Physical determinants of the shape of the psychophysical curve relating tactile roughness to raised-dot spacing: implications for neuronal coding of roughness

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Sutu A, Meftah EM, Chapman CE. Physical determinants of the shape of the psychophysical curve relating tactile roughness to raised-dot spacing: implications for neuronal coding of roughness. J Neurophysiol 109: 1403–1415, 2013. First published December 5, 2012; doi:10.1152/jn.00717.2012.—There are conflicting reports as to whether the shape of the psychometric relation between perceived roughness and tactile element spacing [spatial period (SP)] follows an inverted U-shape or a monotonic linear increase. This is a critical issue because the former result has been used to assess neuronal codes for roughness. We tested the hypothesis that the relation’s shape is critically dependent on tactile element height (raised dots). Subjects rated the roughness of low (0.36 mm)- and high (1.8 mm)-raised-dot surfaces displaced under their fingertip. Inverted U-shaped curves were obtained as the SP of low-dot surfaces was increased (1.3–6.2 mm, tetragonal arrays); a monotonic increase was observed for high-dot surfaces. We hypothesized that roughness is not a single sensory continuum across the tested SPs of low-dot surfaces, predicting that roughness discrimination would show deviations from the invariant relation between threshold (ΔS) and the value of the standard (S) surface (Weber fraction, ΔS/S) expected for a single continuum. The results showed that Weber fractions were increased for SPs on the descending limb of the inverted U-shaped curve. There was also an increase in the Weber fraction for high-dot surfaces but only at the peak (3 mm), corresponding to the SP at which the slope of the psychometric function showed a modest decline. Together the results indicate that tactile roughness is not a continuum across low-dot SPs of 1.3–6.2 mm. These findings suggest that correlating the inverted U-shaped function with neuronal codes is of questionable validity. A simple intensive code may well contribute to tactile roughness.

Keywords: tactile scaling; tactile discrimination; psychophysics; Weber fractions; invariance

Tactile roughness is a complex, multidimensional sensation that is dependent on the physical characteristics of multiple tactile elements (e.g., grains of sand for abrasive papers), including their size, shape, density (or spacing), and composition. To assess the underlying neuronal coding mechanisms, investigators have used the nature of the relation between perceived roughness and surface characteristics (e.g., Cascio and Sathian 2001; Connor et al. 1990; Connor and Johnson 1992; Sathian et al. 1989; Yoshioka et al. 2001).

For relatively coarsely textured surfaces, the dominant view at present is that the neural representation of tactile roughness can best be explained by a spatial variation code whereby differences in the firing rates of slowly adapting type I (SAI) afferents innervating skin regions separated by ~2 mm are computed (Connor et al. 1990; Connor and Johnson 1992; Johnson and Hsiao 1994). This view is based on the work of Johnson and colleagues, who used psychophysical estimates of tactile roughness to test a wide range of neural codes, including an intensive code (mean firing rate) and the spatial variation code. The test surfaces in their initial study consisted of tetragonal patterns of raised dots, whose spacing (center to center) was systematically varied from 1.3 to 6.2 mm. Subjects showed an inverted U-shaped relation between perceived roughness and dot spacing. Roughness increased up to a dot spacing of 3.2 mm and then declined as spacing was further increased to 6.2 mm. Johnson and colleagues ultimately rejected the intensive code because the mean discharge frequency of primary mechanoreceptive afferents (specifically SAI) did not peak at the same dot spacing as the psychophysical results. More recently, Yoshioka et al. (2001) extended these results to finer-textured surfaces (down to spacings of 100 μm), but in this case the intensive code fit the data as well as the spatial variation code. Finer-textured surfaces, with spacings on the order of micrometers (< the range tested by Yoshioka et al.) have been suggested to depend on vibration, signaled by Pacinian (PC) afferents (Bensmaia and Hollins 2003; Hollins and Risner 2000; Mackevicius et al. 2012) and not dependent on SAI afferents (Libouton et al. 2012).

The original psychophysical data of Connor et al. (1990) were, however, strongly influenced by the structure of the surfaces. We have shown that magnitude estimates of tactile roughness show a monotonic linear increase as the spatial period (SP, distance center to center between dots) of rectangular arrays of raised dots is increased from 1.5 to 8.5 mm between adjacent rows (Meftah et al. 2000).

There are three potential explanations for the apparent discrepancy in the psychophysical results (inverted U-shape vs. monotonic). First, there may be fundamental differences in the roughness of textures that change in one dimension (1D) (Meftah et al. 2000) versus two dimensions (2D) (Connor et al. 1990, 1992). This is unlikely, because we have since shown that roughness increases linearly for raised-dot surfaces with 2D changes in dot spacing (Dépeault et al. 2009). The results were indistinguishable from those observed with 1D changes (evaluated at the same time), with the key factor being dot spacing in the direction...
of the scan. Second, it is possible that differences related to a third dimension, dot height, explain the difference. Our raised dots were higher than those used by Connor et al., 1–1.8 mm versus 0.35 mm. This minimized contact between the exploring finger and the smooth floor between dots, thus maximizing skin deformation as dot spacing increased in our experiments. This suggestion is supported by the results of Blake et al. (1997), who reported that roughness estimates increase as dot height is increased over a limited range, from 0.28 to 0.62 mm (only 1 dot spacing tested). Third, it is possible that the subjects with an inverted U-shaped relation between roughness and dot spacing evaluated different qualities of the surfaces over the ascending and descending limbs of the psychophysical curve, i.e., they used different rating scales for each limb. This interpretation would explain why they gave approximately the same rating to surfaces with very different dot spacings, e.g., 2.4 mm versus 5.2 mm. On the ascending limb, the dots were closely packed so that contact was mainly with the tops of the raised dots; on the descending limb, in contrast, the finger would have mainly been in contact with the smooth floor between dots, along with the occasional dot. The suggestion that subjects used different rating scales for each limb of the curve is supported by results from Klatzky and Lederman (1999). Using nonperiodic raised-dot surfaces, their subjects had difficulty in understanding what was meant by “rougher” in the context of a roughness discrimination task when there was considerable contact between the exploring finger and the smooth floor, corresponding to spacings located on the descending limb of the inverted U-shaped curve.

