Title: Representation of tactile curvature in macaque somatosensory area 2

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ABSTRACT

Tactile shape information is elaborated in a cortical hierarchy spanning primary (SI) and secondary somatosensory cortex (SII). Indeed, SI neurons in areas 3b and 1 encode simple contour features like small oriented bars and edges, while higher-order SII neurons represent large curved contour features like angles and arcs. However, neural coding of these contour features has not been systematically characterized in area 2, the most caudal SI subdivision in the postcentral gyrus. Here, we analyzed area 2 neural responses to embossed oriented bars and curved contour fragments to establish whether curvature representations are generated in the postcentral gyrus. We found that many area 2 neurons (26 of 112) exhibit clear curvature tuning, preferring contours pointing in a particular direction. Fewer area 2 neurons (15 of 112) show preferences for oriented bars. Because area 2 response patterns closely resembled SII patterns, we also compared area 2 and SII response time courses to characterize the temporal dynamics of curvature synthesis in the somatosensory system. We found that curvature representations develop and peak concurrently in area 2 and SII. These results reveal that transitions from orientation tuning to curvature selectivity in the somatosensory cortical hierarchy occur within SI rather than between SI and SII.

Keywords: neurophysiology, touch, orientation, neural coding, single unit
Our remarkable perceptual capacity to perceive shapes through touch relies on object representations that are initially encoded in peripheral afferent systems and are subsequently transformed and integrated in somatosensory cortex (Johnson 2001; Phillips et al. 1988). Feature representations carried in the afferent systems are isomorphic with respect to the spatial features of contacted forms (Johnson and Lamb 1981; LaMotte et al. 1998; Wheat and Goodwin 2001). The point-by-point correspondence between a stimulus and its isomorphic representation in peripheral afferents results from the density, size, and simplicity of the slowly adapting type 1 (SA1) afferents’ receptive fields (RFs): Small punctate RFs convey information about skin deformations in only a restricted region (Sripati et al. 2006b). Thus, before integration in somatosensory cortex, shape information like orientation and curvature is only represented in the population responses across peripheral afferents (Khalsa et al. 1998; Wheat and Goodwin 2001).

At the first cortical processing stages in the somatosensory pathway, areas 3b and 1 of primary somatosensory cortex (SI), spatial form is decomposed into contour representations encoded by orientation selective neurons (Hsiao et al. 2002; Hyvarinen and Poranen 1978a). Many 3b and area 1 neurons respond to scanned and indented bars falling within their RFs at particular orientations (Bensmaia et al. 2008a). Orientation tuning in these populations is predicted by the geometry of excitatory and inhibitory response fields comprising these cells’ linear spatial RFs (Bensmaia et al. 2008a; DiCarlo et al. 1998; Sripati et al. 2006b). The sensitivity of orientation-selective neurons is comparable to human psychophysical angular thresholds measured in tactile orientation discrimination tasks (Bensmaia et al. 2008b), suggesting that orientation signals in areas 3b and 1 may account for psychophysical performance (Bensmaia et al. 2008a).
Larger, more complex shape features like contour curvature are encoded by neurons in second somatosensory cortex (SII) (Yau et al. 2009). Individual SII neurons respond selectively to curvature stimuli pointing in particular directions (i.e., curvature direction). Additionally, many SII neurons exhibit consistent response selectivity across RF locations spanning whole finger pads (Thakur et al. 2006; Yau et al. 2009) and over multiple digits (Fitzgerald et al. 2006b). These results indicate that response selectivity transitions from simple-to-complex feature tuning as one ascends the somatosensory cortical hierarchy (Bensmaia et al. 2008a; Phillips et al. 1988; Thakur et al. 2006).

Critically, the nature of contour representations in area 2, the most caudal SI subdivision in the postcentral gyrus (Kaas 1983), has yet to be systematically characterized. Area 2 potentially occupies an important processing stage in the somatosensory cortical hierarchy. Based on anatomical tracer studies, area 2 appears to be the primary route by which information transfers between SI and SII: It is densely innervated by feed-forward projections from other SI regions (Jones et al. 1978; Kaas 1983; Kaas et al. 1979) and connects directly and reciprocally to SII (Friedman 1983; Pons et al. 1992; Pons and Kaas 1986). This connectivity pattern raises the question of how shape representations in area 2 compare to those in areas 3b and 1 and those in SII. This is a critical issue not only because it provides information regarding how contour representations are transformed between SI and SII, but also because somatosensory information from SI, which is used to guide haptic interactions with objects, projects to posterior parietal association cortex via area 2 (Mountcastle et al. 1975). Thus, area 2 may be an important junction where form information is processed before projecting to the dorsal and ventral pathways proposed in somatosensory dual stream models (Reed et al. 1996; Reed et al. 2005). Indeed, evidence from monkey ablation studies (Carlson 1981;
Randolph and Semmes 1974) and neuroimaging studies in humans (Bodegard et al. 2001; Bodegard et al. 2000) support the case for area 2 playing an important role in tactile shape processing.

In the present study, we tested whether area 2 neurons explicitly code for curvature by analyzing single-unit responses to embossed oriented bars and contour curvature stimuli in two awake macaque monkeys. We fit each neuron’s response pattern with separate tuning models designed to capture orientation and curvature selectivity: Direct comparison of model performance allowed us to determine tuning preferences objectively for each neuron. We verified the modeling results using model-free metrics and quantified population response distributions. Lastly, we directly compared the temporal dynamics of area 2 and SII contour responses.

