Neuronal correlates of tactile speed in primary somatosensory cortex

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Dépeault A, Meftah EM, Chapman CE. Neuronal correlates of tactile speed in primary somatosensory cortex. J Neurophysiol 110: 1554–1566, 2013. First published July 10, 2013; doi:10.1152/jn.00675.2012.—Moving stimuli activate all of the mechanoreceptive afferents involved in discriminative touch, but their signals covary with several parameters, including texture. Despite this, the brain extracts precise information about tactile speed, and humans can scale the tangential speed of moving surfaces as long as they have some surface texture. Speed estimates, however, vary with texture: lower estimates for rougher surfaces (increased spatial period, SP). We hypothesized that the discharge of cortical neurons playing a role in scaling tactile speed should covary with speed and SP in the same manner. Single-cell recordings (n = 119) were made in the hand region of primary somatosensory cortex (S1) of awake monkeys while raised-dot surfaces (longitudinal SPs, 2–8 mm; periodic or nonperiodic) were displaced under their fingertips at speeds of 40–105 mm/s. Speed sensitivity was widely distributed (area 3b, 13/25; area 1, 32/51; area 2, 31/43) and almost invariably combined with texture sensitivity (82% of cells). A subset of cells (27/64 fully tested speed-sensitive cells) showed a graded increase in discharge with increasing speed for testing with both sets of surfaces (periodic, nonperiodic), consistent with a role in tactile speed scaling. These cells were almost entirely confined to caudal S1 (areas 1 and 2). None of the speed-sensitive cells, however, showed a pattern of decreased discharge with increased SP, as found for subjective speed estimates in humans. Thus further processing of tactile motion signals, presumably in higher-order areas, is required to explain human tactile speed scaling.

tactile motion; texture; speed scaling; temporal frequency; S1; monkey

MOVEMENT BETWEEN THE SKIN and an object activates all tactile afferent types (both slowly and rapidly adapting) that play a role in discriminative touch (Edin et al. 1995; Essick and Edin 1995; Goodwin and Morley 1987; Greenspan 1992; Lamb 1983) and improves tactile perception. For example, tactile roughness discrimination thresholds are halved during dynamic touch, i.e., with movement, compared with static touch (Morley et al. 1983). While we have a great deal of information about the peripheral and central coding of tactile roughness, little is known about tactile motion coding (speed) and perception, even though it is essential for object manipulation in everyday life (e.g., tactile slip during prehension).

At the receptor level, a number of studies have characterized the sensitivity of primary cutaneous afferents to moving surfaces or brushes. The results showed that cutaneous mechanoreceptive afferents innervating both hairy and glabrous skin, including rapidly adapting (RA), Pacinian (PC), and slowly adapting type I and II (SAI, SAII) 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, 1987b). The signals are complex, covarying with multiple attributes: tactile speed, surface structure (roughness and/or shape of the stimuli scanned over the skin), and contact force (Birznieks et al. 2001; Johnson 2001). At present, it is not clear how these signals are processed at higher levels to extract precise information about tactile speed.

Lesions of primary somatosensory cortex (S1) greatly impair the ability of monkeys to categorize tactile speed (Zainos et al. 1997). Consistent with this, a number of studies have shown that S1 cortical neurons are sensitive to tactile motion, using a variety of approaches including mechanical indentation of the skin (Esteky and Schwark 1994), sequential stimulation of a fixed length of skin (Gardner et al. 1992; Pei et al. 2010; Romo et al. 1996; Whitsett et al. 1972), and tangential scanning of surfaces over a fixed location on the skin with the subject either immobile, passive touch (DiCarlo and Johnson 1999; Sinclair et al. 1996; Tremblay et al. 1996) or moving, active touch (Sinclair and Burton 1991). The results indicate that sensitivity to the speed of tactile motion is present in all three areas that form the primate cutaneous hand representation, areas 3b, 1, and 2. In addition, there is some indication that speed sensitivity is frequently combined with sensitivity to the texture of scanned surfaces. At present, however, we have limited information about the extent to which S1 neuronal discharge has properties consistent with a role in tactile speed scaling and whether the different areas that comprise S1 play differential roles in signaling tactile speed.

This study was prompted by two related observations. First, even though tactile signals are complex and covary with multiple parameters, including texture and speed, human tactile roughness estimates are relatively independent of tactile scanning speed (Lederman 1983; Meftah et al. 2000). This observation indicates that an invariant representation of roughness is extracted from the complex peripheral signals. Second, it appears that the same is not true for human tactile speed estimates. We recently showed that tactile speed scaling is dependent on surface texture in two important ways (Dépeault et al. 2008): 1) some surface structure, specifically texture, is essential because subjects have a great deal of difficulty in estimating the speed of a moving smooth surface, and 2) speed estimates for the roughest surface tested [8-mm spatial period (SP) measured in the direction of the scan] were systematically lower than for two “smoother” surfaces (2- and 3-mm SP). In other words, the physical characteristics of the textured stimuli modified the subjective speed of moving stimuli. We excluded the possibil-
ities that this was explained by a sparser stimulus (fewer raised dots for the rougher surface) or the disposition of the dots (periodic or nonperiodic) and showed that the important parameter was dot spacing in the direction of the scan. These results led us to hypothesize that the discharge of cortical neurons playing a role in scaling tactile speed should covary with the speed and SP of textured surfaces in the same manner seen in human subjects. We further expected that the discharge pattern would be independent of the disposition of the raised dots (periodic vs. nonperiodic), consistent with our psychophysical observations.

Our hypotheses were tested in the present study by recording from single neurons in S1 of awake monkeys as textured tactile stimuli were displaced at different speeds across the receptive field (RF). The stimuli consisted of raised-dot surfaces that varied in terms of roughness (SP) and dot disposition (periodic, nonperiodic). The range of tactile speeds was similar to that used in our earlier psychophysical study, corresponding to speeds often used during tactile exploration (Smith et al. 2002).