In light of the above considerations, we hypothesized that dot height is the critical factor underlying the shape of the psychometric curve relating tactile roughness with dot spacing: monotonic increase versus inverted U-shape. We predicted that the inverted U-shaped relation between roughness and SP would be transformed into a monotonic relation by increasing the height of the tactile elements (raised dots). We tested this prediction, using surfaces with the same 2D spatial characteristics as those used by Connor et al. (1990) but varying dot height [low (0.36 mm) or high (1.8 mm)]. We also investigated the possibility that the subjects rated different sensory qualities on the descending limb of the inverted U-shaped curve, compared with either the ascending limb (low dots) or the monotonic increasing curve obtained with high-dot surfaces. We reasoned that if this was not a single sensory continuum then the ability to discriminate differences in dot spacing would show deviations from the expected invariant relation between discrimination threshold (ΔS) and the value of the standard (S) surface (ΔS/S = a constant, the Weber fraction). Our results confirmed our predictions, showing the importance of dot height for tactile roughness. The results are discussed in relation to putative neuronal codes for roughness and interpreted to suggest that a simple neuronal rate code for roughness may well be sufficient to explain tactile roughness. This finding has important implications for the development of neuroprosthetic devices to substitute for lost sensorimotor function. A preliminary report of these results has been presented in abstract form (Meftha and al. 2010).

MATERIALS AND METHODS

Subjects

A total of 15 healthy, naive adults (8 women and 7 men, all but 3 right-handed for writing, 21–35 yr old) volunteered to participate in the study. The subjects were financially compensated for their participation. The institutional ethics committee approved the experimental protocol, and all subjects gave their informed consent before participating in the experiment. For experiment 1 (magnitude estimation), eight of nine subjects participated in two experimental sessions (1.5 h long) in which they estimated the degree of roughness of surfaces scanned under their immobile right middle fingertip (D3). The remaining subject (female) only participated in one session (series 1, see below). For experiment 2 (discrimination threshold), 10 subjects participated in two experimental sessions (1.5 h long); 4 of them (2 women and 2 men) also participated in experiment 1.

Experiment 1: Magnitude Estimates of Roughness

Surfaces. As shown in Fig. 1A, two series of eight textured surfaces of embossed, cylindrical raised dots (diameter 0.7 mm, measured at the top) arranged in a tetragonal (or diamond) pattern were prepared from flexible letterpress (CML Printing Plates, St Léonard, QC, Canada). Each tetragon on a surface had identical dot spacing (distance center to center between dots) on its four sides. For series 1 (Fig. 1A, top), dot spacing ranged from 1.3 to 6.2 mm (increments of 0.7 mm; see Table 1). This covered the range of spacings tested previously by Connor et al. (1990). For series 2 (Fig. 1A, bottom), a smaller range of dot spacings was used (3.4–6.2 mm, increments of 0.4 mm); this corresponded to the descending limb of the psychophysical curve described by Connor et al. The dimensions of each surface were 2 × 10 cm; four of these “surfaces” were prepared in a single continuous strip (2 × 40 cm); 2 strips for each series, a and b, in Fig. 1A) that was mounted around the circumference of the tactile stimulator for presentation to the finger tip (Fig. 1, C and D). For each series, two sets of eight surfaces were prepared: one set had high dots (1.8 mm), and the other set had low dots (0.36 mm) (Fig. 1B).

Tactile stimulator. The tactile stimulator was similar to that described by Zompa and Chapman (1995). It consisted of a cylindrical drum (40-cm circumference) mounted on a drive shaft and rotated by means of a DC motor through a 100:1 reduction gear. The four strips of the series (2 × high, 2 × low dots) were mounted around the circumference of the drum (details in Fig. 1). As shown in Fig. 1C, the surfaces were accessible for palpation by the pad of the distal phalanx of D3 through twinned rectangular apertures (2.5 × 6.5 cm each). Four markers, numbered 1 to 4, were placed next to the surfaces, corresponding to the four strips (Fig. 1C). These were used to cue the subject as to the surface to touch on the next trial.

Experimental setup. The experimental setup was identical to that described by Meftha et al. (2000). A brief summary is provided here. The subject was seated with the tactile stimulator at about waist level (Fig. 1C). Ambient light was reduced to avoid any visual cues about the surface roughness. The subject wore headphones to mask any auditory cues related to tactile roughness. A yellow light (4 cm²) was placed directly in front of the subject, midline, at eye level (distance 1.2 m). Both arms were comfortably supported on two independent manipulands that allowed only elbow rotation in the horizontal plane. During the experiment the left arm was maintained in a comfortable, resting position. During the intertrial interval, the distal phalanx of the right D3 rested on the marker located distal to the surface to be scanned in the next trial. The direction of the scan was proximal to distal relative to D3 (see arrow, Fig. 1D). The speed of the surface under the finger tip was ~60 mm/s. The subject was told to use a constant, comfortable level of vertical contact force in touching the surface throughout the session.

Perceptual task. At the beginning of the session, the subject was informed that a series of surfaces would be scanned under the
finger pad of the right D3. The subject was asked to evaluate the roughness of each surface presented, after a single presentation. Roughness was not defined. Instead, the subject was instructed to base his/her estimates on his/her personal definition of roughness. Before data collection started, several practice trials allowed the subject to become familiar with the logistics of the experiment. The subject's scale was then established by presenting three different surfaces drawn from examples of the surfaces used in the task. For this, we used surfaces with high dots, presenting the two extremes, and finally a surface from the middle of the range. The subject was told that the surfaces were illustrative examples, and he/she was asked to assign any whole number that seemed appropriate to the third surface; the only constraint was that the number should be proportional to the sensation of roughness. All subjects were tested with series 1 in the first session and series 2 in the second.

