Tactile Speed Scaling: Contributions of Time and Space

Alexandra Dépeault,1,* El-Mehdi Meftah,1,* and C. Elaine Chapman1,2
1Département de Physiologie, Groupe de Recherche sur le Système Nerveux Central and 2École de Réadaptation, Faculté de Médecine, Université de Montréal, Montréal, Quebec, Canada

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Dépeault A, Meftah E-M, Chapman CE. Tactile speed scaling: contributions of time and space. J Neurophysiol 99: 1422–1434, 2008. First published January 16, 2008; doi:10.1152/jn.01209.2007. A major challenge for the brain is to extract precise information about the attributes of tactile stimuli from signals that co-vary with multiple parameters, e.g., speed and texture in the case of scanning movements. We determined the ability of humans to estimate the tangential speed of surfaces moved under the stationary fingertip and the extent to which the physical characteristics of the surfaces modify speed perception. Scanning speed ranged from 33 to 110 mm/s (duration of motion constant). Subjects could scale tactile scanning speed, but surface structure was essential because the subjects were poor at scaling the speed of a moving smooth surface. For textured surfaces, subjective magnitude estimates increased linearly across the range of speeds tested. The spatial characteristics of the surfaces influenced speed perception, with the roughest surface (8 mm spatial period, SP) being perceived as moving 15% slower than the smoother, textured surfaces (2–3 mm SP). Neither dot disposition (periodic, non-periodic) nor dot density contributed to the results, suggesting that the critical factor was dot spacing in the direction of the scan. A single monotonic relation between subjective speed and temporal frequency (speed/SP) was obtained when the ratings were normalized for SP. This provides clear predictions for identifying those cortical neurons that play a critical role in tactile motion perception and the underlying neuronal code. Finally, the results were consistent with observations in the visual system (decreased subjective speed with a decrease in spatial frequency, 1/SP), suggesting that stimulus motion is processed similarly in both sensory systems.

INTRODUCTION

Many years ago, Katz (1925) observed that movement between the skin and the surround is as important to touch as light is to vision. Sensory impressions are more vivid and precise with movement so that, for example, tactile roughness discrimination thresholds are approximately halved with movement (dynamic touch) as compared to without (static touch) (Morley et al. 1983). While we have considerable knowledge about the ability to perceive various qualities of tactile stimuli, including for example light touch, surface roughness, and micro-geometric or local shape (what can be sensed on the fingertip), we know much less about the appreciation of tactile motion itself. This is an important lacuna because tactile motion perception is critically important in everyday life with a practical example being the ability to hold and manipulate objects. This is in turn dependent on sensory feedback from tactile mechanoreceptors to detect and minimize slip (Johansson 1998).

At a simple level, one would expect that the rapidly adapting mechanoreceptive afferents that play a key role in discriminative touch must be particularly specialized to detect tactile motion. As reviewed by Johnson (2001), these include the Pacinian (PC), rapidly adapting, glabrous skin (RA), and various hair follicle afferents (hairy skin). A complementary role cannot, however, be discounted for the slowly adapting afferents (SAI and II). Even though they are specialized to signal static contact, they also discharge more intensely to moving stimuli, and their signal contains information about tactile motion (Edin et al. 1995). Thus tactile motion cannot be presumed to depend on activity in only one or several types of peripheral receptors.

The elegant studies of Mountcastle and colleagues provided the first systematic studies of the neuronal and perceptual correlates underlying motion perception, using punctate vibration as the stimulus (LaMotte and Mountcastle 1975; Mountcastle et al. 1972; Talbot et al. 1968). Their experiments showed that RA afferents are particularly sensitive to lower frequencies of vibration (flutter), whereas PC afferents are exquisitely sensitive to higher frequencies. Vibration does not, however, reflect more than a subclass of the types of tactile motion encountered in daily life. More recent studies have characterized receptor sensitivity to more natural stimuli, including tangential movement (surfaces or local shapes scanned over a skin area) and transverse movement (brush strokes over a fixed length of skin). Such studies have shown that cutaneous mechanoreceptive afferents innervating both hairy skin and glabrous skin, including SAI, SAI, RA, and PC afferents, are sensitive to tactile motion (Darian-Smith et al. 1980; Edin et al. 1995; Essick and Edin 1995; Goodwin and Morley 1987; Greenspan 1992; LaMotte and Srinivasan 1987a,b). Yet the afferent signals elicited by tangential movement, specifically moving surfaces, are complex, reflecting both surface structure (the roughness and/or shape of the stimuli scanned over the skin) and tangential speed. This leads to the general question as to how the brain extracts precise information about the attributes of tactile stimuli from signals that co-vary with multiple parameters.

We know that human tactile roughness scaling (magnitude estimates) is relatively independent of scanning speed (Lederer 1983; Meftah et al. 2000), indicating that information about surface roughness is extracted from these complex signals—possibly using a spatial code (Connor and Johnson 1992; Connor et al. 1990). As regards tactile motion scaling, in contrast, we have little information as to whether tactile motion can be extracted from signals that co-vary with both texture and speed. There have been a few reports showing that humans can scale the subjective speed of either mechanical pulses on
the skin (Franzén and Lindblom 1976) or brush displacement over a fixed length of skin (Essick et al. 1988, 1996). But interpretation of these results was confounded by the fact that stimulus duration covaried with stimulus speed: faster stimuli had a shorter duration. Subjects could, therefore, have based their ratings on either parameter. This is an important gap in our knowledge because such information is critical for identifying the cortical neuronal mechanisms underlying tactile motion perception.

The present study had two aims. First, we determined the capacity of human subjects to scale the tangential speed of surfaces moved under the fingertip (tactile speed), using a paradigm in which stimulus duration was held constant. This was achieved by varying the length of surface presented as a function of speed (faster speeds, longer segment of surface presented). We chose to investigate tactile speeds within the range of speeds often used during tactile exploration, 33–110 mm/s (Smith et al. 2002a), corresponding to speeds over which texture estimates are invariant with changes in scanning speed.