METHODS

Behavioral and neurophysiological methods. We recorded extracellular action potentials from well-isolated somatosensory neurons located in Brodmann area 2 in the postcentral gyri of two awake rhesus monkeys (Macaca mulatta). The animals were trained to sit in a primate chair with their hands restrained while tactile stimuli were indented into the skin surface of the distal pad of digits 2, 3, or 4 on the animals’ right hand. One animal (monkey-S; male; 5.85 kg) was trained to sit passively and was given liquid rewards at random intervals; the other animal (monkey-X; female; 8 kg) was trained to perform a visual vigilance task and was rewarded for maintaining visual fixation within a 5°–radius window on a computer monitor that was positioned in front of the animal but slightly offset to its left (away from the fixed right hand and the motorized stimulator). Despite the fact that the animals were tested under different cognitive conditions with attentional demands that may have differentially influenced area 2 responses (Burton and Sinclair...
2000; Meftah et al. 2002), we confirmed that response properties, over a variety of measures, did not significantly differ between monkeys (see below). Unfortunately, while the animals’ head positions were fixed during the experiments, we did not manipulate or assess their deployment of visual attention, so it is possible that the animals, especially the passively behaving one, directed visual attention toward their partially-visible, stimulated hand. Because vision and deployment of attention can influence somatosensory activity (Forster and Eimer 2005; Taylor-Clarke et al. 2002) and tactile sensitivity (Kennett et al. 2001), this potential unsupervised behavior may have introduced additional variability to the recorded neurophysiological responses; however, systematic selectivity patterns are unlikely to emerge through this behavior alone. All procedures were approved by the Johns Hopkins Animal Care and Use Committee and conformed to National Institutes of Health and US Department of Agriculture guidelines. After the animals’ initial training period, recording chambers (19 mm diameter) were positioned over the central sulcus in the left hemisphere of each animal according to Horsley-Clarke coordinates (anterior 6; lateral 21). Prior to the start of the neurophysiological experiments, a 3-mm craniotomy was trephined within the recording chamber for initial mapping. The craniotomy was gradually expanded in order to expose dura over the region of interest. On each recording day, a custom multielectrode-microdrive system (Mountcastle et al. 1991) was loaded with up to 7 quartz-coated platinum-tungsten (90:10) electrodes (shaft diameter, 80 μm; tip diameter, 4 μm; impedance, 1-5 MΩ at 1 KHz). The microdrive proboscis was inserted into the saline-filled recording chamber and oriented such that the electrodes were perpendicular to the skull. Each electrode was then individually advanced through the dura and into the cortex until multiunit neural activity was detected. When all electrodes were properly positioned in the superficial cortical layer,
each electrode was again advanced gradually while we manually mapped and characterized multiunit RFs. We identified the location of area 2 in the postcentral gyrus by first locating the central sulcus (CS) based on the pattern of neural responses we encountered during the microelectrode penetrations. After locating the CS, the microelectrode array was oriented to be parallel and posterior to the CS to maximize coverage of the SI digit representations in the post-central gyrus. The position of the microdrive was adjusted daily such that the electrode array systematically covered the digit representations in area 2. We identified area 2 recording sites (in contrast to areas 3b and 1) on the basis of RF location transitions in the somatotopic maps encountered during the advancement of the electrodes, RF size (spanning multiple pads and digits), and response properties (the presence of neurons with mixed cutaneous and proprioceptive sensitivities). Recorded extracellular potentials were band-pass filtered and fed into a multi-channel spike sorter (Alpha Omega, Alpharetta, GA), which detected action potentials based on similarity to fitted spike templates. Spike sorting allowed us to isolate up to 3 distinct units per electrode. Although the RFs of units isolated on the same electrode typically spanned the same skin regions, this was not always the case for units isolated on different electrodes. For each recording session, we identified the distal finger pad that was most responsive across the set of isolated units and chose this as the site of tactile stimulation. For this reason, the tactile stimulation may not have been presented at the optimal ‘hot-spot’ location within some neuron’s RFs (see Discussion).

SII recordings. In temporal dynamics analyses (see below), we compared area 2 response time courses to the response dynamics of SII neurons recorded in the same animals. We previously reported on the nondynamic data from these recording experiments (Yau et al. 2009). For SII experiments, recording chambers were positioned
over the animals’ lateral sulcus (Horsley-Clarke coordinates: anterior 6; lateral 28). In
initial mapping sessions the lateral sulcus was located based on the somatosensory,
auditory, and visual responses encountered as the electrodes passed through the gray
and white matter. We characterized isolated units’ response properties and RFs using
handheld probes and the motorized stimulator. A complete description of these
techniques has been detailed previously (Fitzgerald et al. 2004).