METHODS

Two monkeys (Macaca mulatta; monkey B, 8.5 kg; monkey N, 6.3 kg) were used in the present experiment. Recordings were made from three hemispheres contralateral to the stimulated digits (both sides for monkey B; left for monkey N). The institutional animal care and use committee approved all of the procedures, and the guidelines specified by the Canadian Council on Animal Care were followed. The recordings were made outside the context of a tactile perceptual task, and so it was important to control the animal’s attention (Meftah et al. 2002). As in other studies (Fitzgerald et al. 2006), the animal’s attention was controlled by having the monkey perform a simple light discrimination task (see below) while the textured surfaces were displaced beneath the immobile tips of digits 3 and 4 (D34) at different speeds.

Tactile stimulator. The strips of surfaces were affixed to a tactile stimulator, similar to that described by Zompa and Chapman (1995). It was composed of a cylindrical drum (40-cm circumference) mounted on a drive shaft that was rotated by means of a DC motor through a 100:1 reduction gear controlled by a computer. The different surfaces were accessible through openings (18 × 22 mm) giving access to the drum. The tactile stimulator was fixed to the primate chair at waist height, in front of the monkey.

Surfaces. The surfaces were prepared on flexible letterpress plate with a photographic process (CML Printing Plates, St. Léonard, QC, Canada). They were composed of raised dots [truncated cones: 1-mm high and 0.8-mm diameter (top); Fig. 1B]. Two series of surfaces were used, one periodic and the other nonperiodic (see Fig. 1C). Each series consisted of four 10-cm-long surfaces that together formed a single 40-cm strip (Fig. 1A). The surfaces were drawn from sets used in a previous psychophysical study and have been described in detail elsewhere (Dépeault et al. 2009). The periodic surfaces were constituted of rows of dots with a constant transverse SP (center to center) of 2 mm and longitudinal SPs varying from 2 to 8 mm. In the initial recordings, the nonperiodic surfaces were matched for dot density. These were generated by jittering the periodic dots to produce a pseudorandom arrangement. This maintained the same number of dots, but the average spacing in the scanning direction covered a smaller range, 2–4.9 mm. In most recordings, a different set of nonperiodic surfaces was used, in this case matched for longitudinal SP (Fig. 1C). This set was generated by pruning dots from the first nonperiodic set.

Speeds. Surfaces were presented with three nominal speeds of 40, 75, and 100 mm/s (40, 60, and 85 mm/s for the initial cells in monkey B), which covered most of the range used during tactile exploration in humans (Smith et al. 2002). The actual speed varied slightly from the nominal speed (<1.2%).

Behavioral task. When the monkeys were first brought to the laboratory, they were trained to adopt a posture (place one hand on the surface and one on a lever), then to accept moving surfaces under their immobile fingers, and finally to perform a visual discrimination task during the drum rotation (see below). This whole process required a total of 4–6 mo. The monkeys had to attain a performance of ~90% in the visual discrimination task, which required 5–8 wk. Lights (red
and yellow) were placed in front of the monkey at eye level (~35 cm), and the hand ipsilateral to the recorded cortex was positioned on a response lever. The fingertips (D34) of the other hand were placed over the surface in one opening (see Fig. 1D) and stayed immobile for all the trials necessary (monitored visually during acquisition; trial rejected if variation in vertical force was greater than ±0.2 N). Before each trial, the correct positioning of the fingers was verified; thereafter, the experimenter initiated the trial. After a total hold period of 1 s, a red light turned on to warn the monkey that the texture would move and that the visual discrimination task would begin in 2 s (see Fig. 2, A and B). The yellow light was first of low intensity and then increased in intensity after a delay of 1.5, 2.0, or 2.5 s. The monkey had to detect this change and then respond to it by lifting its hand from the lever to receive a drop of water. The reaction time window for a successful trial was 200–700 ms. Performance of the monkeys during recordings was, on average, 80% correct. Monkey B would often withdraw its fingers from the surfaces when the drum was repositioned; monkey N left its digits in place throughout. For each trial, finger position was closely monitored throughout the scan.

Surgical procedures. When the monkey mastered the task, a chronic recording chamber was placed over the hand representation of S1, contralateral to the stimulated hand. The surgical procedure used here for chamber implantation was described previously (Chapman and Ageranioti-Bélanger 1991; Tremblay et al. 1996). Briefly, after sedation with ketamine + glycopyrrolate (15 mg/kg im + 0.01 mg/kg), the animal was intubated for endotracheal administration of isoflurane (2–3%). Physiological parameters (temperature, heart rate, and respiration rate) were monitored during the surgery. Antibiotics (enrofloxacin, 5 mg/kg) were administered prior to surgery and for 10 days postoperatively. Postoperative analgesia was provided for a minimum of 72 h (ketoprofen 0.1 mg/kg and buprenorphine 0.05 mg/kg).

Data acquisition and analysis. Extracellular recordings of single neurons were performed in S1 with glass-coated tungsten microelectrodes (0.2–1 Ω). For each penetration, depths were noted when cell activity was reached, when a cell was recorded, and when there were transitions between active and silent zones. The RF properties of each neuron were carefully determined. Cells were initially characterized according to their modality: cutaneous (sensitive to light or moderate touch) and/or deep (responsive to joint movement and/or muscle palpation). Our recordings concentrated on neurons that 1) had a cutaneous RF on the stimulated digit tips (D3 and/or D4) and 2) showed obvious modulation of their discharge rate in response to the moving textures. The extent of the cutaneous RF was mapped with a hand-held probe. For one monkey (monkey N), the mapping was repeated and confirmed with a von Frey filament (F = 0.02 N). The adaptation rate for each cell was determined: SA neurons continued to discharge for ~2 s during static touch, while RA neurons showed transient responses to static stimulation, along with discharge during the application and removal of the stimulus.