The second aim of the study was to identify the extent to which the physical parameters of the stimuli (textured and smooth surfaces) modify the perception of tactile motion. As pointed out in the preceding text, tactile mechanoreceptors in the glabrous skin do not signal speed independently of surface texture. An invariant representation of tactile texture is extracted from these signals, but we do not know if the brain is also able to extract an invariant representation of tactile motion. To address this issue, we were motivated by studies in the visual system that have shown that subjective visual speed estimates are decreased when the overall visual stimulus is made sparser, either by decreasing the spatial frequency, 1/SP (spatial period) [periodic gratings] or the number of items in the display [dot density] (Campbell and Maffei 1981; Diener et al. 1976; Watamaniuk et al. 1993; cf. Smith and Edgar 1990). We therefore systematically varied the physical parameters of our stimuli (SP and dot density) to determine how these factors influence tactile motion perception.

In this study, subjects scaled the speed of textured (raised dot surfaces) and smooth surfaces. Surface texture was varied by changing the spacing between dots, the dot density, and dot disposition (periodic or nonperiodic). The results indicated that subjects can indeed scale the speed of constant duration tactile stimuli, but the spatial characteristics of the surfaces modified speed perception, and this in a similar manner to that seen in the visual system. A preliminary report of these data has been presented elsewhere (Meftah et al. 2005).

**METHODS**

**Subjects**

Twenty-six naïve paid subjects (17 women and 9 men, all but 2 right-handed for writing, 20–35 yr old), volunteered to participate in the study. The institutional ethics committee approved the experimental protocol, and subjects gave their informed consent before participating. Each subject participated in one session of 2 h. The task was to estimate the speed of surfaces scanned under their right middle fingertip (D3).

**Surfaces**

Ten strips, 2 × 40 cm each, were prepared on flexible letterpress (Jiang et al. 1997): one was smooth (not shown) and the others were textured (Fig. 1, A–C), with embossed, cylindrical raised dots (0.8 mm diameter on the top, 1 mm height, Fig. 1D). The physical characteristics of the nine textured surfaces are summarized in Table 1. As shown in Fig. 1A, one series of textured surfaces (experiment 1, periodic surfaces) consisted of rectangular arrays of dots with identical transverse SPs (2 mm, distance center-to-center between adjacent dots in each row) and three different longitudinal SPs (2, 3, or 8 mm between rows), corresponding to the direction of the scan (Fig. 2A, see arrows). Subjective roughness shows a monotonic increase over this range (Meftah et al. 2000) [Note: this contrasts with the U-shaped relation reported by Connor et al. (1990) when dot spacing is incremented in 2 dimensions, as opposed to the unidimensional change employed here]. The second series (experiment 2, nonperiodic surfaces; Fig. 1B) had the same number of raised dots as the first series, but they were distributed quasi-randomly, with densities of 6.3, 16.7, and 25 dots/cm². The latter surfaces were designed by taking the periodic dot matrices and “jittering” the position of the dots while maintaining, on average, the same spacing between adjacent dots (Lederman et al. 1986). The average SP in all directions was 2.0 mm (25 dots/cm²), 2.5 mm (16.7 dots/cm²), and 4.9 mm (6.3 dots/cm²). Finally, the third series (experiment 3, nonperiodic; Fig. 1C) also consisted of dots distributed quasi-randomly, but with the same average SP in the direction of the scan as in the first series, i.e., 2, 3, and 8 mm. These were prepared by pruning the series from experiment 2 (dots removed) so that the mean dot spacing in the scanning direction was identical to that of the periodic surfaces. Thus this series preserved the same mean spacing in the direction of the scan, but dot density was lower (Table 1). For all three series of surfaces, roughness estimates increase

![FIG. 1. Characteristics of raised dot surfaces. A: periodic surfaces used in experiment 1: spatial period (SP) was constant across the rows (2 mm) and varied between the rows (direction of scan), 2, 3, or 8 mm SP. B: surfaces used in experiment 2 had the same number of raised dots as for experiment 1, but dot disposition was random. C: these nonperiodic surfaces (experiment 3) had the same average SP in the direction of the scan as the periodic surfaces (A), but dot density was lower especially for the roughest surface (see Table 1). D: dot dimensions and SP.](http://jn.physiology.org/)

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TABLE 1. Spatial characteristics of the textured surfaces

<table>
<thead>
<tr>
<th>Surface</th>
<th>Dot Density, dots/cm²</th>
<th>Dot Spacing*, mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Expt 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Periodic</td>
<td>25</td>
<td>2</td>
</tr>
<tr>
<td>Periodic</td>
<td>16.7</td>
<td>3</td>
</tr>
<tr>
<td>Periodic</td>
<td>6.3</td>
<td>8</td>
</tr>
<tr>
<td>Expt 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nonperiodic</td>
<td>25</td>
<td>2</td>
</tr>
<tr>
<td>Nonperiodic</td>
<td>16.7</td>
<td>2.5</td>
</tr>
<tr>
<td>Nonperiodic</td>
<td>6.3</td>
<td>4.9</td>
</tr>
<tr>
<td>Expt 3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nonperiodic</td>
<td>25</td>
<td>2</td>
</tr>
<tr>
<td>Nonperiodic</td>
<td>14</td>
<td>3</td>
</tr>
<tr>
<td>Nonperiodic</td>
<td>2.2</td>
<td>8</td>
</tr>
</tbody>
</table>

*Mean spatial period in the direction of the scan.

monotonically across the range of dot spacings (Dépeault et al. 2006; Meftah et al. 2000).

Tactile stimulator

The strips were affixed to a tactile stimulator (Fig. 2B, 4 strips tested in experiments 1 and 2; 3 strips in experiment 3). This consisted of a cylindrical drum (40 cm circumference, 12 cm length) mounted on a drive shaft that was rotated by means of a DC motor through a 1:100.1 reduction gear (Zompa and Chapman 1995). The surfaces were accessible for palpation by the pad of the middle phalanx of the middle finger through two rectangular apertures (6.5 × 2.5 cm each, Fig. 2B). The direction of the scan was proximal to distal relative to D3 (Fig. 2A, arrows).