Experimental design. For each series, a pseudorandom list of 96 trials was preestablished that interleaved dot spacing and height (low and high). Each dot spacing was presented 12 times (6 low, 6 high). Each trial was preceded by a verbal instruction to position D3 over the surface adjacent to the appropriate number. When the subject was ready to start, the trial was initiated by one of the experimenters. The temporal sequence of the events in the trial was as follows: the yellow light, illuminated just before the onset of drum rotation, cued the subject to quickly lower his/her finger onto the already moving surface; the subject then kept his/her finger in contact with the moving surface for 1.15 s; he/she was asked to remove the finger when the light turned off (end of drum rotation). Thereafter, the subject gave his/her subjective estimate of the perceived roughness, and this was entered into the computer by the experimenter and stored with the trial. If the subject judged that he/she was uncomfortable or perturbed during the trial, the trial was rejected and repeated later. Our exper-

Fig. 1. A: schematic representation of the raised-dot surfaces used in experiment 1, roughness estimation. The dots were arranged in tetragons (see inset). Above each sample (truncated length shown) is the dot spacing (mm) measured center to center along the sides of the tetragon. B: dot height was systematically varied (low, high). C: subject position during the experiment. For each series, the low dots were installed at positions 1 and 4 and high dots at 2 and 3. Dot spacing was alternated (a, b, a, b; see A). D: lateral view of the drum of the tactile stimulator showing one 40-cm-long strip of 4 surfaces (each 2 × 10 cm) affixed around its circumference and the position of the middle finger during surface scanning. SP, spatial period.
Table 1. Spatial characteristics of textured surfaces

<table>
<thead>
<tr>
<th></th>
<th>Series 1</th>
<th>Series 2</th>
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<tbody>
<tr>
<td></td>
<td>Sides</td>
<td>Longitudinal</td>
</tr>
<tr>
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<td></td>
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<tr>
<td>Standard</td>
<td>1.3</td>
<td>1.8</td>
</tr>
<tr>
<td>Increments</td>
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<td>2.8</td>
</tr>
<tr>
<td>Modified</td>
<td>2.7</td>
<td>3.8</td>
</tr>
<tr>
<td>Decrements</td>
<td>3.4</td>
<td>4.8</td>
</tr>
<tr>
<td>Modified</td>
<td>4.1</td>
<td>5.8</td>
</tr>
<tr>
<td>Standard</td>
<td>4.8</td>
<td>6.8</td>
</tr>
<tr>
<td>Increments</td>
<td>5.5</td>
<td>7.8</td>
</tr>
<tr>
<td>Modified</td>
<td>6.2</td>
<td>8.8</td>
</tr>
</tbody>
</table>

Values are dot spacings (mm) measured center to center either along the side of the tetragon or longitudinally (across the diagonal of the tetragon, in the direction of the scan).

The experimental design ensured that information about surface roughness came only from contact with the moving surface. At the end of each session, the subjects were debriefed and questions were posed about the strategy used for estimating surface roughness. They were also asked to rate the overall difficulty of the task using a scale from 1 to 10 (1, very easy; 10, very difficult).

**Data acquisition and analysis.** The task and the data acquisition were under computer control. For each trial, digital events (times of scanning onset and end), drum position, and vertical contact force (200-Hz digitization rate) were recorded. For each trial the vertical contact force was measured by a pair of strain gauges, visually inspected online, and if the contact force during the scanning interval varied by more than ±0.2 N the trial was discarded and repeated later during the session.

For each subject, roughness estimates were normalized off-line by dividing the subject’s responses by the averaged value of all estimates given during the same experimental session. These normalized values were used for the subsequent statistical analyses. For each subject, a two-way analysis of variance (ANOVA) was applied to the data (estimates/dot spacing and height). For the pooled data, a repeated-measures ANOVA was used (estimates/dot spacing and height). The statistical analyses employed parametric tests because the data were normally distributed (Shapiro-Wilk normality test) and variances were similar (Levene's test). These and other analyses were performed with SYSTAT version 11 or MATLAB version 7.3.0.

To describe the nature of the relationship between subjective roughness and dot spacing, linear regression analyses were applied to the data from each subject. The regression parameters (slope, intercept, and $r^2$, the coefficient of determination) were compared across series 1 and 2 with paired $t$-tests. For the high-dot surfaces, all data were included in the regression analysis. For the low-dot surfaces, three regressions were performed. One regression used all data, while the other two were fit to the ascending and descending limbs of the inverted U-shaped curve (see Fig. 3 for example). For the ascending limb, all data points for which roughness ratings increased with an increase in dot spacing were included (first two spacings, Fig. 3). For the descending limb, the regression was fit to all of the rest of the data, including the peak, the plateau (if present), and the descending limb of the curve. This provided a good estimate of the regression since the regression parameters were not different from those obtained when the curve was fit only to data points from the dynamic part of the descending limb. The intersection of the ascending and descending regressions defined the peak of the inverted U-shaped curve (e.g., 2.02 mm for the example in Fig. 3). The level of significance was fixed at $P < 0.01$ for all statistical analyses.

**Experiment 2: Roughness Discrimination**

**Surfaces.** In this experiment, four series of eight surfaces were prepared, with two replicates of each (low, high). Each surface was 2 cm wide × 10 cm long. The general physical characteristics of the surfaces were identical to those used in the magnitude estimation experiments: tetragonal raised-dot patterns, with the same two dot heights and dot diameter. The dot spacings were chosen relative to the general inverted U-shaped curve obtained in series 1/low of experiment 1, so that discrimination threshold was estimated at four different points on the curve (see Fig. 4C), corresponding to the origin, either side of the peak (+ and -), and the end of the curve. Each series included one standard surface and seven modified surfaces (see Table 1). The standards were 1.3 mm (increments of 0.05 mm for the modified surfaces; range 1.35–1.65 mm), 3 mm (3–; decrements of 0.1 mm, range 2.9–2.3 mm; 3+; increments of 0.1 mm, range 3.1–3.7 mm), and 6.2 mm (decrements of 0.25 mm, range 5.95–4.45 mm). The absolute value of the increment or decrement was adjusted as a function of the standard (~4%; value estimated from Lamb 1983).

**Apparatus.** In experiment 1, we used the same method for stimulus presentation as in Meftah et al. (2000). It was not practical to use the same approach here because only a limited number of surfaces can be mounted on the tactile stimulator. This would have required eight sessions/subject since a lengthy calibration is required each time the surfaces are changed. We therefore developed a new apparatus for stimulus presentation that allowed us to test four conditions/session. This was, in part, made possible by using active touch to minimize the delay between scans. This was justified since there is no evidence that tactile discrimination is modified by the mode of touch, active versus passive (reviewed in Chapman 1994). As shown in Fig. 2, pairs of surfaces were mounted on a horizontal plate (30 × 46 cm) that was in turn mounted on a fulcrum and counterbalanced with a weight of 50 g, so that the vertical contact force was constant throughout the exploration. The choice of counterweight was arbitrary, falling well within the range commonly used during exploration of textured surfaces (Smith et al. 2002). The surfaces were mounted on small plaques (11.5 × 11.5 cm) that were affixed onto the plate with the long axis of the surface (corresponding to the direction of the scan) being oriented perpendicular to the subject. These were changed after every trial. The apparatus was placed on a table, at wrist height, directly in front of the subject. The apparatus was hidden from the subject’s view by a curtain. The midpoint of the apparatus was aligned with the subject’s right shoulder; the distance between the subject and the apparatus was adjusted so that there was an angle of 35° between the shoulder and the elbow when the digit contacted the surface. The experimenter helped the subject to position D3 at the start position for each surface (Fig 2). Subjects were instructed to push down gently on the surface so that the mobile plate just moved, and then to make their scan (from left to right). Ambient light and auditory feedback were decreased as for experiment 1.