Data collection was under computer control (see Tremblay et al. 1996). During each trial, the following data were collected: neural spike intervals, vertical contact force, drum position, and specific timing of events in the trial (e.g., light change, time of the response). Cell recording started with the last 500 ms of the hold period and lasted for a total of 6.5 s. During each trial, 8 cm of surface was presented (proximal to distal), and drum rotation time was varied to generate a range of speeds (40–105 mm/s). The speed was constant.
throughout the trial (see Fig. 2A). For each cell, there was a total of 120 trials presented pseudorandomly, consisting of 5 repetitions of each speed-texture combination (3 speeds and 4 textures) for both periodic and nonperiodic series. The tactile stimulator was displaced horizontally after the first 60 trials (periodic or nonperiodic series) to expose the other series of surfaces; this ensured that the monkey’s arm remained in the same position relative to the surfaces throughout data acquisition.

The activity during the stimulation period (when the surface was displaced under the digit tips) was the focus of this study. Rasters and peri-event histograms were used to examine the discharge pattern of each cell. For each trial, mean cell discharge rate was calculated during five different epochs (see Fig. 2B): 1) hold period corresponding to the 500 ms before the red light turned on; 2) instruction period; 3) first half of stimulation period; 4) second half of stimulation period; and 5) complete stimulation period (epochs 3 + 4). The number of spikes during epochs 3–5 was also calculated.

For each cell, the following analyses were performed for epochs 3–5. First, the mean discharge rate during epochs 3–5 was compared with epoch 1 to see whether there was a significant difference (Wilcoxon test, \( P \leq 0.05 \)) and therefore determine whether the cell was modulated by the moving surfaces. Second, an analysis of variance (ANOVA) (dependent variable: mean discharge rate during epoch 3, 4, or 5; independent variables: speed and SP) was applied to the results of each data file (1 set of surfaces, periodic or nonperiodic) to classify cells as speed and/or texture sensitive. Third, linear regressions were applied to each data file to describe the nature of the relationship between mean discharge rate and scanning speed. In general, similar results were obtained with epochs 3, 4, and 5. The measure of interest was the strength of the relationship between mean discharge frequency and scanning speed as quantified by the coefficient of determination, \( r^2 \). We chose to concentrate on the measures from the complete stimulation period, epoch 5, in RESULTS because \( r^2 \) values were highest for this measure across the population of speed-sensitive cells. Further analyses are described in RESULTS. Statistical analyses used Systat version 11.0 for Windows (SPSS, Chicago, IL). The minimum level of significance for all analyses was \( P \leq 0.05 \).

Our main analyses were based on the assumption that the underlying neuronal code for tactile speed is mean discharge rate. We also tested the possibility that a spike count code might provide a better fit to the data. This was motivated by Luna et al.’s (2005) suggestion that a spike count code explains flutter discrimination better than a mean rate code. Our results (not shown) suggested, however, that the relations were substantially weaker (lower \( r^2 \) values) with the spike count code. Such findings led us to concentrate the population analyses on measures obtained with mean discharge rate.

Histological methods. Electrocorticograms were performed near the end of the recordings. After that, the monkey was euthanized with an overdose of pentobarbital (35 mg/kg ip) and perfused through the heart with a formol-saline solution. The brain was then removed and parasagittally sectioned in 50-μm slices to be stained with cresyl violet. The areas of S1 were distinguished according to the criteria established by Powell and Mountcastle (1959) and Jones et al. (1978).

RESULTS

Recordings were made from three hemispheres of two monkeys in the cutaneous hand region of S1 (areas 3b, 1, and 2). A total of 119 cells were recorded, with 94 cells having complete acquisition files for both the periodic and nonperiodic surfaces (~60 trials for each set of surfaces). Seventy-two neurons were recorded in monkey B and 47 neurons in monkey N. All cells had a cutaneous RF that included the digit tip of D3 and/or D4 and so were stimulated by the moving surfaces. All were sensitive to light touch. The adaptation type was determined for almost all cells with manually applied stimuli: 56 RAs and 62 SAs. Histological reconstructions (see Table 1) showed that the sampling covered all three areas that form the S1 cutaneous hand representation: 25 cells were located in area 3b, 51 in area 1, and 43 in area 2. SA responses were encountered in all three areas and made up, respectively, 44%, 52%, and 58% of the sample.

Cell discharge was recorded while the monkey performed the visual discrimination task, ensuring that attention was controlled throughout the time of data acquisition. When possible (isolation maintained, monkey willing to work), two blocks of trials were recorded for each neuron: one set with the periodic surfaces and the other with the nonperiodic surfaces (order counterbalanced across sessions). Four different textures were presented in each block, at three different scanning speeds. These data were used to evaluate the extent to which cell discharge covaried with scanning speed, surface texture, and dot disposition (periodic, nonperiodic). Individual cell examples are presented first, followed by the population analyses.

Single-cell examples. The most common response pattern encountered was sensitivity to both surface texture and scanning speed. Figure 3A shows a representative cell recorded in area 2. Trials in the rasters and peri-event histograms (aligned on scanning onset) were sorted according to dot disposition [Fig. 3A, top (periodic) and middle (nonperiodic)] and scanning speed. Within each raster, trials are shown in increasing order of longitudinal SP. During the period of drum rotation (thick bar above the raster in Fig. 3A), discharge rate showed an abrupt increase shortly after drum rotation began, followed by a modest degree of adaptation during the period of constant-velocity scanning. When scanning speed was increased (Fig. 3A, left to right), the discharge rate increased. The change in dot disposition (Fig. 3A, top vs. middle), in contrast, had little effect on neuronal sensitivity to tactile scanning speed. An ANOVA was applied to the data for each acquisition file (periodic, nonperiodic). Discharge rate during the stimulation period (epoch 5, Fig. 2) was significantly modulated by both speed and SP (\( P \leq 0.003 \)) for the periodic and nonperiodic surfaces. Figure 3A, bottom, summarizes the results, plotting cell discharge rate as a function of speed, with separate regression lines shown for each set of surfaces (periodic, nonperiodic). There was a monotonic increase in discharge rate as scanning speed increased in each case, and both regressions were significant (\( P < 0.0005 \)). The two regression curves were parallel, indicating that speed sensitivity was the same for the periodic and nonperiodic surfaces. This was confirmed by the observation that the \( r^2 \) values (shown in Fig. 3A, bottom) were similar for both sets of surfaces. These data are replotted in Fig. 4A with separate regression lines for each SP. Inspection shows that the relation with speed was preserved across the four SPs tested, with lower discharge rates with the smoothest surface (2-mm SP) compared with the roughest surface (8-mm SP).