Experimental setup

The subject was seated (Fig. 2B) with the tactile stimulator at waist level. Ambient light was reduced to avoid any visual cue concerning the surface and its speed. White noise was delivered through earphones to eliminate any auditory cue from the rotation of the drum. Both arms were comfortably supported on two horizontal manipulanda. The right one was positioned so that, during the inter trial interval, the distal phalanx of D3 rested just above the surface to be scanned. A yellow light (2 × 2 cm) was placed at eye level and 1.2 m distance in front of the subject. This cued the subjects to lower their finger onto the moving surface (see following text).

Perceptual task

Before the experiment, the subjects were informed that surfaces would be displaced under the distal pad of D3 at different speeds. They were asked to estimate the speed of the surface motion. The subjects were free to choose a comfortable contact force while touching the surface in motion and were requested to use the same force throughout the experiment. No force feedback was provided during the trials apart from the occasional reminder to use a relatively constant force. They were not informed about the number of speeds or surfaces used. Six practice trials were first performed to familiarize the subjects with the various events in the trial (see following text). The subjects were then provided with sample stimuli so that they could establish their own scale: one surface (3 mm SP or the corresponding non periodic surface) was presented at three different speeds, the slowest, the fastest, and then one intermediate. The subjects were told that these were three illustrative examples, and were asked to estimate the perceived speed of the last trial (intermediate) using any representative whole number. Thereafter data collection began.

Experimental design

For experiments 1 and 2, each session consisted of two blocks of trials (textured, smooth); experiment 3 had only a single block of trials (textured). In the first block, the three textured surfaces (periodic or non periodic) were presented at eight different nominal speeds: 33, 43, 53, 65, 76, 86, 98, and 110 mm/s. Speed increments averaged 11 mm/s (range, 10–12 mm/s). The actual speed varied slightly from the nominal speed (<1.2%). Figure 2C shows the superimposed force, displacement, and speed profiles from one subject. Each surface-speed combination was repeated six times for a total of 144 trials. A preestablished pseudo-random list of trials that interleaved the three surfaces and the eight speeds was used. In the second block of trials (experiments 1 and 2), only the smooth surface was presented (8 speeds * 6 repetitions, total of 48 trials).

During the intertrial interval, the drum was rotated to the start position (Fig. 2A, start). The subject was then asked to position D3 over one of the surfaces (position 1, smooth; 2–4, textured). After the subjects signaled their readiness, the trial was initiated by the experimenter. The temporal sequence of events in the trials is shown in Fig. 2C. Drum rotation began 0.3 s after the start of data acquisition; this was followed by the light onset (0.8 s). The light signaled the subjects to quickly lower their finger onto the surface that was already in motion and estimate its speed. The light was extinguished 2.5 s later; this was the cue for subjects to raise their finger, ending their contact with the surface. At the same time, the signal for drum rotation ended. Due to inertia, drum rotation ended 200–600 ms later depending on the speed, generally after contact with the surface ended. Thereafter the subjects provided their numerical estimate of the perceived speed. At the end of the session, the subjects were debriefed and questions posed as to the strategy for rating speed as well as the number of speeds and surfaces presented.

One critical element in the experimental design was that the duration of all presentations was identical (3 s), thus ensuring that the subjects had no temporal cue, specifically stimulus duration, on which to base their subjective magnitude estimate of speed. This was achieved by increasing the length of surface presented for higher speeds (see Fig. 2, A and C, a–h) from 99 mm (33 mm/s, a) to 330 mm (110 mm/s, h). Higher speeds could not be tested as this would have required more than one revolution of the drum, and so the subjects would have felt the gap where the two ends of the 400-mm-long strip met.

Data acquisition and analysis

The task and data acquisition were under computer control. Digital events (times of onset and offset of drum rotation, light signal), and vertical contact force (200-Hz digitization rate) were recorded for each trial. The subjective magnitude estimate was entered by the experimenter and stored with the trial. If the subject felt uncomfortable or was unable to estimate speed after the trial, the trial was rejected and repeated later. Contact force was visually inspected on-line, and the trial was rejected and later repeated if the contact force during the scan varied by more than ±0.2 N.

To pool the data, magnitude estimates were normalized off-line by dividing each subject’s responses (raised dot and smooth surfaces) by the arithmetic mean value of all the estimates given for the raised dot surfaces during the same session. The grand mean (textured and smooth surfaces) was not used for normalization because one experiment, 3, did not include a block of smooth trials. Thus the results of experiments 1 and 2 would have been skewed relative to the final experiment, making direct comparisons impossible. The normalized values were used for the subsequent statistical analyses.

For each trial, the speed of surface motion was calculated over the time that speed was constant (from 300 ms after motor onset to motor offset, see Fig. 2C). These data were also used to calculate the temporal frequency of the stimulus (speed/mean SP in the direction of the scan). For each trial, we measured contact force during the
scanning period over a 500-ms period of constant force (shaded rectangle, Fig. 2C).

The statistical analyses employed parametric tests because the data were normally distributed (Shapiro-Wilk normality test) and showed similar variances. For the magnitude estimates, an ANOVA (Systat version 11) was applied to the data from each subject (scanning speed, surface included as factors). For the pooled data, a repeated-measures model was used (estimates/scanning speed, surface). To describe the nature of the relationship between subjective magnitude estimates and the objective (tactile) speed of the surfaces, linear regression analyses were applied to the data obtained from each subject. The level of significance was fixed at $P < 0.05$.

**RESULTS**

All subjects were able to scale the speed of the textured surfaces and showed a monotonic relationship between perceived speed and objective speed (linear regressions, $P < 0.0005$).