**Perceptual task.** The experimental design was a two-alternative forced-choice (2AFC) method. In each trial, the subject scanned, from left to right, a pair of surfaces (1 standard, 1 modified; order counterbalanced) using the distal phalanx of D3 and then reported verbally which felt rougher (1st or 2nd explored). The response was recorded by one of the experimenters. Note that for the two decrementing series (–), the graphical representation of the results (see Fig. 6) was
reversed (proportion judged smoother). As for experiment 1, subjects were encouraged to use their own personal definition of roughness. No feedback on performance was provided to the subjects. If the subject judged that he/she was uncomfortable or perturbed during the trial, the trial was rejected and repeated later. Before the experiment, subjects were given several practice trials with the exploration; at this time they were trained to move at $\sim$100 mm/s (1-s-duration scan). Speed was modestly faster than for experiment 1, to minimize the length of the session (2 scans for each trial), while remaining well within the range of speeds used for tactile exploration (Smith et al. 2002) and below speeds at which the perception of tactile stimuli is suppressed (Cybulska-Klosowicz et al. 2011). This initial practice was followed by a second series of trials to give the subject a general idea about the range of textured surfaces to be presented (the standard surface paired with the modified surface having the largest difference in dot spacing); the latter practice was repeated before each block of trials.

Data acquisition and analysis. The experiment was organized into two separate sessions. Each session consisted of four blocks (2 low dot and 2 high dot) of 56 trials (8 repetitions of the 7 modified surfaces presented with the standard surface). All parameters were counterbalanced across subjects and sessions. At the end of each block of trials, the subject was asked to rate the difficulty of the task and the unpleasantness of the surfaces using a scale from 1 to 10 (1, easy or pleasant; 10, very difficult or very unpleasant).

For each subject and each standard, the data were fit to a logistic function (proportion correct vs. dot spacing; Voisin et al. 2002). From this, discrimination threshold (ΔS: 75% correct, with 50% corresponding to chance performance for this 2AFC method) was calculated. The Weber fraction was also calculated (ΔS/S, where S corresponded to the center-to-center dot spacing along the sides of the tetragon for the standard surface). The pooled data were analyzed with nonparametric statistical tests (Wilcoxon and Friedman tests) since these data were not normally distributed.

RESULTS

Experiment 1: Magnitude Estimates of Roughness

Series 1. Figure 3 shows the individual results of one subject tested with the wider range of dot spacings, 1.3–6.2 mm. The normalized roughness estimates for the raised-dot tetragonal patterns are plotted as a function of dot spacing measured along the sides of the tetragons. The results from both the low and high dots are shown, along with curves fitted to the mean estimate for each dot height. Inspection of the curves reveals that roughness estimates for high dots increased in a nearly linear fashion as the dot spacing increased. For low dots, the inverted U-shaped curve described by Connor et al. 1990 (see introduction) can be seen: there was an increase of roughness estimates up to 2 mm; thereafter, roughness plateaued and then declined as the dot spacing further increased. There was almost complete separation between the two curves for dot spacings >3 mm. A two-way ANOVA applied to these data (dependent variable: roughness estimate) showed that both dot spacing and dot height were significant factors ($P < 0.0005$). The interaction was also significant ($P < 0.0005$).

The individual psychometric curves for all nine subjects are plotted in Fig. 4. A (high) and B (low). For the high dots, inspection of the individual curves indicates that roughness estimates showed a monotonic increase as dot spacing increased. For the low dots, two different response patterns were observed. Six of nine subjects had an inverted U-shaped psychophysical curve, with the peak of the curve varying across subjects (see below). Three other subjects showed an initial increase in their roughness estimates as dot spacing increased up to 3.4–4.8 mm, followed by a plateau (i.e., no descending limb). The data of each subject were subjected to
an ANOVA. The results indicated that roughness estimates significantly covaried with both dot height and spacing; the interaction was also significant in all cases ($P < 0.0005$). The pooled results plotted in Fig. 4C show that the two curves, low and high, were clearly separate for all dot spacings >2 mm. There was, however, a trend for the slope of the high-dot psychometric curve to decrease for spacings of 3.4 mm and greater. All subjects showed this decrease in the rate of rise of the roughness estimates as dot spacing increased (Fig. 4A), but the spacing at which this occurred varied across subjects (2.7–6.2 mm, mean 3.9 mm). This result confirms previous observations by Meftah et al. (2000) and Dépeault et al. (2009), with the change in slope occurring at roughly the same longitudinal dot spacing (≈4.8 mm here vs. ≈5.5 mm in our previous studies; see Table 1).

The nature of the relationship between the subjective estimates and dot spacing was examined with linear regressions applied to the data from each subject. The mean slopes, intercepts, and $r^2$ values are summarized in Table 2. In the case of high dots, all subjects showed a significant, positive relationship between perceived roughness and dot spacing ($P < 0.0005$). The $r^2$ values were high (mean 0.83), indicating that the linear regression model provided a good fit to the data. For low dots, the regression applied to the entire data set was significant for only five of nine subjects. The mean slope was close to 0, and the $r^2$ values were low, explaining only 19% of the variance in the roughness estimates (Table 2). Paired comparisons showed that all regression parameters were significantly different for the two dot heights ($P < 0.0005$).