<table>
<thead>
<tr>
<th>Table 1. S1 cell distribution</th>
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<tr>
<td>Area 3b</td>
</tr>
<tr>
<td>-------</td>
</tr>
<tr>
<td>Monkey B</td>
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<tr>
<td>Monkey N</td>
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\( n = 119 \) neurons. S1, primary somatosensory cortex.

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Speed sensitivity independent of texture sensitivity was much less frequently observed. Nevertheless, a few such cells were encountered, and an example from area 2 is presented in Fig. 3B. There was a marked increase in discharge with increasing speed for both sets of surfaces, with modestly higher discharge rates for the data set acquired with the nonperiodic surfaces. The regressions with speed (see summary plot in Fig. 3B, bottom) showed a monotonic increase with increased speed.
In this case, the \( r^2 \) values were higher than those obtained for the cell shown in Fig. 3A, reflecting the importance of speed as a factor explaining the variations in discharge rate. Inspecting the rasters, there is little evidence for any sensitivity to texture. Consistent with this, Fig. 4B shows that the four curves relating rate to speed as a function of SP are superimposed. This result was confirmed with the ANOVAs: speed was a significant factor for both the periodic and nonperiodic surfaces (\( P < 0.0005 \)), while texture was not (\( P > 0.15 \)).

Although not the focus of these analyses, a substantial proportion of cells (see below) were sensitive only to texture (longitudinal SP) independent of scanning speed. An example is shown in Fig. 3C (area 3b). For both sets of surfaces, cell discharge increased as SP was increased (see rasters in Fig. 3C and Fig. 4C). Texture was a significant factor in the ANOVAs (\( P \leq 0.01 \)), but speed was not (\( P > 0.85 \); see summary plot in Fig. 3C, bottom). Consistent with this, the linear regressions with speed had slopes approaching 0 (\( P > 0.9 \)), and \( r^2 \) values of 0 were obtained (both sets of surfaces). Inspection of Fig. 4C, however, shows a clear separation between the curves sorted on SP, reflecting this cell’s sensitivity to texture.

The dependence of cell discharge on both speed and SP in many cases (e.g., Fig. 3A and Fig. 4A) suggested that temporal frequency (speed/SP) might be a factor. When cell discharge was plotted as a function of temporal frequency, however, the cell sensitive to both texture and speed (Fig. 4D) showed no significant relation (\( P = 0.82 \)). Instead, we obtained families of nonoverlapping curves that reflected the underlying SP of the surfaces, emphasized here with separate regressions for each SP. For the speed-sensitive cell (Fig. 4E) the regression with temporal frequency was significant, but this factor explained substantially less of the cell variance compared with speed (poled \( r^2 \) values of 0.226 and 0.609, respectively).

**Fig. 4.** Single-cell examples (same as Fig. 3, A–C) showing the influence of SP on speed sensitivity. A–C: discharge rate during the scan is plotted as a function of speed, with separate regressions shown for each SP. D–F: discharge rate is plotted as a function of temporal frequency (speed/SP); separate regressions are shown for each SP, and isocontour lines (dotted) join equivalent speeds. These plots show families of nonoverlapping curves. The coefficient of variation, \( r^2 \), for the pooled relationship (periodic and nonperiodic surfaces) is shown on each panel. The \( r^2 \) values for the temporal frequency plots of the 2 speed-sensitive cells (D and E) were substantially lower than for the plots with speed (A and B).

Neuronal sensitivity to scanning speed and texture. As indicated above, cell sensitivity to speed and texture was assessed by an ANOVA applied to the data collected with each set of surfaces. The results are summarized in Table 2. The vast majority of cells recorded were sensitive to one or both factors (109/119). Inspection shows that texture sensitivity was more frequently encountered than speed sensitivity (95 vs. 76 cells). Speed sensitivity was frequently combined with texture sensitivity (62/76, 82%) and rarely seen in isolation (14/76, 18%). In contrast, texture sensitivity independent of tactile scanning speed was seen in 35% of texture-sensitive cells (33/95).

**Table 2.** Sensitivity to speed and texture as function of cytoarchitectonic area

<table>
<thead>
<tr>
<th></th>
<th>Area 3b (n = 25)</th>
<th>Area 1 (n = 51)</th>
<th>Area 2 (n = 43)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Texture + speed</td>
<td>12</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td>Speed</td>
<td>1</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>Texture</td>
<td>10</td>
<td>15</td>
<td>8</td>
</tr>
<tr>
<td>Ns</td>
<td>2</td>
<td>4</td>
<td>4</td>
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\( n = 119 \) neurons. Ns, nonsignificant.
Table 3. Adaptation rates of cells tested with both sets of surfaces, periodic and nonperiodic, as a function of area and speed/texture sensitivity

<table>
<thead>
<tr>
<th></th>
<th>Area 3b (8 RA/7 SA)</th>
<th>Area 1 (19 RA/23 SA)</th>
<th>Area 2 (14 RA/23 SA)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Texture + speed</td>
<td>5/3</td>
<td>10/11</td>
<td>7/16</td>
</tr>
<tr>
<td>Speed</td>
<td>0/0</td>
<td>3/3</td>
<td>2/4</td>
</tr>
<tr>
<td>Texture</td>
<td>3/4</td>
<td>5/8</td>
<td>4/3</td>
</tr>
<tr>
<td>Ns</td>
<td>0/0</td>
<td>1/1</td>
<td>1/0</td>
</tr>
</tbody>
</table>

Values are expressed as numbers of rapidly adapting (RA)/slowly adapting (SA) afferents; n = 94 neurons.