**Periodic surfaces (experiment 1)**

The individual psychophysical curves, mean normalized magnitude estimates as a function of scanning speed, are...
plotted in Fig. 3A. Inspection of the individual curves indicates that the results were similar for the three periodic surfaces with SPs of 2, 3, and 8 mm. The data of each subject were subjected to an ANOVA: speed was a significant factor for all subjects and SP for 6/8 subjects. No subject showed a significant interaction (speed × SP). The pooled results, plotted in Fig. 4A, indicate that subjective magnitude estimates of speed were lower for the roughest surface (8 mm SP) as compared with the smoother surfaces. A repeated-measures ANOVA applied to the pooled data confirmed that subjective magnitude estimates varied as a function of SP as well as scanning speed (Table 2) with no interaction between the two factors. The nature of the relationship between subjective speed and objective speed was examined using linear regression analyses applied to the data from each subject. The mean slope \((m)\), intercept \((b)\), and coefficient of determination \((r^2)\) are summarized in Table 3. For all three surfaces, the \(r^2\) values were high (0.551–0.703). Although slopes were closely similar across the three surfaces (0.013–0.014), a repeated-measures ANOVA showed that the intercepts varied across the three SPs \([F(2,14) = 4.886, P = 0.025]\), being lower for the 8 mm SP surface (mean of −0.05) as compared with the other two surfaces (means of 0.15 and 0.12, respectively). The latter impression was confirmed with post hoc contrasts \((P = 0.036\) for both). Overall subjective

![Graphs](https://journals.physiology.org/doi/fig/10.1152/jn.00663.2007)
magnitude estimates were significantly lower, mean 17.1%, for the surface with the largest SP. A multiple regression analysis indicated that the major part of the variance of the subjective magnitude estimates was explained by scanning speed (75%) as compared with only 18.5% for SP.

**Nonperiodic surfaces (experiments 2 and 3)**

The surfaces used in experiment 2 preserved the same number of dots as in experiment 1, but their disposition was different, quasi-random versus periodic. The individual results for 10 subjects (different from those used in experiment 1) are plotted in Fig. 3B. Once again, the results were similar for all three nonperiodic surfaces with densities of 25, 16.7, and 6.3 dots/cm². Speed was a significant factor in all cases, but dot density was only significant in 3 of 10 subjects (ANOVA). None of the subjects showed an interaction between speed and dot density. The pooled results (Fig. 4B) showed there was considerable overlap across the three curves. The repeated-measures ANOVA (Table 2) was significant for speed but not dot density. Consistent with these observations, the results of the linear regression analyses indicated that neither the intercepts \( F(2,18) = 1.34, P = 0.29 \) nor the slopes \( F = 2.33, P = 0.13 \) showed a change across the three surfaces. Finally, a multiple regression indicated that dot density contributed only 1.2% to the variance in subjective magnitude estimates of speed as compared with 75% for tactile motion itself. Thus subjective speed did not systematically vary across the three nonperiodic surfaces.

The results of experiment 2 suggested that periodicity, and not the number of raised dots, may have contributed to the underestimation of speed for the 8 mm SP surface in experiment 1. Another explanation for the difference was, however, that dot spacing, and not periodicity, was responsible for the underestimation of speed for the 8 mm SP periodic surface. Dot spacing (SP) in the direction of the scan was different for each series: 2–8 mm (periodic) versus 2–4.9 mm (nonperiodic). This factor was controlled in experiment 3 (nonperiodic surfaces, mean dot spacings of 2, 3, and 8 mm). The individual psychophysical curves are summarized in Fig. 3C, and the pooled data are shown in Fig. 4C. The results were now very similar to those obtained in experiment 1 with subjective magnitude estimates of speed being lower for the roughest surface, 8 mm mean SP, as compared with the two smoother surfaces (2 and 3 mm mean SP). As in experiment 1, the individual ANOVAs showed that speed was a significant factor in all cases, and mean spacing was significant in a majority of subjects (5/8). Both factors were significant in the pooled analysis (Table 2). No significant interactions were found either in the individual or pooled analyses. As for experiment 1, the intercepts of the linear regressions varied across the three surfaces \( F(2,14) = 5.853, P = 0.014 \), and slope showed no change (Table 3). The intercepts were lower for the surface with an average 8 mm SP (−0.26) compared with the other two surfaces (means of −0.07 and −0.15); the difference was, however, only significant between the two extremes (post hoc contrast, 8 vs. 2 mm, \( P = 0.012 \)). As in experiment 1, the major part of the variance of the subjective magnitude estimates was

![FIG. 4. A–C: pooled data from the 3 experiments. Mean normalized magnitude estimates (±SE across all estimates) are plotted as a function of scanning speed, and the spatial characteristics of the scanned surface.](image)

TABLE 2. Results of repeated-measures ANOVAs for experiments 1–3

<table>
<thead>
<tr>
<th></th>
<th>Speed</th>
<th>SP or Density</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( F ) df*</td>
<td>( P )</td>
<td>( F ) df</td>
</tr>
<tr>
<td>Experiment 1</td>
<td>89.16  7, 49</td>
<td>&lt;0.0005</td>
<td>8.34  2, 14</td>
</tr>
<tr>
<td>Experiment 2</td>
<td>58.42  7, 63</td>
<td>&lt;0.0005</td>
<td>1.53  2, 18</td>
</tr>
<tr>
<td>Experiment 3</td>
<td>173.89  7, 49</td>
<td>&lt;0.0005</td>
<td>6.33  2, 14</td>
</tr>
<tr>
<td>Smooth/Expt 1</td>
<td>10.55  7, 49</td>
<td>&lt;0.0005</td>
<td></td>
</tr>
<tr>
<td>Smooth/Expt 2</td>
<td>12.55  7, 63</td>
<td>&lt;0.0005</td>
<td></td>
</tr>
</tbody>
</table>

\( n = 8, 10, \) and 8 for experiments 1–3, respectively. *Degrees of freedom.
TABLE 3. Mean values of the parameters describing the linear regressions, mean normalized magnitude estimates versus speed, for each surface in each of the 3 experiments