Stimulus set and tactile stimulator. Tactile stimuli were 2D angles and arcs machined
onto the surface of a 20-mm square plastic block (Ultem, General Electric). For each
stimulus, background material was removed to leave a 0.5-mm wide contour at a relief
height of 5 mm (Fig. 1A). The stimuli were positioned such that angle vertices and arc
midpoints fell at the center of the square block. A 1.25-cm stalk on the opposite side of
the plastic block served as a handle for the stimulus gripper (Fig. 1B). Contour stimuli
included three angles (45, 90, and 135°) and three circular arcs (radius of curvature: 1,
5, and 7.5 mm) (see Fig. 2A, angles and arcs alternate across columns). Stimuli were
presented at 8 directions (45° intervals) (see Fig. 2A, rows). The full stimulus set thus
comprised 48 unique spatial patterns that were defined by curvature direction (0–315°),
subtense (angle subtended by the curvature fragment), and whether they contained a
sharp corner (angles vs arcs). We also tested for responses to a straight bar presented
at 8 orientations (22.5° intervals) (see Fig. 2C). For all stimuli, the contours extended to
the block boundaries to ensure that they reached beyond the finger pad contact area.
This design guaranteed that only continuous contour fragments (and no abrupt
terminations) contacted the single stimulated finger pad in each experiment: The stimuli,
therefore, were entirely contained within the boundaries of the RFs of area 2 neurons.
(For comparison, these stimuli would extend beyond the more restricted boundaries of
RFs in areas 3b and 1, which would confound characterizations of contour tuning properties in these neural populations.) The two smallest arcs (1 and 5-mm radius) subtended 135° and continued with straight line segments to the block edges. The arc stimuli were designed such that their spatial profiles closely matched those of the angle stimuli (i.e., subtense spanning 45–135°).

The stimulator (Fig. 1B) was a servo-controlled linear motor (Baldor Electric Company, Inc., Santa Clarita, CA) that mounted onto a magnetic forcer and translated with 0.01-mm precision across a downward-facing horizontal plane on a frictionless air cushion (Aerotech, Inc., Pittsburgh, PA). The linear motor provided 40 mm of vertical travel with an accuracy of ~1 μm. A small rotary stepper motor (Arsape, Inc., Switzerland) attached to the bottom of the linear motor provided a full range of stimulus rotation. A pneumatic ‘gripper’ motor (Pisco USA, Bensenville, IL), fixed to the bottom of the rotary motor, was used to retrieve individual stimulus blocks under computer control from a cassette containing all of the machined stimuli. Detailed specifications for this stimulator have been described previously (Lane et al. 2010).

Experimental design. At the outset of each experimental session, we first mapped the RFs of the isolated area 2 neurons by presenting oriented bars to the distal pads of digits 2, 3, and 4 (Fig. 1A). This procedure enabled us to identify quantitatively the most responsive distal finger pad and we centered the contour and bar stimuli on this pad in the main experiment. Critically, because our stimuli enable characterization of contour responses on only a single finger pad, it is important to note that we typically palpate larger objects that span multiple digits. Shape processing, therefore, requires the integration of cutaneous information simultaneously acquired over multiple hand
locations (Hsiao 2008; Pont et al. 1997), and our experiment, like other studies focusing on a single pad, offers a first approximation of coding for shape 'primitives' which may serve as fundamental building blocks for tactile shape synthesis. Stimuli were indented perpendicular to the skin's surface to a displacement of 1.3 mm beyond the point of initial skin contact (which was recalibrated for each session). Stimuli were presented for 500 msec with an inter-stimulus interval ranging from 0.5 to 2.5 sec. Each stimulus was randomly presented at all 8 directions before another stimulus was retrieved. All stimuli were presented in random order without replacement, and the entire procedure was repeated five times. The tactile stimulus was not visible to the animals.

Data Analysis

We first identified neurons that exhibited statistically significant response modulation due to tactile stimulation: The inclusion of neurons in subsequent analyses (112 of 121 recorded neurons) depended on whether evoked responses were significantly greater than baseline activity (one-tailed, unpaired t-test, $P < 0.05$). For each stimulus, the response rate was calculated by summing spikes over the 500-ms presentation period and averaging across 5 repetitions. Baseline responses were calculated from blank trials, interspersed throughout the experiment, in which no stimulus was presented.

Characterizing curvature selectivity. The curvature direction, $\theta_i$, for each stimulus was the direction of a vector along the stimulus axis of symmetry pointing away from the interior of the angle. This corresponds to the direction in which angles and arcs are typically described as pointing toward (e.g. a 90° angle stimulus pointing to the right has a $\theta_i$ value of 0). For each cell, we determined the response rate to the $i$th stimulus, $R_i$, at
direction $\theta_i$, by summing spikes over the 500-ms presentation period and averaging across 5 repetitions. We fit the responses with a 4-parameter curvature-tuning model based on a von Mises function (circular normal function), a gain term, and a baseline term, using a nonlinear least-squares algorithm (lsqnonlin; Matlab, Mathworks Inc.). The population distribution of preferred curvature directions (von Mises function peaks) was assessed for circular uniformity with a Rayleigh test.

We quantified the significance of direction tuning by computing a direction index ($DI$) based on vector strength for each neuron (Yau et al. 2009):

$$DI = \sqrt{\left[ \sum R_i \sin(\theta_i) \right]^2 + \left[ \sum R_i \cos(\theta_i) \right]^2 \sum R_i}$$