Nature of relationship between cell discharge and scanning speed. Our entire sample of speed-sensitive cells showed an increase in discharge when speed was increased. We characterized the relationship between mean discharge and scanning speed (all SPs pooled) as either graded (monotonic increase as speed increased) or nongraded (saturation at higher speeds; verified with Kruskal-Wallis test). For the neurons sensitive only to speed, 12 of 14 were classified as graded (e.g., Fig. 3B). For the texture + speed-sensitive cells, the vast majority (55/62) were also classified as graded (e.g., Fig. 3A). The remaining cells were nongraded.

To describe the nature of the relationship between discharge rate and speed, linear regressions were applied to the data from each set of surfaces (Fig. 3, A–C, for the 3 single-cell examples, respectively). Since speed estimates in humans are closely similar for periodic and nonperiodic surfaces (Dépeault et al. 2008), we expected that neurons involved in tactile speed scaling should signal tactile speed independent of dot disposition. A total of 94 neurons were tested for sensitivity to speed with both sets of surfaces (Table 3). Of these, 64 were categorized as speed sensitive, either alone (n = 12) or in combination with texture sensitivity (n = 52). The majority of neurons (42/64) were sensitive to speed for both sets of surfaces, with 30 showing the same pattern of discharge for both periodic and nonperiodic surfaces (27 graded, 3 nongraded). The remaining cells, 34 of 64, were sensitive to speed for only one set of surfaces (11 periodic only, 11 nonperiodic only) or changed their discharge pattern (n = 12, graded for one set and nongraded for the other).

The linear regressions for all 64 cells with a significant relationship with speed are plotted in Fig. 5, A and B (periodic and nonperiodic, respectively). To determine the extent to which the speed signals were comparable for the periodic and nonperiodic surfaces, we compared the parameters of their linear regression curves (slope, intercept, $r^2$). A comparison of the slopes is shown in Fig. 5C, periodic vs. nonperiodic. The corresponding data from the texture-sensitive cells (n = 27) are also plotted. Speed-sensitive cells had steeper slopes than the texture-only cells (close to 0). Inspection shows that for the two groups of speed-sensitive cells the Gaussian bivariate confidence ellipses (95%) are oriented along the equality line, consistent with no difference in slope as a function of dot disposition. This impression was confirmed with paired comparisons (Wilcoxon tests), which showed no differences in slope ($P = 0.784$), intercept ($P = 0.799$), or $r^2$ values ($P = 0.063$) for the periodic vs. nonperiodic surfaces. Similar results were obtained when the comparison was restricted to cells showing a graded pattern of discharge for both sets of surfaces.

Linear discriminant analyses indicated that there was a significant difference between speed-sensitive (speed only and texture + speed combined) and texture-only neurons as regards both slope ($P = 0.0001$) and $r^2$ values ($P < 0.0005$) but not intercepts ($P = 0.89$). Slopes were higher for speed-sensitive neurons (periodic, 0.45 ± 0.06; nonperiodic, 0.47 ± 0.08) than for texture-only neurons (0.06 ± 0.02 and 0.12 ± 0.05, respectively). The $r^2$ values showed a similar trend: speed-sensitive cells (0.178 ± 0.019 and 0.21 ± 0.021, respectively) > texture-only cells (0.019 ± 0.004 and 0.024 ± 0.005, respectively).

To summarize, the results indicated that speed sensitivity was common and usually combined with texture sensitivity. More importantly, we found no difference in the relation with speed as a function of dot disposition, consistent with the results of our human psychophysical experiments. This observation led us to pool data across both series of surfaces for most other analyses.

Neuronal sensitivity to temporal frequency. The results of our psychophysical study (Dépeault et al. 2008) indicated that...
tactile speed scaling was not a function of temporal frequency. We therefore expected that neurons playing a role in speed scaling would share this property. The analysis presented in Fig. 4, D–F, was extended to all cells tested with both sets of surfaces. For the neurons that had a significant relationship with speed (n = 64), less than half (n = 28) showed a significant relation with temporal frequency. Moreover, the slopes were variable (22 with a negative relation; 6 positive). This contrasted with the regressions with speed, in which case all speed-sensitive cells showed a significant positive relation between discharge rate and speed. These findings were thus consistent with our psychophysical results.

Applying the same analyses to the texture-only cells resulted in a higher proportion of significant relations with temporal frequency (18/27; e.g., Fig. 4F). The sign of the relationship was negative for all but one cell, so lower discharge rates with higher temporal frequencies, corresponding to smoother surfaces. This result undoubtedly reflected the contribution of SP to their discharge.

Comparison across areas 3b, 1, and 2. Texture sensitivity and speed sensitivity were encountered in all three areas that comprise the S1 hand representation (χ²-test, P = 0.64; Table 2). There were, however, two regional differences. First, the speed-only cells were almost entirely restricted to areas 1 and 2 (13/14, Table 2). Second, cells with a graded increase in discharge with speed for both sets of surfaces were also restricted to areas 1 and 2 (26/27).

The general pattern of discharge in response to speed was, nevertheless, similar across all three areas. Figure 6 presents ensemble averages of cell discharge for all of the texture + speed and speed-only cells recorded from one monkey (monkey N; all tested with the same range of speeds and the same surfaces) as a function of the cytoarchitectonic location of the cells. Note that cell discharge was normalized to the average duration of the rotation. For comparison, we only illustrate the response to the lowest and highest speeds in Fig. 6. For the texture + speed cells, the speed signal showed little change across the three areas. Consistent with this, the mean increase in discharge rate at the highest speed (vs. low) was similar in all three areas (3b, 64%; 1, 74%; 2, 59%). For the speed-sensitive cells, the increases were also largely similar (increases of 80%, 71%, and 123%, respectively). Note that the larger value for area 2 is explained by the low n and one cell (Fig. 3B).