<table>
<thead>
<tr>
<th>Dot Spacing*</th>
<th>Slope</th>
<th>Intercept</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Expt 1, Periodic (n = 8)</strong></td>
<td>Smooth</td>
<td>0.005 ± 0.001</td>
<td>0.353 ± 0.108</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.013 ± 0.001</td>
<td>0.149 ± 0.096</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.014 ± 0.002</td>
<td>0.115 ± 0.099</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>0.013 ± 0.001</td>
<td>-0.049 ± 0.089</td>
</tr>
<tr>
<td><strong>Expt 2, Nonperiodic (n = 10)</strong></td>
<td>Smooth</td>
<td>0.005 ± 0.001</td>
<td>0.340 ± 0.095</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.013 ± 0.002</td>
<td>0.071 ± 0.120</td>
</tr>
<tr>
<td></td>
<td>2.5</td>
<td>0.015 ± 0.002</td>
<td>0.012 ± 0.131</td>
</tr>
<tr>
<td></td>
<td>4.9</td>
<td>0.014 ± 0.001</td>
<td>-0.031 ± 0.105</td>
</tr>
<tr>
<td><strong>Expt 3, Nonperiodic (n = 8)</strong></td>
<td>Smooth</td>
<td>0.016 ± 0.001</td>
<td>-0.071 ± 0.061</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.017 ± 0.001</td>
<td>-0.147 ± 0.087</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>0.016 ± 0.001</td>
<td>-0.260 ± 0.072</td>
</tr>
</tbody>
</table>

Values are means ± SE. *Mean spatial period in the direction of the scan. r², coefficient of determination.

explained by tactile speed (81.8%) as compared with only 14.2% for SP. Overall, subjective speed was, as found for the periodic surfaces, systematically lower, 14.6%, for the surface with the largest average SP, 8 mm. This finding suggests that dot spacing, and not periodicity, was the critical factor for the speed underestimates with the roughest surface.

**Smooth surface**

In experiments 1 and 2, subjects also estimated the speed of a smooth surface displaced under the finger tip. To compare directly across the two sets of results obtained from the same subjects in the same experimental session (smooth vs. textured), the smooth estimates were normalized using the corresponding mean from the textured surfaces. The individual and pooled (thick line) psychophysical curves are plotted in Fig. 5. The results were much more variable across subjects than for the main experiments. Moreover, some subjects initially found it difficult to even perceive the movement of the smooth surface. As there was no difference between the results obtained in the two experiments (P = 0.48, 2-way ANOVA), the results were pooled. Overall subjective magnitude estimates of speed for the smooth surface were ~28% lower than for the corresponding raised dot surfaces (P < 0.0005). Most subjects (15/18) could, nevertheless, scale the speed of the smooth surface (linear regressions, P < 0.05). The slopes of the regressions were significantly lower than for the corresponding textured surfaces (P < 0.0005; see Table 3). This latter result was independent of the normalization procedure because slope was still significantly lower (P = 0.001) when these data were normalized relative to the mean of all ratings given during the block of trials with the smooth surface. The r² values were also lower (P < 0.0005), explaining only 28% of the variance in the subjective magnitude of speed as compared with 55–70% for the raised dot surfaces in the same subjects. Finally, although subjects may have changed their rating scale across the blocks of trials (smooth, textured), all subjects commented that the speeds used during the smooth trials were lower than in the textured trials. Together the results indicate that subjects had difficulty in scaling speed in the absence of raised dots on the surface.

**STIMULATION CONDITIONS.** For each trial, normal contact force during the exploration was calculated off-line for a period of 500 ms during the scan (shaded rectangle, Fig. 2C). Contact force was under the subject’s voluntary control and normal force varied across subjects (ANOVA, P < 0.0005). Mean force was higher for the textured surfaces (0.47 ± 0.02 N) than for the smooth surface (0.29 ± 0.02 N; paired t-test: P = 0.001). This observation likely reflects the fact that the coefficient of friction relative to the skin (tangential/normal force) is higher for these raised dot surfaces as compared with the smooth surface (Cadoret and Smith 1996; Smith and Scott 1996; Smith et al. 2002a). In general, subjects used relatively

![Fig. 5](http://jn.physiology.org/ 10.2307/journals.jn)
low contact forces, lower than those used during texture estimation with this same tactile stimulator (Meftah et al. 2000), but comparable to those used during active tactile exploration (Smith et al. 2002b). To determine whether variations in contact force contributed to the results in the main experiments (subjective magnitude estimates for the raised dot surfaces), we categorized the applied force into two categories, low or high contact force, for each speed. The results of one subject are shown in Fig. 6A. Contact force showed no change across the range of speeds tested (left), and magnitude estimates likewise did not vary with contact force (right). Similar results were obtained with the pooled data (Fig. 6, B–D). Thus variations in contact force did not contribute significantly to the results obtained with the textured surfaces.

SUBJECT COMMENTS. Most subjects (21/26) correctly recognized that each surface touched was different from the others. They estimated that about seven to nine different speeds were employed for the textured surfaces, although there were differences between subjects (range, 5–15 different speeds). For the periodic surfaces, subjects reported that the smoothest of the textured surfaces (2 mm SP) seemed faster than the other textured surfaces. For the smooth surface, the subjects judged that there were fewer speeds (4–5) than for the textured surfaces and, as mentioned in the preceding text, they also reported that the speeds were slower, consistent with the estimates given during the psychophysical testing. In addition, subjects often volunteered their estimate while the surface was moving, especially for the smooth surface.

