses of a population in which the fibers are arranged in a uniform configuration with a density of 0.7 mm\(^{-2}\) (spacing, 1.2 mm) but in which sensitivity varies between fibers. These panels show slices taken through a population response profile at right angles to the gap axis at \(x\) values 0, 2.4, and 4.8 mm (chosen arbitrarily); stimulus gap width was 2.8 mm presented orthogonally. The degree of distortion produced by differences in fiber sensitivity is marked and can be appreciated by comparing these profiles with that in the top panel which shows responses of fibers with uniform sensitivity.

**Innervation geometry and density**

While we have been able to establish the statistical distribution of sensitivities within peripheral SAI populations, the geometric arrangement of SAI innervation of the skin of the fingerpad is not known. It is unlikely to be precisely uniform, however, and we need to determine how this will impact on the spatial form of the population response. Another factor that will impact on the spatial form of population responses is the position of the stimulus relative to the fiber matrix. The profiles described for the single fiber data in earlier sections were constructed with the center of the gap positioned symmetrically about the center of the receptive field, and the simulated population profiles shown in Fig. 6, A and B, were constructed with the stimulus positioned over the receptive field center of the fiber at the center of the population. To determine how variations in population geometry and stimulus position impact on the population response profile, we varied the position of fibers by adding a random component to the position of each

![Figure 5](https://example.com/figure5.png)
fiber in one dimension (at right angles to the axis of the gap) and shifted the stimulus relative to a uniformly spaced fiber matrix. The outcome of these modifications is illustrated in Fig. 6C by slices through response profiles of populations with a variety of innervation configurations.

It is evident from these few examples that nonuniform spacing of receptive fields or offsets in the position of the stimulus relative to the receptive field matrix will produce a range of profile distortions. This figure further demonstrates that even if the CNS “knows” the sensitivity of individual fibers and normalizes responses on the basis of this “knowledge” (effectively uniform sensitivity), thus removing distortions such as those shown in Fig. 6B, the profiles are still distorted as a result of nonuniformity in the population geometry. In all of the scenarios illustrated in the preceding text, the neural image of the stimulus is changed as the sampling population becomes asymmetrical relative to the stimulus.

The influence of innervation density on performance was investigated by approximately doubling the fiber density from a population with uniform fiber spacing and varying fiber sensitivity (2nd panel from the bottom), and uniform fiber spacing and uniform sensitivity (bottom). Note that for the bottom panel slices at all x values would be the same.

Response variability

Random variation in the responses of individual afferents will also distort population responses. The model takes account of random noise by incorporating variability associated with peripheral mechanisms and also noise associated with central structures and processing. A noise component $\epsilon_{ij}$ is added to the response of each afferent modifying Eq. 1 to

$$r_{ij} = s_{ij}(a + b_e^{-|x|^2} - d e^{-|y|^2}) + \epsilon_{ij}$$

(2)

Two broad categories of noise are used (see DISCUSSION for justification). In one category, termed “proportional noise,” the noise is proportional to the magnitude of the response of each fiber, and in the second category, “additive noise,” the noise is independent of the magnitude of the afferent’s response. In the case of proportional noise, $\epsilon_{ij}$ is a normally distributed random variable with a mean of zero and either a standard deviation $\sigma_{ij}$ proportional to $r_{ij}$ or a variance $\sigma_{ij}^2$ proportional to $r_{ij}$. In the case of additive noise, $\epsilon_{ij}$ is a normally distributed random variable with a mean of zero and a standard deviation $\sigma$ which is the same for all $i$ and $j$.

Effects of population variables on performance

Given the distortions in the response profiles produced by realistic variations in fundamental population characteristics,
the question is how information about gap width is extracted from population responses such as these and how do such distortions affect the resolution of the stimulus? There are a number of response measures that may be used as indices of gap width within the population response, such as the depth or width of the response trough, or the peak-to-trough height. We used a response index that measures how the gap is reflected in the whole population response and is therefore more robust (see DISCUSSION). Our response measure is the absolute magnitude of the deviations in response from the mean response to the shoulders of the stimulus, that is the combined volume of the response troughs and peaks (equivalent to the shaded area in Fig. 7A). It is calculated as follows

$$\sum_{\delta} |r_{ij} - \bar{R}|\delta\delta_{ij}$$

where $\delta$ and $\delta_{ij}$ are the separations between the receptive field centers of individual fibers within the model in the $x$ and $y$ directions respectively, and $\bar{R}$ is the mean response to the shoulders of the stimulus (Fig. 1B).