RA and SA cells were identified in each of the three areas, but there was no obvious trend for the adaptation rate of the cell (RA vs. SA) to influence these categorizations (Table 3). Thus equal proportions of cells that were only texture sensitive or only speed sensitive were RA and SA.

Comparison with speed scaling estimates. To qualitatively compare the neuronal relations with speed to human tactile speed estimates, Fig. 7 plots the pooled data from a subset of the speed-sensitive cells (Fig. 7, A, texture + speed, and B, speed) along with the pooled results from the scaling experiments (Fig. 7C, replotted from Dépeault et al. 2008). Cell selection was limited to those showing a graded increase in discharge with speed for both sets of surfaces (periodic and nonperiodic), i.e., cells with characteristics consistent with a role in speed scaling. Note that some cells (monkey B) were tested with a narrower range of speeds. Inspection shows that discharge rates and scaling estimates both showed a monotonic increase as speed increased. The influence of SP can be seen by comparing the results from the smoothest (SP = 2 mm) and roughest (SP = 8 mm) surfaces (both SPs employed in the speed scaling experiments). For the texture + speed-sensitive cells (Fig. 7A) discharge rates were systematically higher for the rougher texture, while SP had no influence on the discharge of speed-only cells (Fig. 7B, curves superimposed). This contrasted with the results from the human psychophysics, in which case scaling estimates were lower for the rougher texture. While the speed-varying signals in S1 cortical neurons agree well with the human results, the neuronal data do not explain the reduced speed estimates for the rougher texture.

A second comparison (neural vs. human data) is illustrated in Fig. 8. This plots the distribution of the r² values from the linear regression analyses (discharge rate vs. speed) as a function of cell classification along with the corresponding human results (speed estimates vs. speed). The data sets are the
same as in Fig. 7. These data give an indication of the degree to which variance in the dependent variable (discharge rates or scaling estimates) was explained by tactile speed. Inspection shows that there is minimal overlap between the neural and psychophysical $r^2$ values, with the former having lower values than the latter. This suggests that speed scaling most likely depends on the discharge of a population of speed-sensitive cells. The distribution of the $r^2$ values for the neuronal data was distinctly bimodal, with no evidence that one category of cell (speed only, texture + speed) had higher $r^2$ values than the other. Finally, the large majority of the cells showing a stronger relation with speed ($r^2 > 0.2$, 20/21; 4 speed and 17 texture + speed) were located in areas 1 and 2.

**DISCUSSION**

Consistent with our hypothesis, we identified a population of S1 speed-sensitive neurons that showed a graded increase in discharge with increasing speed, independent of dot disposition (periodic, nonperiodic). Such S1 cells thus have properties consistent with playing an important role in the human ability to scale tactile motion. The observation that these neurons were concentrated in areas 1 and 2 suggests, moreover, a critical role for caudal S1 in the processing of tactile motion signals.

**Sources of tactile speed signals.** The sensitivity of peripheral mechanoreceptive afferents to tactile speed has been addressed in a number of earlier studies. As detailed in the introduction, all of the cutaneous mechanoreceptors that play a role in discriminative touch are sensitive to tactile speed, including afferents categorized as slowly adapting (SAI, SAIL) as well as rapidly adapting (RA, PC). In the present study, we categorized each cell according to its adaptation rate since it is known that cortical neurons retain their adaptation properties (Sretevan and Dykes 1983; Sur et al. 1984). In these recordings, no cells with properties consistent with receiving PC inputs were observed (large RF and sensitive to an air puff directed to the field). This is not too surprising since PC-like responses are only rarely encountered in S1 (Hyvärinen and Poranen 1978; Iwamura et al. 1983, 1985; Tremblay et al. 1996). Overall, we found that speed-sensitive neurons had approximately equal proportions of RA and SA (40%, 60%) responses to maintained touch. Identical proportions were observed for the neurons sensitive only to texture. These findings suggest that all types of afferents contribute to tactile speed appreciation. Although our classification (RA/SA) was based on qualitative responses elicited by manual stimulation, we emphasize that the proportions of SA units identified in areas 3b and 1 (44% and 52%, respectively) are fairly close to those reported by Pei et al. (2009), who used controlled mechanical stimulation (58% and 46%) to classify cell types. Our modestly lower estimate in area 3b may represent sampling bias since SA responses are restricted mainly to middle cortical layers (Sur et al. 1984).

**Tactile speed signals in S1 cortex.** Speed sensitivity in S1 bore several similarities to the discharge patterns seen at the level of primary afferents. First, the sign of the relationship between discharge frequency and speed was in all cases positive, i.e., discharge rate increased as a function of speed. This observation is consistent with a number of previous studies in S1 that have shown that discharge rates generally increase with increased speed of various stimuli including brushes, scanned
surfaces, and simulated moving bars generated with multiprobe arrays (DiCarlo and Johnson 1999; Gardner et al. 1992; Romo et al. 1996; Tremblay et al. 1996; Whitsel et al. 1972). The absence of negative (“inhibitory”) responses to speed in our sample compared with earlier studies (e.g., DiCarlo and Johnson 1999; Sinclair and Burton 1991) can be explained by the sampling procedure, since only neurons showing an increase in discharge during surface scanning were tested. Second, cells generally showed a monotonic increase in discharge rate as speed was increased. We found only a few cells (~12% of the speed-sensitive cells) with some evidence of saturation at higher speeds (nongraded), but the range of speeds tested, corresponding to speeds used during tactile exploration, was limited. We likewise found no evidence for cells tuned to a particular speed, as seen in the visual system. Again this may be a function of the restricted range of speeds tested (see below). Third, speed sensitivity was often associated with texture sensitivity, consistent with the discharge properties of peripheral afferents.