When the regressions (low dots) were restricted to the ascending limb of the curve, all subjects showed a positive and significant relationship and the $r^2$ values were higher (mean 0.77). The parameters of the regression curves were now Table 2. Parameters describing linear regressions from experiment 1: mean normalized magnitude estimates vs. dot spacing

<table>
<thead>
<tr>
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<th>Dot Height</th>
<th>Slope</th>
<th>Intercept</th>
<th>$r^2$</th>
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<tbody>
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<td>-0.05 (0.10)</td>
<td>0.83 (0.04)</td>
</tr>
<tr>
<td></td>
<td>Low</td>
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<td>0.53 (0.10)</td>
<td>0.19 (0.06)</td>
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<tr>
<td></td>
<td>$P$ values (H vs. L)</td>
<td>0.0005 &amp; 0.0005 &amp; 0.0005</td>
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</tr>
<tr>
<td></td>
<td>Low/ascending</td>
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<td></td>
<td>Low/descending</td>
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<td>1.30 (0.11)</td>
<td>0.35 (0.08)</td>
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<tr>
<td>Series 2</td>
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<tr>
<td></td>
<td>Low</td>
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<td>1.13 (0.15)</td>
<td>0.32 (0.11)</td>
</tr>
<tr>
<td></td>
<td>$P$ values (H vs. L)</td>
<td>0.0005 &amp; 0.0005 &amp; 0.0044</td>
<td></td>
<td></td>
</tr>
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</table>

Values are means (SE) of the parameters describing the linear regressions from experiment 1, mean normalized magnitude estimates vs. dot spacing (side of the tetragon, center to center). L, low; H, high; $r^2$, coefficient of determination.
similar to those obtained with the high dots (paired t-tests: slope, \( P = 0.04 \); intercept, \( P = 0.019 \); \( r^2, P = 0.40 \)). For the larger dot spacings, the majority of subjects (6 of 9) showed a significant negative correlation with dot spacing. The two regressions (ascending and descending) intersected at 2.3 mm (range 2.0–3.4 mm). The regressions for the remaining 3 subjects were all nonsignificant, i.e., the slope was not different from 0. Their roughness ratings plateaued for larger dot spacings (beginning at 3.4 mm for 2 subjects, 4.8 mm for the other), and their results contributed to the low mean \( r^2 \) value, 0.35. When taken at face value, the latter three subjects could not discriminate any differences in tactile roughness over a large range of spacings (3.4–6.2 mm). Plateaus were not seen in a previous study (Connor et al. 1990), but differences in experimental design (mode of touch, active vs. passive, here; length of surface available for exploration, 11 mm vs. 100 mm) and/or the compliance of the surfaces (rigid vs. flexible) may have contributed to the results.

Altogether, the results showed that there were clear differences between the high- and low-dot conditions, but there seemed to be some ambiguity in the roughness estimates assigned to the low dots over the range of 3.4–6.2 mm, with some subjects reporting that roughness decreased over this range and others reporting no change. Consequently, we repeated this experiment, using a range of dot spacings that was restricted to the “descending” limb identified in the first series.

**Series 2.** Dot spacings in this series ranged from 3.4 to 6.2 mm. The individual and pooled results of six subjects (all of whom participated in **series 1**) are plotted in Fig. 4, D and E, and Fig. 4F, respectively. Eight subjects were tested, but the results of two were excluded (1 subject could not scale the surfaces; the other changed his strategy for the high-dot surfaces, increased roughness for increased dot spacing in **series 1** vs. decreased ratings for **series 2**, consistent with a change in the operational definition for roughness).

The results for the high dots (Fig. 4, D and F) were very similar to those obtained in **series 1**, with all subjects showing a monotonic increase in roughness across the entire range. The parameters of the linear regressions (Table 2) were closely similar to those obtained with **series 1** (paired t-tests: slope, \( P = 0.6 \); intercept, \( P = 0.14 \); \( r^2, P = 0.019 \)).

In contrast, the results obtained with the low dots were very different from **series 1**. There was no longer an inverted U-shaped relation; instead all subjects showed a decrease in roughness estimates as dot spacing increased (4/6 significant including 2/3 subjects with a plateau for **series 1**/low). Consequently, comparisons of the regression parameters, high versus low, were all significant (see Table 2). Inspection of the results indicated, however, that there was still some ambiguity for the smaller dot spacings tested (3.4 and 3.8 mm), so that the pooled data peaked at 3.8 mm and declined thereafter.

To determine the extent to which subjects were consistent in their roughness ratings across the two series of surfaces, Fig. 5 plots, for each subject who participated in both sessions (\( n = 6 \)), the mean normalized roughness estimates for four of the dot spacings used in **series 2** that had comparable spacings tested in **series 1** (see legend for details). The data (Fig. 5A) were fit well by a linear regression (\( r^2 = 0.903 \)), and inspection suggests that there was a continuum from smooth to rough, with high-dot surfaces being rated as rougher than low-dot surfaces. When the same data were categorized according to dot spacing (Fig. 5B), it is clearly evident that this “continuum” was critically dependent on both dot height and dot spacing. Thus the largest dot spacing was found at both extremes corresponding to the low and high dots.

For subjects tested with both series of surfaces, difficulty ratings were identical for both series. There was, however, a wide range of ratings across subjects (1.5–8/10). The personal definitions of roughness were likewise widely variable, ranging from the level of hardness or the degree of prickling to the degree of resistance offered by the surfaces.

**Skin contact with the smooth floor.** To determine whether the skin contacted the smooth floor of the surfaces, the skin of the digit in three subjects was coated with ink and the surfaces were displaced under the immobile digit tip. Inspection of the low-dot surfaces indicated that the digit contacted the floor for all surfaces with spacings \( \geq 3.4 \) mm, corresponding to the descending arm of the psychophysical curves. Skin contact with the floor of the high-dot surfaces was restricted to the largest dot spacing (6.2 mm) and was intermittent.

**Experiment 2: Roughness Discrimination**

The results of experiment 1 indicated that there was ambiguity in the estimated roughness of the low-dot surfaces, particularly when the dot spacings were near or greater than the peak of the inverted U-shaped curve. One interpretation of our results is that subjects used two different scales for the ascending and descending portions of the inverted U-shaped curve, i.e., different sensory qualities were evaluated. We reasoned

![Fig. 5](https://example.com/f5.png)

**Fig. 5.** Mean normalized roughness estimates in **series 2** vs. **series 1** for 6 subjects who participated in both series. Data were taken from surfaces with identical (3.4 and 6.2 mm) or closely similar dot spacings (4.1 vs. 4.2 mm; 5.4 vs. 5.5 mm). Data are categorized as a function of dot height (A) and dot spacing (B). Roughness estimates were similar across the 2 series of surfaces tested in experiment 1, forming a continuum from smoother to rougher that was critically dependent on both dot height (A) and spacing (B), with spacing having opposite effects depending on dot height.
that if this was not a single sensory continuum then the ability to discriminate differences in dot spacing would show deviations from the expected invariant relation ($\Delta S/S = $ a constant).