The degree to which this measure reflects changes in gap width was tested by presenting the model with a range of gap widths and calculating $V$. Figure 7B (C and $\triangle$) shows that when fiber sensitivity was uniform across the population (in the absence of response noise), $V$ increased monotonically with increasing gap width for both stimulus orientations but with a greater slope when the gaps were presented in the parallel orientation (—). When fiber sensitivity was allowed to vary randomly across the population within the range measured experimentally (□ and $\Delta$), the results were similar but the magnitude of $V$ was greater for any particular gap width and the function for orthogonal orientations became even flatter. Thus while variation in fiber sensitivity produces distortions in the response profile as Fig. 6B shows, the measure is still able to extract information about gap width from the blurred image although the precision of that identification for stimuli presented orthogonal to the skin ridges is likely to be poor. Furthermore the introduction of random noise had little effect on the shape and magnitude of the $V$ functions (Fig. 7B, *), illustrated here for a combination of proportional noise ($s_{ij} = 0.06 r_{ij}$) and additive noise ($\sigma = 3$ imp/s).

We used signal detection theory to determine the precision with which the model could discriminate two stimuli differing in gap width and thus determined the degree to which particular population characteristics may limit acuity. The paradigm adopted was a two-alternative forced-choice approach equivalent to that used in our human psychophysics experiments. Two stimuli, the standard and the comparison, were presented to the model in pairs. For 100 pairs, the first and second stimuli were both the standard (gap width, 2.0 mm), and for an additional 100 pairs the first standard and the second stimulus (the comparison) had an increased gap width. The response measure $V$ was calculated from the population response to each stimulus. For each pair, the second stimulus was judged to be different if $|V_{ij} - V_{il}| \geq \delta$ the decision boundary (defined as half the difference between the mean value of $V$ for the comparison stimulus and the mean value for the standard stimulus), otherwise the two stimuli were judged to be the same. From the resultant conditional probabilities, the index of discrimination $d^{'}$ was calculated and discrimination thresholds determined in the same manner as for the psycho-physics experiments—Goodwin and Wheat (1999) detail the calculations and rationale for this approach.

In the following section, we examine the resolution of realistic populations of SAIs as a number of parameters were successively varied. First we examine how resolution was affected by innervation density when the pattern of innervation was uniform. Innervation densities for this and subsequent analyses were 0.463, 0.7, and 1.56 mm$^{-2}$ (fiber spacings, 1.47, 1.2, and 0.8 mm, respectively). Initially we used a low level of noise, which we know exists in the periphery (Phillips and Johnson 1981a; Wheat et al. 1995), and then we added extra
noise to take account of variability at the CNS level. Next we present the results of varying the relative position of the afferents in the population to create a nonuniform pattern of innervation at different innervation densities and test resolution with a range of increasing noise levels. The performance of the model is measured in terms of difference threshold values (the difference in gap width that could be discriminated in 75% of trials) and is compared with human performance. When making these comparisons, it must be borne in mind that the ridge pattern on human fingerpads is not as uniform as in monkeys. Thus the alignment of the gap axis in the human experiments was only approximately parallel to the ridges over the majority of the contact area.

The population that produced the results illustrated in Fig. 8, A and B, had a sensitivity distribution identical to the population illustrated in Fig. 6B. Figure 8A shows that with peripheral noise alone (N1), that is, proportional noise equivalent to that observed experimentally in the responses of peripheral SAIs ($\sigma_0^p = 0.06 \ r_{ij}$), the performance of the model for orthogonal presentations was around the performance level of our human subjects for whom the axis of the gap was approximately parallel to the ridges. However, when the stimulus was presented to the model in the parallel orientation (Fig. 8B), performance was far superior to that of our human subjects. Furthermore this was true when innervation density was approximately double (●) or half (■) that of the normal human fingerpad (□). The relative performance between populations of different densities is addressed in the DISCUSSION.