Nature of the relationship between subjective magnitude estimates and tactile scanning speed

The main analyses were based on the assumption that the relation between subjective speed and tactile speed could best be explained by a linear regression model. This was supported by the results of the single degree of freedom polynomial contrasts performed with the repeated-measures ANOVAs (pooled data). In all three experiments, the linear relation had a higher $F$ value than did higher-order polynomial tests. Nevertheless, power functions have been used in previous studies to describe the relation between tactile speed and either the firing rates of peripheral afferents (Essick and Edin 1995; Greenspan 1992) or speed scaling (Essick et al. 1988). In all cases, the range of scanning speeds was much larger than that used here (e.g.; 5–320 mm/s for Essick and Edin; 0.4–1,000 mm/s for Greenspan). To compare the two approaches, the pooled data from each experiment/surface were fit to both linear and power functions. The $r^2$ values with the power functions were systematically higher than with the linear regression analyses, but the difference was very small (mean difference, 0.027). Moreover, the exponents of the power functions were close to 1 (1.12–1.34), i.e., close to a linear function. Together the results suggest that our data were well fit by linear functions.

To determine the extent to which temporal cues related to the surface structure, specifically the frequency with which the raised dots passed over the skin (temporal frequency = speed/mean SP in the direction of the scan), contributed to the results,

![Fig. 6. Contribution of vertical contact force to the results. A: results from 1 subject (experiment 1). Left: data from each speed were divided into low and high contact forces. Contact force during scanning was low and independent of speed, yet varied across trials (low vs. high force). Right: magnitude estimates for the same subject did not vary with contact force. B–D: pooled results from experiments 1 to 3 showing that subjective speed did not vary with contact force, low vs. high. All data shown with SE.](http://jn.physiology.org/10.1152/jn.00328.2007)
we plotted the scaling estimates for each surface and each experiment as a function of temporal frequency. Such an analysis has been used previously to argue for the importance of temporal cues to roughness appreciation (Cascio and Sathian 2001; Gamzu and Ahissar 2001; Morley and Goodwin 1987). If temporal frequency was the sole determinant of tactile motion estimates, then the subjective magnitude estimates of speed would be expected to show a monotonic increase with temporal frequency. As shown in Fig. 7, A–C, however, families of nonoverlapping curves were obtained for each experiment (green, roughest surface; purple, intermediate; red, smoothest). Estimates reflected more the actual tangential scanning speed (same speeds joined by isocontour lines, see Fig. 7A) than the temporal frequency. A fourfold increase in temporal frequency, for example from 13.8 Hz (8 mm SP at 110 mm/s) to 55 Hz (2 mm SP at 110 mm/s, Fig. 7A), led to only a 12% increase in roughness estimates. These data were subsequently reduced to a single monotonic continuum (overlapping green, purple and red curves, Fig. 7, D–F) by “normalizing” the results to the same spacing (all ratings divided by the mean SP in the direction of the scan) and plotting the results as a function of temporal frequency. To determine the net effect of the transformation, an $r^2$ total value (3 surfaces pooled together) was calculated for each subject from the linear regression, estimates/SP versus temporal frequency. The mean values are shown on Fig. 7, D–F. Overall the transformed data explained a significantly higher proportion of the variance in the magnitude estimates, 71–83% (paired t-test, $P < 0.0005$), than did the untransformed data, 62–72% (Table 3, note that these were separate calculations for each surface, averaged together for the comparison). Moreover, repeated-measures ANOVAs demonstrated that the transformation abolished the significant change in intercepts across SP for the two experiments with the same range of mean SP [experiments 1 and 3; untransformed data, $F(2,28) = 10.36, P < 0.0005$; transformed data, $F(2,28) = 1.89, P = 0.17$]. Together the results indicate that speed scaling is dependent on temporal frequency, but this ability is consistently modified by the spatial characteristics of the tactile stimuli.

Contribution of periodicity to the results

Although the transformation of the results (preceding text) indicated that periodicity did not contribute to the results, we considered the possibility that the subjective magnitude estimates might have been more reliable (less variable, lower SE) when the events were regularly spaced (periodic surfaces) as compared with irregularly spaced (nonperiodic surfaces). To

**FIG. 7.** A–C: mean normalized subjective estimates of speed (±SE) plotted, for each surface and each experiment, as a function of the temporal frequency (scanning speed/mean SP in the direction of the scan). Isocontour lines join equivalent speeds (nominal speeds indicated in A). For each experiment, a family of 3 nonoverlapping curves was obtained. D–F: the magnitude estimates from A to C were themselves divided by mean SP, and are replotted relative to temporal frequency. This reduced the results from each experiment to a single continuum relative to temporal frequency. The mean $r^2$ total values (±SE), estimate/SP vs. temporal frequency (individual subject analyses), are indicated.
address this, the data from the two experiments that were matched for dot spacing are plotted together in Fig. 8. The magnitude estimates were pooled across all SPs, and the SEs were calculated from all trials. Inspection shows that the two curves, periodic (solid line) and nonperiodic (interrupted line), were superimposed with, if anything, a steeper slope for the nonperiodic surfaces (see also Table 3). Although the SEs were not obviously different, we also computed the SE for each speed and texture in each subject. A repeated-measures ANOVA showed a modest increase in the variability of the magnitude estimates for the nonperiodic surfaces as compared with the periodic surfaces ($P = 0.022$), corresponding to a 0.9% increase in variability for the former when expressed as a % of the mean ratings (9.1% for periodic surfaces, 10% for nonperiodic surfaces). Thus while stimulus regularity contributed to the results, the effect was small.

**Discussion**

The present study showed that humans can estimate tangential tactile motion across a range of behaviorally relevant speeds, and this in the absence of explicit cues related to stimulus duration. We also demonstrated that subjective magnitude estimates of scanning speed covaried with surface texture, consistent with single unit recordings which indicate that information about speed and surface texture is confounded in the signals of peripheral mechanoreceptive afferents (see **Introduction**). Figure 7 suggests that speed and texture signals, at least as relates to tactile motion perception, may remain confounded at all levels of processing within the CNS.