We tested this prediction by determining discrimination threshold at four points on the inverted U-shaped psychophysical curve for roughness (see Fig. 4C, top), corresponding to its origin (1.3 mm), peak (3 mm: $-$, decrementing; $+$, incrementing), and end (6.2 mm, $-$). We expected that threshold would increase as the value of the standard stimulus increased, reflecting the well-known dependence of discrimination threshold on the value of the standard, and that the results would differ as a function of dot height.

The results of a representative subject are shown in Fig. 6. For the testing on the ascending portion of the inverted U-shaped curve (Fig. 6, left: standards 1.3+ and 3$-$), performance did not vary as a function of dot height (low, high), and thresholds (0.75 correct) were identical (see legend for details). When discrimination performance was tested on the descending limb of the curve (Fig. 6, right: standards 3+ and 6.2$-$), there was a large separation between the high- and low-dot curves, and threshold was lower with high dots (respectively, 0.21 and 0.25 mm) compared with low dots (0.51 and 0.65 mm).

The results of 10 subjects are summarized in Fig. 7 and Table 3. Discrimination threshold (individual and means shown) varied significantly with the dot spacing of the standard for both low and high dots (Friedman’s tests, $P < 0.0005$). Inspection of the results (Fig. 7A) shows that threshold increased as the dot spacing of the standard increased, so that threshold was significantly higher for the roughest standard compared with the smoothest standard for both low and high dots (Wilcoxon tests, $P = 0.005$). The data from the ascending limb of the curve (S, 1.3+ and 3$-$) were pooled, and a paired comparison, low versus high, showed no difference in threshold with dot height (Wilcoxon, $P = 0.96$). On the descending limb (S, 3+, 6.2$-$), in contrast, threshold was significantly higher for the low-dot surfaces ($P = 0.007$).

In Fig. 7B the mean and individual Weber fractions are plotted. For the low dots, the Weber fraction was low for the two series that tested discrimination performance on the ascending limb of the inverted U-shaped curve (1.3+ and 3$-$). As expected, the mean Weber fraction was higher for the 3+ and 6.2$-$ standards, corresponding to the descending limb of the curve. For the high dots, the Weber fraction was low and unchanging for three of the standards (1.3+; 3$-$, and 6.2$-$), but there was an increase for the 3+ standard. For both low and high dots, there was a significant change in the Weber fraction across the four standards (Friedman’s tests, $P < 0.0005$ and $P = 0.003$, respectively). For the low dots, higher values for the 3+ and 6.2$-$ standards explained the result (no change when these were excluded, $P = 0.2$). For the high dots, in contrast, only the 3+ data contributed to the difference (no change across the other 3 standards, $P = 0.27$).

As for experiment 1, the difficulty ratings varied widely across subjects. Median ratings were similar for low (5: range, 2–9) and high (4.5: 1–9) dots. Although no difference in difficulty ratings were observed across the four standards for either the low or the high dots, the ratings covaried with the Weber fractions, with subjects rating the series with higher Weber fractions as most difficult (low, 9/10 subjects rated...
After careful consideration, we opted to modify the approach described by Blake et al. (1997), and so passive touch was found to be comparable to our previous study of roughness scaling (Meftah et al. 2000). The rationale for this decision was to keep conditions identical to our previous study of roughness scaling (Table 1, 1.8–8.8 mm). Dépeault et al. (2009), however, showed that roughness per se is not a continuum across this range of dot spacings (≤3–3.1 mm). There was some contact, generally intermittent, for low-dot spacings of 3.1–3.7 mm. In contrast, skin contact with the floor of the high-dot surfaces was restricted to the largest dot spacings and intermittent in all cases: ≥5.95 (n = 1) or 6.2 (n = 2) mm.

**DISCUSSION**

The present study demonstrated that subjects show a monotonic linear increase in tactile roughness as 2D raised-dot spacing is increased over 1.3 to 6.2 mm. The majority of these subjects (same session) showed an inverted U-shaped relation between subjective roughness and dot spacing when dot height was reduced from 1.8 to 0.36 mm. Thus the height of the tactile elements is a critical factor for determining both the perceived intensity of roughness (high > low) and the nature of the relation between roughness and dot spacing. More importantly, we also showed that Weber fractions for low-dot surfaces are not constant across this same range of dot spacings, showing a large increase as spacing was increased >3 mm, corresponding to roughly the peak of the inverted U-shaped curve (low dots). The results are consistent with our suggestion that roughness per se is not a continuum across this range of dot spacings (1.3–6.2 mm) for low-dot surfaces. These findings have important implications for neuronal coding of tactile roughness.

**Methodological Considerations**

Before discussing the results, we need to consider whether methodological differences between experiments 1 and 2 might have influenced the results. There were two differences: the mode of touch (passive and active touch, respectively) and the direction of the exploration (proximal-distal and medial-lateral). The rationale for experiment 1 was to keep conditions identical to our previous study of roughness scaling (Meftah et al. 2000), and so passive touch + proximal-distal exploration. After careful consideration, we opted to modify the approach in experiment 2 by using a new apparatus that allowed us to fully test each subject in eight conditions, involving eight sets of surfaces (7 pairs for each condition), within two experimental sessions (see also MATERIALS AND METHODS). We have no reason to think that either methodological difference contributed substantially to the results. Although the mode of touch is critical for perceiving simulated local shapes (Smith et al. 2009), there is a large body of evidence showing that the mode of touch, active versus passive, has no effect on tactile discrimination (reviewed in Chapman 1994). Likewise, there is no difference in texture discrimination for proximal-distal versus medial-lateral explorations (see, e.g., Lamb 1983).

**Table 3. Summary of results obtained in experiment 2: mean discrimination threshold and mean Weber fraction as function of dot spacing of standard surface and dot height.**

<table>
<thead>
<tr>
<th>Standard Dot Spacing, mm</th>
<th>1.3+</th>
<th>3.0–</th>
<th>3.0+</th>
<th>6.2–</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Discrimination threshold, mm</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>0.05 (0.01)</td>
<td>0.15 (0.02)</td>
<td>0.37 (0.07)</td>
<td>0.51 (0.08)</td>
</tr>
<tr>
<td>High</td>
<td>0.07 (0.01)</td>
<td>0.14 (0.01)</td>
<td>0.25 (0.02)</td>
<td>0.25 (0.03)</td>
</tr>
<tr>
<td><strong>Weber fraction</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>0.041 (0.006)</td>
<td>0.051 (0.006)</td>
<td>0.123 (0.024)</td>
<td>0.082 (0.012)</td>
</tr>
<tr>
<td>High</td>
<td>0.055 (0.005)</td>
<td>0.047 (0.005)</td>
<td>0.082 (0.007)</td>
<td>0.041 (0.004)</td>
</tr>
</tbody>
</table>

Values are results obtained in experiment 2: mean (SE) discrimination threshold and mean (SE) Weber fraction (ΔS/S) as a function of the dot spacing of the standard surface (S) and dot height (n = 10 subjects).

either 3+ or 6.2– series as most difficult; high, 7/10 rated 3+ series as most difficult). There was no difference in unpleasantness ratings when comparing the low and high dots (P = 0.074), with both sets of surfaces being rated as moderately unpleasant (median 4.0 for low; 5.0 for high).