More noise was introduced to simulate the presence of noise in both peripheral and central mechanisms—proportional noise with $\sigma_0^p = 0.15 \ r_{ij}$ plus additive noise with $\sigma = 3 \text{ imp/s}$ (columns labeled N2 in Fig. 8, A and B). Discrimination thresholds increased dramatically from around 0.2 mm to at least 0.8 mm for orthogonal presentations (Fig. 8A), but for parallel presentations (Fig. 8B), performance remained superior to that measured for our human subjects with thresholds less than 0.2 mm for all three innervation densities. Data depicted with white columns superimposed over the data in the N2 columns show that if fiber sensitivity was uniform across the population (in other words, if the CNS compensates for varying sensitivity), there was negligible improvement in performance for parallel presentations. Conversely for orthogonal presentations, there was considerable improvement, although performance was still poorer than that of our human subjects. This was the case at all three innervation densities. Other populations with different sensitivity distributions were tested with similar results to those for the population illustrated in Fig. 8, A and B.

A comparison between Fig. 8, B and C, with noise N2 (proportional $\sigma_0^p = 0.15 \ r_{ij}$ and additive $\sigma = 3 \text{ imp/s}$) shows that offsetting the stimulus relative to the population matrix or introducing nonuniformity into the geometric configuration of...
the population matrix had little effect on performance. This was so for both orientations, but Fig. 8C shows performance for parallel orientations only. In the remaining analyses illustrated in Fig. 8C, we explore the effect of increased levels of noise on performance. The population tested had the same sensitivity distribution as the population illustrated in Fig. 6B but with the scattered fiber distribution illustrated in the second panel of Fig. 6C. We have no clear idea of the level of noise imposed by central mechanisms so we tested this population at a range of noise levels—proportional noise with $\sigma_r^2 = 0.15 \ r_p$, 0.4 $r_p$, and $r_p$, in combination with additive noise with $\sigma = 3$ or 6 imp/s. The results suggest that proportion noise is not the major factor limiting performance because even at high levels of proportion noise ($\sigma^2_r = r_p$) performance for the parallel orientation is comparable to human performance provided additive noise is low. It is clear that additive noise is potentially the greater limiting factor. As could be expected from the results illustrated in Fig. 8A, at higher noise levels, the discrimination performance of the model for orthogonal presentations was only marginally above chance at all population densities, therefore these results are not shown.

So far we have assumed that the CNS knows the relative location of the receptive field centers of the fibers innervating the fingerpad and thus the results presented here were calculated using the precise locations of the receptive field centers. However, as a comparison, we also carried out these same analyses on the basis that the CNS does not have this “knowledge” and assumes a uniformly distributed matrix. The results were similar with either form of computation.

DISCUSSION

Tactile spatial acuity—human performance

Our subjects were able to discriminate changes in gap width of around 0.2 mm for both 2.0- and 2.9-mm gap width standards. This is comparable with previous studies of spatial acuity that have used tasks similar to ours. For example, Loomis (1979) reported a threshold of 0.3 mm for the discrimination of the spatial interval between two bars separated by approximately 5 mm and Morley et al. (1983) reported a discrimination threshold of 0.1 mm for gratings with periods around 1 mm. Other measures traditionally employed to examine spatial acuity have produced much larger thresholds. For instance, studies that have used grating orientation as a measure report thresholds levels of approximately 0.8–1 mm (Craig 1999; Craig and Kissner 1998; Johnson and Phillips 1981; Sathian et al. 1997b; Van Boven and Johnson 1994a,b). The reason for the discrepancy in these measures is pursued in the final section of the DISCUSSION.

Neural representation

The features of our gap stimuli were clearly represented in the spatial modulation of single SAI responses. The gap was represented by a trough in the response profiles and the edges of the gap produced corresponding peaks in the profiles similar to those reported by Phillips and Johnson (1981a) for bars, edges and gratings. We found that different gap widths produced differences in the degree of response profile modulation and that these differences were easily resolved as response variability was low. Stimulus orientation also influenced the degree of profile modulation—presenting the gaps orthogonal to the skin ridges resulted in a relative flattening of the profiles. This is consistent with the effect noted by Phillips and Johnson (1981a) when aperiodic gratings were presented with the grooves oriented orthogonal to the ridges of the monkey fingerpad.