Speed sensitivity was distributed across all three areas of the S1 cutaneous hand representation, consistent with our previous observations (Tremblay et al. 1996). The proportion of speed-sensitive cells in area 3b, 52%, was lower than that reported by DiCarlo and Johnson (1999), 90%, possibly reflecting their use of a different range of speeds (20–80 mm/s vs. 40–105 mm/s here) and/or differences in the physical characteristics of the surfaces (dot height, material, etc.). Our results suggested that there is a trend for a rostrocaudal gradient in speed sensitivity: areas 3b, 52%; 1, 63%; and 2, 72%. Moreover, the speed-only cells were almost entirely restricted to areas 1 and 2. When combined with the observations that areas 1 and 2 contained the large majority of the cells showing a stronger relation with speed ($r^2 > 0.2$, 20/21) along with almost all of the cells showing a graded increase in discharge with speed for both sets of surfaces (26/27), we suggest that these two areas likely play an important role in tactile speed. We have previously suggested that the rostral areas (3b and 1) are particularly concerned with tactile texture (Meftah et al. 2009), and this is in agreement with the work of others (e.g., Darian-Smith et al. 1982; Sinclair and Burton 1991). We now suggest that caudal S1, specifically areas 1 and 2, is preferentially involved in extracting speed signals. This scenario is supported by the observation that only 24% of texture cells in area 2 were insensitive to scanning speed, compared with 45% for area 3b and 38% for area 1.

Our observation of speed-only ($n = 14$) and texture-only discharge patterns ($n = 33$) in S1 is consistent with earlier reports (Jiang et al. 1997; Tremblay et al. 1996). The peripheral signals themselves, however, covary with both parameters. We have previously suggested (Meftah et al. 2000) that the texture-only response pattern may reflect the result of a central transformation, subtracting the speed signal online from the original texture- and speed-varying signal to generate an invariant representation of texture. Alternately, texture invariance may represent the output of the SAI-mediated spatial variation code for tactile roughness (Connor et al. 1990). This code is insensitive to changes in scanning speed (DiCarlo and Johnson 1999, and Johnson and Hsiao (1992) proposed that the spatial code is eventually transformed into a mean rate code at some level in the processing of tactile inputs. To explain the speed-only cells, the necessary speed-invariant texture signal is present in S1 and this may be subtracted from the texture- and speed-varying signal. The speed-only cells were mainly found in areas 1 and 2, while the texture-only cells were especially characteristic of areas 3b and 1. Thus the transformation likely occurs in the more caudal parts of S1 where speed-only cells were found (areas 1 and 2).

Interactions between speed and texture are, however, a key component of tactile speed scaling. As described in the introduction, surface structure (texture) is essential because subjects have great difficulty in scaling the speed of a moving smooth surface. Yet texture modifies speed perception, since rougher surfaces are systematically rated as moving more slowly than smoother surfaces (Dépeault et al. 2008). In the latter study, we showed that SP (longitudinal) and not dot density was the critical factor underlying the underestimation of tactile speed with rougher surfaces, and this is independent of dot disposition. While we identified a sizable proportion of neurons that met most of our criteria for cells underlying tactile speed perception (graded with speed, insensitive to dot disposition), one key criterion was not met, namely, decreased discharge for rougher vs. smoother surfaces while preserving a graded pattern of discharge with tactile speed. Tactile speed scaling must therefore depend on further processing of tactile motion signals. This is likely to be a function of higher-order areas, e.g., posterior parietal cortex (areas 5 and/or 7) or secondary somatosensory cortex (S2).

**Texture sensitivity in S1 cortex.** The discharge of a high proportion of the S1 neurons, 80% of the sample, covaried with the longitudinal SP of the periodic and/or nonperiodic raised-dot surfaces. The relationship to SP was not analyzed in detail in this report, but it is of note that a proportion of these showed a monotonic increase in discharge rate across the range of SPs tested here, 2 to 8 mm (e.g., Fig. 4C). Such a discharge pattern, along with insensitivity to scanning speed (Fig. 3C), is consistent with such a neuron playing a key role in scaling the roughness of textured surfaces, since roughness estimates (same surfaces) also show a monotonic increase as SP is increased (Dépeault et al. 2009) and are insensitive to changes in scanning speed (Meftah et al. 2000).

**Neuronal code for tactile speed.** The main measure of cell sensitivity to tactile speed was the mean discharge rate during the entire stimulation period. We tested the possibility that tactile speed might be signaled in S1 by a spike count code (see METHODS), but our analyses showed that the mean rate code gave results superior to those obtained with the spike count measure. Indeed, for the obviously speed-sensitive neuron illustrated in Fig. 3B spike count showed no change across the three scanning speeds, whereas the discharge rate increased significantly. This most likely reflects Darian-Smith et al.’s (1980) observation that cutaneous mechanoreceptive afferents generate fewer spikes per raised dot when scanning speed is increased. Our results are consistent with those of Essick and Edin (1995), who showed that primary tactile afferents sensitive to tactile motion use a mean rate code and not a spike count code. Indeed, spike counts actually decline as brushing speed increases. Thus we rejected the possibility that tactile speed is signaled by a spike count code.

The choice of analysis interval (epoch 5, Fig. 2) was in turn based on the results of preliminary analyses that showed that the strength of the relationship between discharge rate during this period and speed was higher than for measures restricted to either the first or second half of the surface scans. We were,
however, surprised that the measures based on the first half of the surface presentation did not give stronger correlations. This measure gives greater weight to the initial part of the surface presentation, and Luna et al. (2005) had suggested earlier that S1 may rely on a forward-weighted code to signal differences in flutter vibration frequencies. Although we cannot discount the possibility that task differences (somatosensory discrimination task in Luna et al. vs. diversionary task here) contributed to our negative result, the difference can more likely be explained by the neuronal code used—a mean rate code here vs. a spike count code for Luna et al.—which, as explained above, was not well suited for the present data.