Skin contact with the smooth floor. The digit of three subjects contacted the floor for all low-dot surfaces scanned using active touch except those with the smallest dot spacings (≤3–3.1 mm). There was some contact, generally intermittent, for low-dot spacings of 3.1–3.7 mm. In contrast, skin contact with the floor of the high-dot surfaces was restricted to the largest dot spacings and intermittent in all cases: ≥5.95 (n = 1) or 6.2 (n = 2) mm.

**What Is Tactile Roughness?**

Roughness-smoothness is an important perceptual dimension of tactile surface texture along with hardness-softness and surface elasticity (stickiness-slipperiness) (Hollins et al. 1993; Yoshioka et al. 2007). As pointed out in the introduction, roughness is a function of many factors. The perceived roughness of abrasive papers, for example, increases with an increase in average particle size (decreased grit value). When particle size is increased, however, the spacing between adjacent particles also increases (Stevens and Harris 1962). In this study, we independently manipulated two components of roughness: dot height (keeping dot diameter constant) and dot spacing (distance between raised dots). In these experiments, subjects were asked to use their own definition of roughness for the scaling and discrimination studies. Although the personal definitions of roughness varied between subjects, the results for the high-dot surfaces were very consistent across subjects. The results for the low-dot surfaces were clearly different from the high-dot surfaces, and there was also more variability across subjects. This is considered further below.

**Magnitude Estimates of Roughness**

The results with the high-dot surfaces demonstrated that roughness increases linearly when tetragonal dot spacing is increased, extending our earlier results with a 1D change in dot spacing to a 2D change in spacing (Meftah et al. 2000). The range of dot spacings along the sides of the tetragons (1.3–6.2 mm) was nominally less than that used in our earlier study (1.5–8.5 mm). Dépeault et al. (2009), however, showed that the critical measure is dot spacing in the direction of the scan, and this was similar in both studies (Table 1, 1.8–8.8 mm). Consistent with Blake et al. (1997), we found that roughness estimates were higher for high compared with low dots. Their results were, however, restricted to a single dot spacing (3.5 mm, corre-
difference according to dot height. For the high dots, subjects could discriminate changes in dot spacing of 4.1–5.5% over most of the range. Comparable performance measures were obtained for the low-dot surfaces (4.1–5.1%), but only when testing was restricted to the ascending limb of the inverted U-shaped curve. For testing on the descending limb, subjects required proportionally larger changes in low-dot spacing, 8.2–12.3%, in order to discriminate a change in dot spacing. An increase was also observed for the high-dot surfaces, but this was restricted to one series, 3+. The Weber fractions (% difference discriminated) obtained from the series located on the ascending limb of the inverted U-shaped curve are comparable to those reported in previous studies (2–5%) using either rectangular arrays of raised dots or gratings (Lamb 1983; Morley et al. 1983), i.e., in studies where dot spacing was changed in 1D (corresponding to the direction of the scan) and not 2D as here. The similarity of the results (1D vs. 2D) is consistent with our previous suggestion that the key factor for tactile roughness is dot spacing in the direction of the scan (Dépeault et al. 2009). Some caution is needed, however, since there was one other difference in the experimental design. In this study, subjects were constrained to a single scan over the standard and modified surfaces; in contrast, the earlier studies allowed unlimited exploration. It remains possible that performance with these 2D changes in dot spacing might have been better (lower Weber fractions) if unrestricted exploration had been allowed (Sinclair and Burton 1991b).

For dot spacings located on the descending limb of the U-shaped curve (3+ and 6.2–series), dot height was a significant factor. Thresholds were significantly higher for low-dot surfaces (vs. high dot). The Weber fractions (low-dot surfaces) were significantly increased relative to the ascending limb values, consistent with our main hypothesis. It is generally accepted that Weber fractions are relatively constant through the midrange of a sensory continuum. Nonlinearities can occur, but these are generally seen at the extremes of the continuum (see, e.g., Güçlü 2007; Mallery et al. 2010). The results from the low-dot series suggest that the range of dot spacings studied, 1.3–6.2 mm, does not represent a single continuum of roughness. We believe that subjects rated roughness magnitude on the ascending limb. Consistent with this, the results were closely similar for both high- and low-dot surfaces, and this for both experiments. The higher Weber fractions on the descending limb of the curve (low dots), along with the adoption of a rating scale that varied inversely with dot spacing, suggests that subjects rated some other sensory quality here. We do not know what they were rating, but the most obvious candidate is dot density. The latter declined as dot spacing increased, and the subjects’ estimates also declined. Given that the finger was in contact with the smooth floor over this range of spacings, the subjects may well have switched to evaluating dot density as this became the salient stimulus superimposed on the smooth floor.

Unexpectedly, however, we also found that the Weber fractions from one of the high-dot standards (3+) were also high (mean 8.2%). Unpublished data (D. Cohen, E.-M. Meftah, and C. E. Chapman) suggest that the spacings over which threshold is increased is quite narrow, since Weber fractions measured with standards of 1.25, and 3.5 mm (raised dots: 1.4-mm height, 1D increases in spacing) are invariant. Inter-

Roughness Discrimination

As expected, discrimination threshold increased as the dot spacing of the standard surface increased but there was a clear
estingly, the dot spacing at which the Weber fractions were increased corresponds to the dot spacing at which the slope of the magnitude estimation curve (high dots) showed a modest decline. This suggests that there was a degree of ambiguity as to the perceived roughness of surfaces specifically located at the peak of the inverted U-shaped curve. Consistent with this interpretation, most subjects rated the 3+ (high dots) series as most difficult. For the low dots, difficulty ratings were highest for the 3+ and/or the 6.2− dot series, i.e., those with higher Weber fractions.