Our single fiber response profiles were similar for all fibers and could be described by a difference of Gaussians with the form $r = sa + be^{-cu^2} - de^{-fu^2}$ where the gap width and orientation defined the constants $a$, $b$, $c$, $d$, and $f$, and where $s$ was a multiplicative constant representing the sensitivity of the individual fiber. One way of describing the profile modulation produced by variations in the stimuli would be to use a contrast index similar to that described by Phillips and Johnson (1981a) to quantify changes in single fiber responses as a function of grating period. That same index applied to our data yields values of 0.15 and 0.38 for gap widths of 2.0 and 2.8 mm presented in the orthogonal orientation and 0.49 and 0.6 for gaps of 2.0 and 2.8 mm in the parallel orientation.

Population responses

Single fiber receptive field profiles, however, do not give us a complete understanding of the signaling capacity of populations of SAI s nor do they allow an examination of the degree to which population factors like innervation density, response noise, and variation in fiber sensitivity affect resolution. Some sort of model or simulation is required to study these issues. We simulated the responses of populations of human SAI s using the single fiber response function described in the preceding text as a basis and built onto this, parameters that allowed us to emulate realistic population characteristics including neural noise. We were then able to assess the impact of these critical population characteristics on acuity by measuring the ability of the model to discriminate changes in gap width under a variety of population and stimulus conditions. The performance of the model was measured using a simple response index $V$, which measured how the stimulus gap was reflected in the whole population response.

Fiber sensitivity

There is considerable variation in the sensitivity of fibers within peripheral populations (Goodwin et al. 1995, 1997; Knibestol 1975) that produces large distortions in the population profile (Fig. 6B). It is difficult to know whether variations in fiber sensitivity are important in terms of higher level processing of population signals because it is possible that the CNS has knowledge of the sensitivity of the input fibers and thus responses may be effectively normalized. We found that while such normalization provided little advantage for parallel stimulus orientations, it improved performance for orthogonal presentations, albeit not to the level of performance we found when the stimulus was presented in the parallel orientation even without normalization. It is easy to appreciate why sensitivity variation had a greater effect for orthogonal presentations than for parallel presentations by considering that while random fluctuations produced by differing sensitivities will tend to average out over the relatively large area activated, the stimulus-related peaks and troughs will be much less salient in this “noisy” signal for orthogonal orientations because the
modulation in response profiles is smaller than for parallel orientations.

**Innervation geometry and density**

The CNS has two possible options in performing its computations to extract information from the peripheral signal—it may "know" the relative location of the receptive fields of the input peripheral fibers and base subsequent calculations on that knowledge or it may assume uniformity in geometric arrangement. We found that there was little difference in outcome if the response measure was calculated using the precise location of the receptive fields or alternatively, if it was based on an assumed uniform innervation pattern. With either form of computation, small variations in geometry, such as are likely to exist in the normal innervation pattern of human skin, had little effect on performance. Similarly if the stimulus was presented off-center relative to the sampling array, which is likely to be the case in a real situation, performance was little affected even though the neural image was changed because the sampling points became asymmetrical relative to the stimulus.

Performance levels were not severely degraded by halving the innervation density estimated by Johansson and Vallbo (1979) for the human fingertip (similar densities have been reported for the monkey fingertip by Darian-Smith and Kenins 1980). This finding may seem surprising in view of the reported changes in acuity with age (Sathian et al. 1997a; Stevens and Patterson 1995) where there may be a decline in receptor density, as there is for Meissner's corpuscles, or changes in the nerve endings associated with the Merkel cells (Bolton et al. 1965; Cauna 1965). However, there are other factors associated with aging such as changes in skin mechanics, which our model did not take account of, and possibly cognitive factors that will affect performance. Notwithstanding this, it is possible that the reduction in receptor density with age produces a patchy distribution pattern rather than a uniform loss, and this may be more severe than the perturbations we simulated. At this stage, we have not used the model to study degradation in resolution such as occurs in peripheral neuropathies, nerve injury, or with aging where there are likely to be large "silent" areas in the fingertip (Dyck et al. 1966; Sathian et al. 1997a; Stevens and Patterson 1995; Van Boven and Johnson 1994a).