Values of $DI$ range from 0 (uniform response to all directions) to 1 (non-zero response to only one direction). For each neuron, we determined the statistical significance of $DI$ by randomizing responses across the 48 stimuli 50,000 times and recalculating $DI$ each time to obtain a distribution of values expected by chance (Yau et al. 2009). A separate randomization distribution was calculated for each cell. We defined tuning to be significant when the actual $DI$ value exceeded 95% of the values in the randomized distribution. We also used a randomization test to determine whether the numbers of significantly curvature-tuned neurons were greater than expected by chance (Yau et al. 2009). In this population test we randomized responses across stimuli within neurons. For each neuron we tested whether the $DI$ of the randomized responses exceeded its previously determined significance threshold, and we counted the number of neurons in the entire sample that exceeded significance. This procedure was repeated 50,000 times to generate a distribution of numbers of tuned neurons expected by chance. The actual number of significantly curvature-tuned neurons was larger than any point in the
Characterizing orientation selectivity. This analysis tested the hypothesis that area 2 responses to the curvature fragments could be explained simply by orientation tuning. In order to relate the contour stimuli to orientation, each contour stimulus was decomposed into 2 component orientations (joined at the angle vertices or arc midpoints) whose orientation values were determined by the orientation of perpendicular bisectors. For example, a 90° angle stimulus pointing to the right consisted of components oriented at 45° and 135°. The response rate to each contour stimulus was assigned to both of its component orientations. We fit these responses in the orientation domain with a 4-parameter orientation-tuning model based on a Gaussian function, a gain term, and a baseline term, using a nonlinear least-squares algorithm (lsqnonlin; Matlab, Mathworks Inc.). This procedure allowed us to objectively relate preferred orientations identified from the contour responses with preferred orientations identified independently based on fitting a Gaussian orientation model to each neuron’s responses to the oriented bar stimuli only. Furthermore, the performance of the orientation-tuning model fit to the contour responses could then be directly compared to the performance of the curvature-tuning models fit to the same dataset, thereby providing an objective method for identifying each neuron’s tuning preferences (i.e., orientation vs curvature).

For each neuron, we quantified significance of orientation tuning using vector strength by computing an orientation index (OI) an analogous metric to DI:

\[ OI = \sqrt{\frac{\left(\sum R_B \sin(2\theta_B)\right)^2 + \left(\sum R_B \cos(2\theta_B)\right)^2}{\sum R_B^2}} \]
where $R_b$ is response rate to a bar stimulus (spanning the entire finger pad) presented at orientation $\theta_B$. Values of $OI$ range from 0 (uniform response to all orientations) to 1 (non-zero response to only one orientation). We determined statistical significance of $OI$ for each cell by randomizing its response rates across the bar stimulus trials 50,000 times and recalculating $OI$ each time to obtain a distribution of values expected by chance. We defined tuning to be significant when the actual $OI$ value exceeded 95% of the values in the randomized distribution. Furthermore, as in the curvature analysis, we determined whether the actual number of significantly orientation-tuned area 2 neurons was greater than expected by chance using a randomization test.

Comparison of curvature and orientation tuning. We compared curvature and orientation model performance in neurons exhibiting significant tuning by computing Bayesian information criterion (BIC), a statistical measure used in model selection (Bensmaia et al. 2008a):

$$BIC = n \cdot \log \left( \frac{RSS}{\bar{r}} \right) + k \cdot \log(n)$$

where $n$ is the number of trials, $k$ is the number of model parameters, and $RSS/\bar{r}$ is the summed squared residuals normalized by average response rate. This metric weights model performance against model complexity, and the best fitting model is that which yields the smaller criterion measure.

We computed a single metric relating each neuron’s tuning for curvature direction and component orientation with a tuning strength ratio index:

$$TR = \frac{r_C^2 - r_O^2}{r_C^2 + r_O^2}$$
where $r_C^2$ and $r_O^2$ is the response variance explained by the curvature and orientation models, respectively. Positive tuning strength ratio values indicate stronger curvature preferences, 0 indicates equal selectivity for curvature and orientation, and negative values indicate stronger component orientation preferences.

**Position consistency index.** Each contour stimulus was repeated at 5 positions uniformly spanning 4 mm across the finger pad (Fig. 6A). As a measure of tuning consistency across stimulus contact positions, for each neuron we computed the correlation between the response pattern at the center position and the average response pattern across positions. High correlation values indicate consistent contour selectivity across the finger pad. We determined the statistical significance of each neuron’s position consistency index by randomizing contour responses across all contact positions 1,000 times and recalculating correlation each time to obtain a distribution of index values expected by chance. We defined position consistency to be significant when the actual consistency index exceeded 95% of the values in the randomization distribution.

**Characterizing curvature response modulation.** We supplemented the curvature-tuning analyses based on model-fitting and vector strength with more general analyses of variance designed to identify specific stimulus factors contributing to response variation. We first performed a full two-way ANOVA with main effects of stimulus type (6 levels corresponding to 3 angles and 3 arcs) and direction (8 levels) and an interaction term. To assess the extent to which subtense (45, 90, and 135°) modulated response rates, we collapsed responses across the direction domain and across angles and arcs before conducting a one-way ANOVA with subtense as the single factor. Lastly, we collapsed
responses across the subtense and direction domains and performed paired t-tests contrasting responses to angles and arcs.

Contour response time course analysis: Overview. We characterized the temporal dynamics of neural responses in area 2 and SII (from the same animals) whose curvature responses we have described previously (Yau et al. 2009). In separate analyses, we compared response dynamics between 1) all responsive neurons in area 2 (n = 112) and SII (n = 210) and 2) only curvature-tuned neurons in area 2 (n = 26) and SII (n = 37).

Spike density functions. We computed instantaneous response rates (PSTH bin size, 1 ms) by convolving the spike trains with a spike density function comprising two exponentials:

\[ R(t) = \left(1 - \exp\left(-t / \tau_g\right)\right) \cdot \left(\exp\left(-t / \tau_d\right)\right) \]

where \( \tau_g \) and \( \tau_d \) are the time constants for the growth phase and decay phase (1 ms and 20 ms, respectively). The time constants were chosen to fall within the range of values previously used to generate smoothing kernels (Thompson et al. 1996; Yau et al. 2012). Smoothing spike trains with asymmetric spike density functions yields more accurate instantaneous rate estimates by avoiding backward biasing (Thompson et al. 1996). We averaged PSTHs across the area 2 and SII samples to generate separate population response curves (Fig. 9).