**Present results**

To the best of our knowledge, this is the first demonstration that subjects can scale tactile speed in a situation in which stimulus duration was held constant. Thus the only source of information on which subjects could base their estimates was tangential motion of the surfaces under the fingertip. All subjects showed a monotonic increase in their subjective magnitude estimates as scanning speed increased with virtually identical slopes for the psychometric curves across a range of textured surfaces. The ability to scale tactile motion was, however, critically dependent on surface structure. When subjects rated the speed of a smooth surface, their magnitude estimates of speed were significantly lower as compared with the results obtained with textured surfaces in the same subjects. Moreover, while all subjects were able to scale the speed of the textured surfaces, some were unable to scale the speed of the smooth surface. This latter observation was not explained by lack of familiarity with the task, as testing with the smooth surface occurred, in all cases, after the subject had already performed the experiment using the textured surfaces. While the dramatically lower $r^2$ values for the psychometric functions (44–45% of the values from the textured surfaces) might have reflected the contribution of other factors to the results obtained with the smooth surface, we believe that this finding more simply reflected the inability of subjects to scale the speed of the smooth surface. Consistent with this explanation, the slopes (smooth) were only one-third of the values for the textured surfaces.

The present results also showed that tactile magnitude estimates of speed were dependent on the spatial characteristics of the scanned surfaces. Specifically, the roughest surfaces (8 mm dot spacing) were estimated to move ~15% slower than the smoother, textured surfaces (2–3 mm dot spacing). This result was independent of dot disposition because similar results were obtained with raised dots arranged in either periodic arrays of dots or quasi-randomly distributed across the surface. Dot density was likewise not responsible for the speed underestimates seen in the first experiment (periodic surfaces) because we were not able to reproduce this result when subjects rated the speed of nonperiodic surfaces matched for dot density (experiment 2). In creating the nonperiodic surfaces, however, the range of dot spacing in the direction of the scan was also altered, decreasing from 2–8 to 2–4.9 mm. The importance of this factor was addressed in the final experiment where we reproduced the initial results, but this time using nonperiodic arrays of raised dots. Thus the underestimation of speed for the roughest surface (8 mm dot spacing) was attributed to the spacing between dots in the direction of the scan with the critical range being >4.9 mm, the maximum spacing tested in experiment 2. This effect was, however, small relative to the main effects of tactile speed. Multiple regression analyses indicated that tactile motion explained 75–82% of the variance in the magnitude estimates of speed in the three experiments, as compared with only 14–19% attributed to dot spacing in experiments 1 and 3 and 1.2% in experiment 2.

**Comparisons with previous studies**

Earlier studies (Essick et al. 1988, 1996; Franzén and Lindblom 1976) reported that subjects can scale tactile speed, but stimulus duration covaried with speed in their experiments. Thus it was not clear if subjects were scaling speed or stimulus duration. Indeed, Essick et al. actually proposed that stimulus duration was the key factor explaining their results. This likely explains why the mean exponent for the power functions fit to their data (0.61) was lower than the values obtained in the present study (1.12–1.34). Another explanation for the different results cannot, however, be discounted: the high exponents obtained here might reflect a difference between hairy and glabrous skin. Consistent with this suggestion, Essick and Edin (1995) reported that ~50% of RA afferents innervating the glabrous skin of the hand have exponents $>1$ (mean discharge
rate vs. speed), whereas those innervating hairy skin have lower exponents. Further experiments are needed to address this latter possibility.

Methodological consideration

The speed range used here covers only partially the range studied by Essick et al. (1988, 1996), 5–640 mm/s. We were not able to test speeds >110 mm/s because we were limited by the length of surface available for presentation (400 mm). This in turn was limited to the physical dimensions of the tactile stimulator. The tested range, 33–110 mm/s, nevertheless corresponds to a behaviorally important range of the tactile speeds. For example, subjects use speeds of 10–157 mm/s during tactile exploration (Smith et al. 2002a) and 60–190 mm/s during Braille reading (Grunwald 1966).

Friction

Friction, the ratio of tangential to normal force, may have been a contributing factor to the present results. The skin of the finger is compliant and offers resistance to surface displacement. This resistance can moreover be higher for rougher surfaces. Thus Smith et al. (2002a) showed that the rate of change of tangential force during active tactile exploration increases with surface roughness, at least for periodic surfaces with the same range of dot spacings as tested here. How this contributes to the subjective estimates of speed is not known. We found that normal force was constant across the speeds tested consistent with previous observations (Smith et al. 2002a,b) of invariances in normal force during active tactile exploration of smooth and textured surfaces, but technical limitations of our apparatus did not allow us to monitor tangential force. We can say, on the other hand, that the contribution of friction is likely to be complex: speed was underestimated with the roughest surface and this independent of dot disposition (periodic or nonperiodic). If friction had been a critical factor, then we would have expected a greater effect with the periodic surfaces as the regular and widely spaced rows should have offered more resistance than the randomly distributed dots, and so more friction. The results were, however, independent of dot disposition.

Mechanoreceptors contributing to encoding tactile motion

For the smooth surface, the initial contact would have produced an initial stretch of the skin, activating discharge in all types of cutaneous mechanoreceptive afferents innervating the glabrous skin, SAI, RA, and PC (Srinivasan et al. 1990). During the speed plateau, only SAI afferents would have continued to discharge given their sensitivity to skin stretch, although we cannot exclude a potential contribution from RA and PC afferents because the smallest imperfection on the smooth surface would have been sufficient to activate these receptors (LaMotte and Whitehouse 1986; Srinivasan et al. 1990; see also Bensmaia and Hollins 2005). We believe that feedback during the speed plateau contributed little to the results because some of the subjects did not even perceive the motion of the smooth surface without prompting. Because subjects often volunteered their estimate while the smooth surface was still moving, we suggest that they likely gathered most of the relevant information from the initial contact with the moving surface. Contact with the moving surface would have been accompanied by both normal and tangential forces on the skin of the fingertip. We suggest that these signals were likely used to estimate the speed of the smooth surface and that differences across subjects may reflect differences in skin friction as a result of, for example, difference in skin moisture (see also preceding text).