Comparing the effects of different innervation densities for a fixed area of skin, as we have done with our simulations, can lead to apparently anomalous results; performance may improve as innervation decreases. The reason for this is that changing density, in a fixed area of skin, also changes other properties of the population such as the positions of the receptive fields, the distribution of sensitivities, etc. Thus when comparing two, necessarily different, populations at two densities, spurious results may occur because of the characteristics of those two populations (e.g., see Fig. 8A). Of course averaged over a large number of populations, a decrease in innervation density must degrade performance.

**Response variability**

Noise of the type and magnitude observed for peripheral responses (Edin et al. 1995; Phillips and Johnson 1981a; Wheat et al. 1995) had only minimal effects on the performance of the model. Given that noise at the peripheral level is small, this is not a surprising result. However, as one would expect, performance deteriorated as noise levels increased to resemble those likely to exist at the CNS level with by far the largest impact stemming from additive noise. For retinal ganglion cells and neurons in the lateral geniculate nucleus, a number of studies have described variability that is independent of the magnitude of the response, i.e., "additive" noise (Croner et al. 1993; Edwards et al. 1995; Schiller et al. 1976) while in visual cortex, motor cortex and parietal areas 2/5, variability of response increases as the response of the neuron increases, usually with the variance approximately proportional to the mean (Dean 1981; Heggelund and Albus 1978; Lee et al. 1998; Snowden et al. 1992; Vogels et al. 1989). There is little documented in the literature to indicate the level of noise in CNS somatosensory areas (e.g., Gardner and Costanzo 1980; Tremblay et al. 1996; Whitset et al. 1978), and therefore the levels chosen by us may not truly reflect what occurs in real tactile processes. In spite of our lack of quantitative data in this regard, our analyses nevertheless serve to highlight the relative effects of noise in the processing of tactile information. The important finding is that the greatest impact on gap discrimination performance appears to be additive noise. This makes perfect sense given that additive noise will reduce the difference between peak and trough responses, thereby reducing the effective signal. It must be stressed, however, that additive noise will not necessarily have that same limiting effect on discrimination performance for all tactile stimuli. In a previous study, which simulated the discrimination of the curvature, position, and contact force of spherical stimuli, we found that proportional and additive noise had different effects on performance depending on which stimulus parameter was being discriminated because for each a somewhat different response measure was employed (Goodwin and Wheat 1999).

Response indices, such as that described by Phillips and Johnson (1981a), which are based on maximum and minimum responses, provide a clear measure of response modulation for ideal populations. However, in the case of real SAI populations, defining the maximum or minimum responses within a profile containing multiple peaks and troughs due to random variations in response and also in fiber sensitivity (Fig. 6B) may give spurious indicators of the location of the edges of the gap and thus the effectiveness of the indices will be weakened.

**Stimulus orientation**

The fundamental factor responsible for the orientation effects in our study is the small degree of modulation in the response profiles, and the low slope of the V function with increasing gap width, for the orthogonal orientation as compared with those for the parallel orientation. Neural noise degraded the signal substantially and the differential effect of stimulus orientation on the population response became more evident. For orthogonal presentations, the performance of the model was little above chance at more realistic noise levels. The reasons for the strong orientation effect seen in our single fiber responses are complex and not fully resolved. The simplest explanation is that the beam-like structure of the ridges (Halata 1975) results in skin stiffness that is greater in a direction parallel to the ridges than in the orthogonal direction. There are no direct measurements that we know of to test this
then it should be reflected in the receptive field characteristics, reported. If differential skin stiffness is a significant factor, tranverse direction,” but the pattern of skin ridges was not indentation extended further in the longitudinal than in the (1975) observed that “dimpling of the skin produced by an mm parallel to the ridges and 1.7 mm orthogonal to the ridges. fingerpad was elongated with its long axis parallel to the skin profiles and found that widths at half-height were similar parallel to the ridges (3.8 mm) and orthogonal to the ridges (3.2 mm). The direction of this small difference is consistent with the observations of Khalsa et al. (1998) who found that when a sphere of radius 5 mm was indented into the monkey’s fingerpad, the orientation of the SAI population response was biased toward the long axis of the finger. In an extensive study in which receptive fields on the monkey fingerpad were mapped with an array of probes 0.5 mm in diameter, Vega-Bermudez and Johnson (1999) found no relationship between receptive file orientation and ridge orientation.