Curvature response dynamics. For the area 2 and SII samples, we computed curvature response time courses for the \( i \)th neuron by defining a temporal index of curvature modulation:
where $R_{\phi_p}(t)$ is the mean response of the neuron to its preferred curvature direction, $\phi_p$, and $R_{\phi_{np}}(t)$ is the mean response to its least preferred curvature direction, $\phi_{np}$, at time $t$.

We computed separate area 2 and SII population curvature time courses by averaging curvature modulation indices over curvature-tuned neurons (Fig. 9B) and over all neurons exhibiting significant evoked responses in each sample (Fig. 9E).

Time course comparison tests. We compared the curvature modulation time courses in the area 2 and SII populations by comparing the times at which population traces developed and peaked in the two brain areas. Separate analyses were conducted on samples including only curvature-tuned neurons and all responsive neurons.

Specifically, we computed the first time point at which each population curvature modulation time course exceeded baseline (mean response from –50 to +50 ms relative to stimulus onset) by a response threshold defined as a percentage of its baseline-to-peak range (60, 65, 70, 75, 80, 85, 90, 95, and 100%). We performed the area 2 and SII comparisons with latency defined over a range of thresholds to establish the robustness of these statistical results, and the difference (i.e., offsets) in area 2 and SII latencies provided a measure of how curvature modulation strength increased differentially in the two cortical areas (Fig. 9C,F). A randomization procedure (Yau et al. 2012) was then used to test the statistical significance of the observed time differences: Each neuron’s curvature modulation time course was randomly assigned to area 2 and SII samples and offsets were recomputed. This process was repeated 50,000 times to generate a distribution of offset values expected under the null hypothesis that area 2 and SII curvature modulation latencies are equivalent. Observed offsets were considered
statistically significant if they exceeded 95% of the null hypothesis distribution (Manly 1997). For a global measure of offset measures, we tested the statistical significance of the mean offset averaged over the full range of tested latency thresholds. In addition, we used a randomization Kolmogorov-Smirnov procedure (Yau et al., 2012) to test whether the cumulative difference between area 2 and SII curvature modulation time courses was significant across the 0–300 ms time period. This analysis provided an agnostic complement to the peak offset analysis (which depended on latency threshold definitions), and enabled us to compare the growth of curvature modulation strength over an interval during which the area 2 and SII curvature modulation time courses peaked. The same randomization procedure was used to generate a distribution of maximum cumulative difference between area 2 and SII curvature modulation time courses. The observed maximum cumulative difference was considered significant if it exceeded 95% of this null hypothesis distribution.

RESULTS

We recorded the responses of 121 area 2 neurons in the left hemisphere of two macaque monkeys (monkey-S: \( n = 55 \); monkey-X: \( n = 66 \)). We combined neurons from both monkeys in population summaries because response measures (linearity index, position consistency indices, direction indices, and variance explained by ANOVA) did not differ significantly between monkeys (two-sample t-tests; \( P > 0.05 \)). Tactile stimuli (Fig. 1A) presented to a single distal finger pad significantly modulated \( (P < 0.05) \) response rates in approximately 93% of area 2 neurons (112 of 121). Systematic response selectivity was clear in individual neurons’ raw activity and we characterized population distributions of curvature selectivity (observed in 26 neurons) and orientation selectivity (observed in 15 neurons) using tuning models and model-free response metrics (see below).
Figure 2 shows example neurons that exhibit curvature selectivity. Average response to each stimulus (during the 500-ms presentation period) is indicated by the background gray level (see scale bar). The average response pattern of the first neuron (Fig. 2A) revealed systematic preferences to a small subset of contour stimuli: This response pattern reflected tuning for specific curved contour stimuli pointing to the left (180°) and upper left (135°) that was captured by a von Mises function (Fig. 2A, marginal plot) fit to responses sorted by curvature direction (Methods). Concentrated activity in a single peak along the curvature direction domain is also obvious in the central bouquet plot summarizing the neuron’s sorted raster plots and peri-stimulus time histograms (Fig. 2B). Notably, the banding that is visible in the direction-sorted raster data (which displays the spike trains of all tested contours that point in one direction) reflects this curvature-tuned neuron’s robust responsiveness to specific contours rather than all leftward-pointing curvature stimuli. In contrast, the responses of the second example neuron (Fig. 2D,E), which revealed clear selectivity for curvature stimuli pointing to the right (0°), were more evenly distributed over narrow and broad contours. We previously observed a similar diversity in contour selectivity patterns across SII neurons (Yau et al. 2009). Notably, these curvature-tuned neurons responded less well to oriented bar stimuli (Fig. 2C,F).

Figure 3 features two neurons that produced average response patterns that revealed characteristic tuning for orientation rather than curvature. While orientation-tuned neurons also responded selectively to particular contour stimuli, the projection of spiking rates into the curvature direction domain (Fig. 3A,D, marginal plots) yielded 2 distinct response peaks that cannot be easily modeled with the von Mises curvature-tuning
functions. Thus, the bimodal response pattern, also clear across the raster plots and PSTHs (Fig. 3B,E), is inconsistent with tuning for curvature. Such response patterns are consistent with stimulus preferences based on orientation sensitivity, which is evident in the neurons’ responses to the oriented bar stimuli (Fig. 3C,F). Indeed, when we fit the contour responses of orientation-tuned neurons (Fig. 3A,D) with a model designed to capture sensitivity to the component orientations comprising the larger stimuli (i.e., two oriented line segments joined at the stimulus vertex or midpoint; see Methods) we found that the preferred orientations of smaller contour segments matched the preferred orientations for the larger bar stimuli. In other words, an orientation-tuned neuron preferring bar stimuli oriented near 90° tended to respond more strongly to curvature stimuli containing component segments oriented near horizontal (Fig. 3A,C). Similarly, a neuron preferring bar stimuli oriented near 45° tended to respond more strongly to curvature stimuli consisting of components matching this oblique orientation (Fig. 3D,F).