Overall, we suggest that the neuronal basis for tactile speed estimates can best be explained by the discharge properties of the speed-sensitive neurons located in areas 1 and 2, specifically those cells with higher $r^2$ values. These two areas contained almost all of the speed-only cells. Moreover, areas 1 and 2 contained almost all of the cells showing the best fit between mean rate and speed, and all were speed sensitive for both sets of surfaces (periodic and nonperiodic) as predicted from the human psychophysics.

It remains to be determined, however, whether all of the speed-sensitive neurons contribute to subjective tactile speed estimates or if the speed-only cells might subserve this function, representing a form of sparse coding (Olshausen and Field 2004). The latter were not, however, texture sensitive as predicted by our finding of SP-varying speed estimates. Moreover, a proportion of the texture + speed cells (Fig. 8) were as well related to speed as some of the speed-only cells. Together, the present results do not allow us to reject the possibility that both cell types contribute to tactile speed scaling. As proposed above, however, it is clear that this must be a function of other higher-order regions.

Finally, our suggestion that speed-sensitive neurons contribute to subjective tactile speed estimates is limited to the range of speeds and surface textures investigated here. The present experiments need to be extended to include finer textures, since these can be more effective stimuli for other types of cutaneous mechanoreceptive afferents, including PC afferents (Bensmaia and Hollins 2003).

Parallels with visual motion. Sensitivity to motion is a general characteristic shared across the major sensory systems (somatosensory, visual, auditory, and vestibular). In the present study, we were struck by the general lack of obvious speed tuning. In contrast, speed tuning in visual cortices has been reported in both cats and monkeys, and this can take many forms including velocity low-pass, high-pass, broad-band, and tuned responses (e.g., Orban et al. 1981, 1986). Such tuning is present in retinal ganglion cells (Cleland and Lee 1985). In contrast, primary cutaneous mechanoreceptive afferents (Edin et al. 1995; Essick and Edin 1995; Goodwin and Morley 1987; Greenspan 1992; Lamb 1983) do not show tuning, suggesting that motion is not processed in the same manner in the visual and somatosensory systems. Alternately, the lack of tuning may be a function of the limited range of speeds tested, restricted here to speeds used during active touch. Thus our testing covered a range of speeds associated with monotonically increasing rates of discharge in cutaneous afferents (Essick and Edin 1995). Saturation of discharge can occur, but this is associated with higher speeds than those tested here.

Motion sensitivity in vision is generally associated with the “dorsal” pathway, which is specialized for action (Goodale and Milner 1992; Milner and Goodale 2008; Ungereider and Mishkin 1982). Within the visual system, motion sensitivity is generally a property of higher-order visual areas [e.g., the middle temporal (MT) and medial superior temporal (MST) areas] (Britten et al. 1993; Celebrini and Newsome 1994; Liu and Newsome 2005; Wurtz and Duffy 1992). There is some suggestion that somatosensory processing is also organized into dorsal and ventral streams (Friedman et al. 1986; Mishkin 1979). Although our recordings in S1 were at a relatively low level of processing, it is interesting that the speed-only cells were mainly found in the more posterior areas of S1, areas 1 and 2. Since speed and texture signals are confounded in the discharge of primary mechanoreceptive afferents, this pattern of discharge must represent the result of central processing to extract the portion of the signal related to speed. It is interesting to speculate that these speed-only cells might preferentially project to posterior parietal cortex, and so the dorsal stream, rather than to S2 (the ventral stream). The present recordings were extended to include S2 to determine the extent to which the properties seen in S1 are also seen in S2 (Cybulskaklosowicz A, Meftah EM, Chapman CE, unpublished observations). Preliminary analyses do not, however, support this suggestion, since speed-only cells are also found in S2, and in about the same proportion as seen in S1. An alternate interpretation is that both streams of processing require basic information about tactile motion both for planning and executing movements (dorsal stream) and for perception (ventral stream).

As also seen in the visual system (Campbell and Maffei 1981; Diener et al. 1976; cf. Smith and Edgar 1990), tactile speed scaling varies with the physical characteristics of the moving patterns, and so is dependent on both temporal and spatial cues (Dépeault et al. 2008). Specifically, a decrease in spatial frequency (1/SP) causes a decrease in perceived speed for both modalities. Together such findings suggest that important parallels exist between the somatosensory and visual systems as regards the processing of stimulus motion.

Concluding remarks. We identified a population of neurons, mainly located in areas 1 and 2, with discharge properties mostly consistent with playing a role in scaling tactile speed. Specifically, their discharge rate showed a monotonic relation with speed for testing with both periodic and nonperiodic surfaces. Our results also suggest that the underlying neuronal code is a simple rate code, the same code that is used by the primary mechanoreceptive afferents that are sensitive to tactile speed (Essick and Edin 1995). This latter observation raises an interesting question. Work from Johnson and collaborators (Connor et al. 1990; Connor and Johnson 1992; Yoshioka et al. 2001) has promoted the hypothesis that tactile roughness is not signaled by a mean rate code but by a spatial variation code. Although we recently challenged their rejection of a rate code for tactile roughness (Sutu et al. 2013), the spatial variation code does have the interesting property of being insensitive to scanning speed (DiCarlo and Johnson 1999), and so can account for the invariance of roughness estimates at different speeds (Lederman 1983; Meftah et al. 2000). So, do peripheral afferents use different neuronal codes to signal various physical attributes, a spatial variation code for texture and a mean rate code for speed and force (see, e.g., Wheat et al. 2010)? We
are currently investigating the neuronal code for tactile roughness, reexamining the mean rate code.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS


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