Implications for Neuronal Coding of Tactile Roughness

For the low-dot surfaces, our results suggest that tactile roughness is not a continuum across the range of tested dot spacings, 1.3–6.2 mm. The importance of this observation rests in the fact that, as summarized in the introduction, Johnson and colleagues (Connor et al. 1990) rejected a simple intensive code for tactile roughness (mean discharge rate) because the mean discharge rate of the primary mechanoreceptive afferents, and in particular SAI afferents, peaked at a lower dot spacing, 2.4 mm, than their psychophysical estimates of roughness magnitude, 3.2 mm. This led the authors to develop an alternate neuronal code, the spatial variation code, whereby the perception of roughness is based upon local spatial variations in the firing rates of SAI afferents. This is a robust code that accounts for the invariance of roughness estimates across different scanning speeds (DiCarlo and Johnson 1999; Lederman 1974, 1983; Meftah et al. 2000). Although there is now an impressive body of evidence in support of the spatial variation code (Blake et al. 1997; Connor et al. 1990; Connor and Johnson 1992; DiCarlo and Johnson, 1999, 2000; Yoshioka et al. 2001), the same group also provided evidence that an intensive code (SAI afferents) could explain equally well the perception of roughness of finer-textured surfaces (Yoshioka et al. 2001).

We believe that the present results show convincingly that the original rejection of an intensive code for the coding of roughness was unjustified. First, our magnitude estimation results indicated that the peak of the inverted U-shaped curve when calculated for individual subjects is lower than the value read off from the pooled psychometric function (Fig. 4C), 2.5 and 3.4 mm, respectively. Interestingly, the former value is close to the reported peak of mean discharge rates for the main types of mechanoreceptive afferents (SAI, RA, and PC) that are activated by these textured surfaces, 2.4 mm (Connor et al. 1990). Second, subjects were able to discriminate small differences in dot spacing near the peak of the inverted U-shaped curve, corresponding to a range where roughness estimates (see Figs. 3 and 4) did not distinguish between the surfaces (plateau in the roughness estimates). Third, the results of the roughness discrimination experiments suggested that subjects were not evaluating the same sensory quality for low-dot surfaces on the ascending and descending limbs of the inverted U-shaped curve. Together, our results suggest that it was not valid to use the psychophysical results, specifically the inverted U-shaped curve, to test models for neuronal encoding of tactile roughness.

We suggest that the monotonic increase in magnitude estimates with dot spacing in the case of the high-dot condition argues in favor of the idea of an intensive code: as dot spacing increases, the effective stimulus intensity also increases because the skin has more time to resume its usual convex contour when traveling from one contact to the next, and so offers a greater surface area for stimulation. Consistent with this, neuronal discharge rates in S1 also increase over the same range (high-dot surfaces) (Dépeault et al. 2007; Jiang et al. 1997). Moreover, many S1 cutaneous neurons signal roughness independent of scanning speed (Sinclair and Burton 1991a; Tremblay et al. 1996), consistent with roughness invariance with speed (see above). Our suggestion of intensive coding is consistent with earlier suggestions that the perceived roughness of scanned periodic gratings, an ability that is critically dependent on the spacing between adjacent ridges (Lederman 1983), is explained by the mean discharge rate of the mechanoreceptive afferents, including SAI, RA, and PC afferents (Goodwin et al. 1989; Sathian et al. 1989). Cascio and Sathian (2001) further developed this hypothesis, favoring a rate (intensive) code particularly for SAI afferents to explain increased roughness of periodic gratings as groove width was systematically increased over a limited range (0.75–1.97 mm).

While we demonstrate that a rate code can explain tactile roughness across the range of conditions tested here, it remains that we cannot be certain what quality the subjects were scaling on the low-dot surfaces with larger dot spacings. In this regard, roughness may contain multiple dimensions. For example, grating roughness estimates decline modestly when ridge width is increased while groove width is held constant (Lederman 1983) and ratings covary with speed in a manner consistent with the use of a temporal code based on temporal frequency (speed/SP) (Cascio and Sathian 2001). Indeed, the latter authors suggested that multiple codes may contribute to tactile roughness with the potential advantage of removing potential confounds introduced by nonspecific factors, like contact force. Our suggestion that an intensive code contributes to tactile roughness, possibly supplemented with a temporal code, does not discount the potential importance of the spatial variation code for other related tactile abilities, for example, encoding of 2D spatial form as required, e.g., for Braille reading, which is dependent on a very precise and fine-grained representation of spatial details.

While the use of multiple coding mechanisms for tactile roughness (intensive, temporal, and spatial) may seem overly complex, it should be recognized, as pointed out by Sathian et al. (1989), that texture is a complex stimulus and different cues based on different codes may be used by different subjects to evaluate roughness in different tasks. For example, roughness constancy for a wide range of materials (corduroy, rubber, etc.) may be maintained across different speeds using concomitant proprioceptive signals when the exploration involves limb movement (Yoshioka et al. 2011). In the present study, the similarity in the psychometric curves across subjects, at least for any one condition (high or low dots), suggests that the subjects all employed the same cues for evaluating roughness. This result was, moreover, independent of the variable operating definitions of roughness reported by these same subjects. Thus our experimental design, intermixing high and low dots for experiment 1 and testing series of high and low dots in the same session for experiment 2, was successful in minimizing changes in the cues used.
Implications for Neuroprosthetics

In recent years, there has been considerable interest in developing neuroprosthetic devices to replace lost motor or sensory function (Green et al. 2011a, 2011b). Most of the methods currently employed to provide substitute control and/or feedback signals are, in fact, based on the use of electrical stimulation either through surface electrodes or implanted devices (including at the cortical level). The basic assumption, at least on the sensory side, is that the brain can interpret signals provided through electrical stimulation and make perceptual judgments based on variations in signal strength and frequency. Indeed, this forms the basis for cochlear implants, which can replace lost auditory function. For the somatosensory system, this approach is firmly based on results from both psychophysical experiments in humans (e.g., Chapman et al. 1987) and monkeys (Romo et al. 1998). Thus subjects (human or monkeys) can reliably discriminate small differences in either the amplitude or frequency of electrical stimuli. Humans can also easily scale a range of different intensities of innocuous electrical stimuli applied to the skin. Given these abilities, the idea that tactile roughness is encoded by a simple rate code is consistent with eventually using simple electrical stimulation to mimic this sensory quality and so provide, for example, realistic sensory feedback during object manipulation with a prosthetic hand.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS


REFERENCES