In short, selective contour responses of some area 2 neurons are explainable in terms of orientation sensitivity, rather than curvature tuning.

For each neuron exhibiting significant response modulation, we modeled tuning for curvature with von Mises functions that capture a single response peak in the curvature direction domain (Methods). We quantified tuning significance with vector strength indices (Methods). Across 112 significantly responsive area 2 neurons, tuning strength did not correlate with response strength indexed by maximum response rate ($r = 0.11$, $P = 0.25$) or average response rate ($r = 0.06$, $P = 0.54$). Of this sample, 26 neurons displayed significant tuning for curvature (Fig. 4A, filled circles). This proportion of neurons (23%) was significant based on a randomization test ($P < 0.0001$). Curvature models explained on average 27% ± 3% of the response variance in significantly tuned
neurons. In general, curvature models tended to account for more response variance in neurons with larger and significant vector strength values (Fig. 4A). Some response variance unexplained by these models was likely attributable in part to tuning for stimulus characteristics other than curvature direction, like subtense selectivity or differential sensitivity to angles and arcs (see below), which these simple models ignore.

Orientation tuning (Fig. 4B) was significant in 13% of the sample (15 of 112 neurons; filled circles; randomization test, \( P < 0.001 \)). We modeled tuning for orientation with Gaussian functions that capture a single response peak in the orientation domain (Methods). For neurons with significant tuning, orientation models fit to curved contour responses explained a substantial amount of response variance (mean \( r^2 = 0.18 \pm 0.02 \)). Critically, we validated these orientation models by separately fitting models to bar responses (mean \( r^2 = 0.87 \pm 0.02 \)). Preferred orientations (estimated Gaussian peak values) were highly similar between models fit to the two response sets \( (r = 0.73, P < 0.005) \), as was model performance \( (r = 0.29, P < 0.005) \), confirming that contour responses in a subset of area 2 neurons reflected orientation sensitivity.

We determined whether contour responses were better explained by the curvature models or the orientation models using BIC (Methods). In the 38 neurons exhibiting significant tuning (Table 1; curvature (23), orientation (12), both (3)), curvature models generally performed better as these models yielded lower BIC values in 74% of the tuned sample (28 of 38 neurons): Most neurons with significant tuning fell below the unity line (Fig. 4C). This pattern suggests that curvature selectivity better describes area 2 contour responses compared to orientation selectivity. We further compared neural selectivity for curvature and orientation by computing tuning strength ratios (Methods), a
metric that summarizes each neuron’s relative tuning for curvature and orientation (Fig. 5D, larger values indicate greater curvature sensitivity). Across the population, the average tuning strength ratio was 0.10 ± 0.04. This value was significantly greater than 0 (one-tailed t-test, \( P < 0.005 \)), indicating that curvature selectivity was more common than orientation selectivity in area 2. Average ratio value across curvature-tuned neurons (0.42 ± 0.05) was significantly greater than 0 (\( P < 1.8 \times 10^{-8} \)) and also greater than the average across orientation-tuned neurons (\( P < 0.001 \)).

Population distribution of preferred curvature directions. Estimated model tuning peaks (\( \mu \) parameter in the von Mises functions) summarize the preferred curvature direction for each neuron. Tuning functions for 26 curvature-selective neurons span a wide range of direction preferences (Fig. 5A). Preferred curvature directions are uniformly distributed in this sample (Fig. 5B, red histograms; Rayleigh test, \( P > 0.05 \)) and in the entire area 2 population (Fig. 5B, black histograms; \( P > 0.05 \)).

Position consistency of contour curvature tuning. Higher-order somatosensory neurons exhibit consistent response selectivity across multiple positions within single finger pads (Thakur et al. 2006; Yau et al. 2009) and over multi-digit RFs (Fitzgerald et al. 2006b). Curvature tuning for many area 2 neurons is highly consistent across multiple RF locations (Fig. 6). While the example neuron’s responses scaled depending on stimulus position with respect to the contacted finger pad region, its largest responses were generally confined to stimuli projecting in the 135–180° direction range (Fig. 6A). This neuron had a position consistency index of 0.78 (Methods). Across the entire population, 15 neurons (13% of the population) had significant position consistency indices (\( P < 0.05 \)). Average consistency index across this sample was 0.85 ± 0.01 (Fig. 6B, filled
histograms). Position consistency values across the remainder of the population (Fig. 6B, open histograms) were typically lower (0.63 ± 0.01). Notably, significant correlation between position consistency values and curvature tuning strength ($r = 0.42, P < 3.5 \times 10^{-5}$) indicates that the two response traits, both characteristics of nonlinear neural mechanisms (Thakur et al. 2006), may be yoked in the responses of area 2 neurons. However, as also seen in SII (Thakur et al. 2006), area 2 neurons exhibiting only orientation tuning also display position consistent responses (Table 1).