The striking difference between the gap data and the probe data may be due entirely to the geometric differences between the stimuli that could result in substantially different stress patterns in a ridged surface. An additional potential complication is the curvature of the skin surface that is smaller in the direction aligned with the finger axis than perpendicular to it. However, most of the preceding data pertain to the central part of the monkey fingerpad, which is relatively flat, so that curvature differences are unlikely to be a principal factor. In the human, where the ridge patterns are more variable and complex, the situation is even less clear. Johansson and Vallbo (1980) reported that about half of the receptive fields they mapped were elongated and aligned with the longitudinal axis of the hand, but this was a mixed sample of FAIs and SAI on all parts of the glabrous skin with a multiplicity of ridge patterns in a ridged surface. An additional potential complication is the curvature of the skin surface that is smaller in the direction aligned with the finger axis than perpendicular to it. However, most of the preceding data pertain to the central part of the monkey fingerpad, which is relatively flat, so that curvature differences are unlikely to be a principal factor. In the human, where the ridge patterns are more variable and complex, the situation is even less clear. Johansson and Vallbo (1980) reported that about half of the receptive fields they mapped were elongated and aligned with the longitudinal axis of the hand, but this was a mixed sample of FAIs and SAI on all parts of the glabrous skin with a multiplicity of ridge patterns.

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Ambiguities also plague the human psychophysical data for the effects of orientation on discrimination of a grating from a smooth surface. Essock et al. (1992, 1997) found that performance was optimal when the gratings were aligned with the finger axis, but Craig (1999) found no effect of orientation. Craig’s explanation for the discrepancy is that the parameters of the stimuli were different, in particular contact force was 100 gf in Craig’s study and 16.4 gf in the experiments of Essock et al. In none of these studies is it possible to relate the observations to the nature of the ridge patterns. For our subjects, the ridges in the contact area for both gap and grating studies were more or less perpendicular to the finger axis (Fig. 2C), and we found a clear orientation effect in the grating versus smooth study. A psychophysical orientation effect could be due to any combination of a number of factors including orientation preferences in primary afferent receptive fields, patterns of innervation of the skin, and orientation-selective cortical mechanisms (Gardner and Costanzo 1980; Warren et al. 1986).

There is one inevitable weakness in our study. Our model is based on neural responses from monkeys in which all the
ridges are parallel to the finger axis. Extrapolating these data to regions of the human finger where the ridges run approximately in the same direction (Fig. 2C), and where our psychophysical experiments were performed, is straightforward. However, it is not obvious how to use the data for regions of the human finger where the ridges have more complex and variable patterns. Ultimately this is necessary, but it will require a combination of more sophisticated models of skin mechanics and experiments, using appropriate stimuli, in which recordings from human afferents innervating different regions of the finger are correlated with ridge patterns.

Gap discrimination versus grating orientation

Why is the difference limen for discriminating changes in gap width (=0.2 mm) less than the threshold gap width for discriminating grating orientation (=0.8 mm) (Craig 1999)? A major reason becomes evident when considering the types of neural codes that may be used in the two tasks. To determine a change in gap width, it is sufficient to detect a change in some scalar measure of response, such as our measure V. Because such “total response” codes can be averaged over the entire population, they are relatively insensitive to masking by factors such as neural noise and variation in afferent sensitivity. In contrast, to discriminate the orientation of a grating requires a vector calculation, for example, extracting the orientation of lines passing through the response peaks or troughs. This more complex “spatial” computation, over a smaller subset of the population, is more susceptible to the above masking factors, thus requiring a larger gap (greater signal) for reliable discrimination.

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