In contrast, all of the major cutaneous mechanoreceptive afferents contributing to discriminative touch were undoubtedly continuously activated when the textured surfaces were scanned over the skin. It is known that their discharge reflects not only the physical characteristics of the surfaces (texture) but also the parameters of stimulation, specifically speed and contact force (reviewed in Johnson 2001), most likely including tangential force as well as normal force (Birznieks et al. 2001; Smith et al. 2002a). It seems likely that all of these afferents may contribute to tactile speed scaling, although the relative contribution of each remains to be determined. Certainly there is evidence that all afferent types are sensitive to scanning speed, but the results vary depending on the physical characteristics of the stimulus (Edin et al. 1995; Essick and Edin 1995; Goodwin and Morley 1987; Greenspan 1992; Lamb 1983). The closest parallel can be drawn with Lamb’s study: he recorded from primary afferents innervating the glabrous skin of the hand in the monkey as raised dot surfaces (1 or 2 mm SP) were displaced across the receptive field at different speeds. Within the range of temporal frequencies (speed/SP) used here, RA and PC afferent mean discharge increased with increased temporal frequency and so could account for the present results. Such a suggestion is consistent with Essick and Edin (1995)’s observation that only RA afferents innervating glabrous skin (PC afferents not tested) have exponents >1 (log mean discharge rate vs. log speed), consistent with the exponents found here for the log-log plots (also >1). Interestingly, SAI afferent discharge in Lamb’s study was constant over the same range of temporal frequencies. To exclude their contribution to the present results, however, a wider range of SPs, up to 8 mm, should be tested under the same conditions because there is some evidence (Goodwin and Morley 1987) that SAI afferents are sensitive to the speed of rougher surfaces (see their Fig. 4).

Roughness and subjective magnitude estimates of scanning speed

The present finding that magnitude estimates of speed co-varied with surface roughness is in marked contrast to observations that roughness estimates themselves, measured using the same dot spacings as here (1.5–8.5 mm), are independent of scanning speed (Meftah et al. 2000). In the latter study, subjects scaled the roughness of periodic raised dot surfaces moved under the immobile fingertip at 50 or 100 mm/s (speeds randomly interleaved). Roughness estimates showed a monotonic increase with dot spacing but were invariant over a twofold increase in scanning speed and this for speeds within the range tested here. The latter observations were consistent with the predictions of the spatial variation code proposed by Johnson and colleagues (Blake et al. 1997; Connor and Johnson 1992; Connor et al. 1990; Yoshioka et al. 2001). They proposed that tactile roughness is signaled by differences in the firing rates of nearby SAI afferents with the transformation into
a simple intensive code occurring centrally. The spatial code cannot, on the other hand, explain tactile speed scaling and its dependence on tactile roughness because the code is insensitive to scanning speed (DiCarlo and Johnson 1999). Thus tactile speed must be dependent on some other neuronal code, most likely a simple intensive code based on the firing rates of the peripheral mechanoreceptive afferents that are sensitive to both roughness and scanning speed (above). Our results also show that speed and texture signals, at least as relates to tactile motion perception, may remain confounded at all levels of processing within the CNS. Consistent with this suggestion, the $r^2$ values reported here (Table 3) were lower than the corresponding values for subjective roughness estimates (Meftah et al. 2000), 0.551–0.756 versus 0.87–0.91, likely reflecting increased uncertainty about the speed estimates. Finally, we suggest that the discharge of central neurons contributing to tactile speed perception should vary with speed and texture in the manner shown in Fig. 7, D–F (see following text).

Implications of the results

At a more general level, it may seem counterintuitive for the spatial properties of stimuli to influence speed perception because this must ultimately be a temporal property. Nevertheless the effects of space on speed scaling were reduced to a single monotonic continuum by “normalizing” the results to the same spacing and expressing the results as a function of temporal frequency (Fig. 7, D–F). Thus speed scaling was dependent on temporal but also spatial, cues. In contrast, applying the same analysis to our previous roughness scaling data generates a single curve with a slope approaching 0 (not illustrated). Taken together, we suggest that the discharge of central neurons critically involved in speed or roughness scaling must follow these same patterns. In other words, the neurometric functions (discharge rate/SP vs. temporal frequency) should show a monotonic increase for cells that might play a role in speed scaling. The corresponding neurometric functions for cells involved in texture perception should be flat with a slope approaching 0.

Where this extraction of information occurs is, as yet, unknown. We do know that many neurons in areas 3b, 1, and 2 (S1, primary somatosensory cortex) and S2 (secondary somatosensory cortex) discharge in relation to both surface texture and scanning speed (Jiang et al. 1997; Pruett et al. 2000; Sinclair and Burton 1991, 1993; Tremblay et al. 1996). Moreover, lesions of S1 greatly impair the ability of monkeys to categorize tactile speed (Zainos et al. 1997). The present results provide a clear set of criteria that neurons critical for speed scaling must encounter.

Finally the appreciation of properties such as speed and texture is not unique to the somatosensory system but also extends to the visual system. Several studies have shown an interaction between visual speed scaling and the SP of moving gratings (Campbell and Maffei 1981; Diener et al. 1976; cf. Smith and Edgar 1990). Most studies reported that a decrease in spatial frequency (1/SP) causes a decrease in perceived speed. Our results are consistent with these: the surface with the lowest spatial frequency, 8 mm (0.125) was perceived as moving slower than the surfaces with higher spatial frequencies (0.5 and 0.33 for, respectively, the 2 and 3 mm SP surfaces). In a similar vein, Watamaniuk et al. (1993) reported that decreasing the density of a field of moving dots decreases the perceived speed of visual dot motion. Our results extend this observation to the somatosensory system, but it should be noted that an effect was only seen with the lowest dot density used, 2.2 dots/cm², suggesting that dot density effects may be range limited. Together such findings suggest that important parallels exist between the somatosensory and visual systems as regards the processing of stimulus motion.

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