**Stimulus factors contributing to response modulation.** Our curvature models were designed to capture tuning for curvature direction but not selectivity for subtense (i.e. spanned angle) or differential sensitivity to arcs and angles. To characterize response selectivity to these features, we first performed a full ANOVA with response rate as the dependent variable and with stimulus (6 levels) and curvature direction (8 levels) as factors. In this analysis, the interaction effects represented response modulation that depended on the specific combinations of contour stimulus levels and direction levels. For example, the tuning preferences of the neuron in Figure 2A were captured by significant ANOVA main effects ($P < 0.05$) and a marginally significant stimulus x direction interaction ($P = 0.05$): ANOVA accounted for 40% of its response variance. Across the population, 57 neurons (51%) had significant ANOVA effects. Main effects generally dominated in area 2 as 47% (52 of 112 neurons) exhibited either or both significant main effects of stimulus and direction (Fig. 7A). In comparison, interaction effects achieved significance in only 20% of the neurons (22 of 112 neurons). In neurons showing significant response modulation (Fig. 7B, filled histograms), ANOVA models accounted for substantial amounts of response variance (mean $r^2 = 0.30 \pm 0.01$).
We tested whether the 57 neurons with significant response modulation (two way ANOVA, main or interaction effects) were selective for subtense by collapsing directional responses over angle and arc stimuli. Many neurons exhibited differential responses to the 45, 90, and 135° subtense levels (Fig. 8A). Over 25% of the curvature-responsive sample (15 of 57 neurons) showed significant subtense preferences (one-way ANOVA, P < 0.05). The majority of these neurons (8 of 15) responded best to contours with intermediate (90°) subtense values. Significant preferences in the remaining neurons were split between low and high subtense values. We also tested whether the 57 curvature-responsive neurons differentiated between angles and arcs (Fig. 8B). Only 3 neurons responded differently to angle and arc stimuli (paired t-test, P < 0.05).

While contour response patterns in area 2 closely resembled response patterns in SII (Yau et al. 2009), the temporal dynamics of curvature signals in these areas may have differed. Comparison of response time courses can provide information regarding the relationship between area 2 and SII curvature representations. One possibility is that somatosensory curvature representations are synthesized first in area 2, based on processing of feedforward inputs from areas 3b and 1; in this case curvature tuning would emerge earlier in area 2 compared to SII. Alternatively, area 2 curvature signals could merely reflect feedback of curvature representations initially generated in SII; in this case area 2 curvature tuning would appear delayed relative to SII. We tested these possibilities by comparing the response dynamics of curvature-selective neurons in area 2 (n = 26) and SII (n = 37). In area 2 curvature neurons, the average PSTH (Fig. 9A, black trace) peaked 119 ms after the stimulus was indented before it decayed to a lower, sustained response level. Area 2 curvature selectivity (Fig. 9B, black trace) developed more gradually before peaking at 233 ms and the modulation index remained elevated.
throughout the response period. In comparison, despite subtle differences in the temporal profiles (see Discussion), SII curvature neurons displayed a similar, general dynamic: The peak in the SII PSTH (156 ms; Fig. 9A, gray trace) preceded a delayed peak in the curvature modulation time course (244 ms; Fig. 9B, gray trace). This pattern implies that contour selectivity in both areas is initially weak, but gradually refines into clear curvature tuning after approximately 100 ms. Critically, in curvature-tuned populations, curvature signaling in area 2 evolves earlier or concurrently relative to curvature responses in SII (Fig. 9C). Area 2 curvature modulation peaks generally had shorter latencies compared to SII modulation peaks over the range of tested latency thresholds (% of baseline-to-peak range in curvature modulation traces), although no offset reached statistical significance (randomization test, $P > 0.05$). Notably, the average offset over latency thresholds (Fig. 9C, filled circle) was statistically significant (one-tailed t-test, $P < 0.05$) and indicated that curvature modulation in area 2 preceded SII. However, a threshold-independent analysis of the cumulative difference between area 2 and SII curvature modulation traces (over the 0–300 ms interval) revealed similar growth rates of curvature information in the two samples (randomization test, $P > 0.05$). In general, these results indicate that area 2 curvature signals do not lag their SII counterparts, which was also the case in time course comparisons testing all responsive area 2 and SII neurons (Fig. 9D,E). In these larger samples, peak offsets (Fig. 9F) always indicated more rapid area 2 curvature modulation growth, which was significant for a range of latency thresholds (75–85%, filled squares; randomization test, $P < 0.05$) and for the average over thresholds (one-tailed t-test, $P < 10^{-4}$). Together, the temporal analysis results support the hypothesis that area 2 curvature representations are generated in the postcentral gyrus, rather than merely reflective of SII feedback.

**DISCUSSION**
We have characterized area 2 responses to a parametric set of embossed curved contour stimuli and oriented bars, and we tested whether response patterns reflect orientation tuning or curvature selectivity. Our primary finding is that cutaneous neurons in area 2 exhibiting significant response modulation and selectivity tend to display stronger curvature tuning compared to orientation sensitivity: Curvature-tuned neurons prefer contour stimuli pointing in a particular direction. In a subset of neurons, contour response patterns reflected tuning preferences for orientation, which is consistent with their response selectivity to bar stimuli only. A sub-sample of neurons show position consistent tuning within a single finger pad and respond to contours projecting in similar direction ranges over multiple contact locations. Across the population, preferred direction is uniformly distributed. Few curvature-tuned neurons exhibit selectivity for (curvature) stimulus attributes like subtense and few neurons differentiate between arcs and angles. We also found that area 2 curvature tuning emerges earlier or at the same time as SII tuning, which argues against an area 2 coding mechanism that is based exclusively on SII feedback. Together, these results imply that the transition from orientation selectivity to curvature tuning occurs within SI rather than between SI and SII.

Form information in the somatosensory perceptual pathway begins with isomorphic representations carried by peripheral afferent populations (Johnson and Hsiao 1992). These representations undergo little transformation as they are relayed through the ventro-posterior lateral thalamus (VPL), the principal somatosensory nuclei (Jones and Darian-Smith 1984; Jones et al. 1982). Consistent with this, isomorphism is evident in layer IV responses in area 3b (DiCarlo and Johnson, 2000), the cortical target of thalamic projections (Lin et al. 1979). In contrast, 3b neurons in supra- and sub-granular layers encode small oriented bar and edge features (DiCarlo and Johnson 2000).
Feature selectivity in areas 3b and 1 is mediated by linear neural mechanisms:

Responses are reliably predicted by the spatial interaction between shape features and the geometry of excitatory and inhibitory response fields comprising neural RFs (Bensmaia et al. 2008a; DiCarlo et al. 1998; Sripati et al. 2006b). In contrast, tuning for curvature, like that observed in area 2 responses, is difficult to explain with linear neural mechanisms. Computational studies in the visual system posit that curvature processing requires multiplicative integration (i.e. ‘AND’ operations) of contour component inputs (Poirier and Wilson 2006; Zetzsche and Barth 1990). Nonlinear curvature synthesis may arise purely from specific integration patterns of feedforward inputs from earlier processing stages or synthesis may instead result from dynamic network interactions:

Visual response dynamics in V4 support the dynamic network mechanisms hypothesis (Yau et al. 2012). In area 2, our observation of delayed curvature tuning with respect to the earlier PSTH peak suggests that similar network processing operates in the somatosensory system, although this hypothesis remains to be tested explicitly.

Regardless, area 2 contour responses patterns imply that linear responses give way to nonlinear responses as one ascends the processing pathway in primary somatosensory cortex.

Nonlinear processing in area 2 is also supported by our observation that the response selectivity of curvature tuned neurons remained consistent over multiple positions on the finger pad. Tuning that is tolerant to position changes is a hallmark of higher-order object processing and cannot be explained by linear mechanisms (Thakur et al. 2006). There have been few reports of position invariant responses in the somatosensory system. We previously reported that SII neurons signal orientation and curvature direction over contact points spanning finger pads and digits (Fitzgerald et al. 2006b; Thakur et al. 2006; Yau et al. 2009). Similarly, Hyvarinen and Poranen (1978) found that a subset of...
area 2 neurons signaled orientation regardless of stimulus position across the hand. Our results confirm that complex tuning properties are not restricted to SII, but are present in SI populations as well. However, our experimental design was not ideally suited to characterize position invariant responses, and future studies are required to systematically explore this critical response trait by explicitly focusing on tuning consistency in single finger pads and over multidigit RFs.

We observed contour selectivity in a relatively small proportion of area 2 cells (51% based on ANOVA; 23% based on curvature tuning model analyses), although the number of tuned neurons was statistically significant. Even for selective neurons, the ANOVA and tuning models accounted for a relatively limited proportion of response variance in the contour dataset, because these simple models were restricted to particular stimulus domains (e.g., curvature, orientation, and acuteness) though the large stimulus set varied along these simultaneously. (For comparison, the Gaussian function explained substantially more response variance to the smaller set of bar stimuli, which varied along the orientation dimension only.) A complex model including separate orientation and curvature terms (Yau et al. 2012) likely would have accounted for more variance. More importantly, the identified numbers of selective neurons may not reflect the actual incidence of contour tuning in area 2. Because we isolated single-units based on spiking activity to contact and brushing with handheld probes during initial mapping periods, we may have excluded cutaneous neurons with highly specific and complex tuning properties that may have been unresponsive to simple stimulation (Hyvarinen and Poranen 1978a; Iwamura and Tanaka 1978). Furthermore, the numbers of untuned neurons may have been biased by our experimental procedure for selecting each session’s stimulus contact region: During multi-electrode recording, we identified the most responsive distal pad (on digit 2, 3, or 4) across a set of simultaneously recorded...
neurons (Methods), but the selected contact site may not have been optimal for all isolated neurons. Non-optimal stimulation may have produced noisier responses and weaker contour selectivity in some neurons. Additionally, as discussed above, the animals' behavioral states may have influenced response robustness (Burton and Sinclair 2000; Chapman and Meftah 2005; Meftah et al. 2002) thereby limiting our ability to characterize tuning preferences: More rigorous constraints on tactile and visual attention may have revealed clearer selectivity patterns. Lastly, many of the neurons that responded to stimulation, but failed to exhibit contour tuning, may have been selective for other stimulus features that we did not test. Besides spatial form, somatosensory neurons also encode stimulus motion (Pei et al. 2011; 2010; Ruiz et al. 1995; Warren et al. 1986), frequency (Mountcastle et al. 1969; Romo et al. 1998; Salinas et al. 2000), and texture (Chapman et al. 2002; Jiang et al. 1997; Randolph and Semmes 1974; Semmes and Turner 1977). For these reasons, the reported proportion of contour selective neurons should be viewed as a conservative estimate of the prevalence of this tuning property in area 2, though it is notable that a similar proportion of SII neurons (37 of 210) exhibited significant curvature tuning on a single finger pad (Yau et al. 2009). We found that few area 2 neurons differentiate between angle and arc stimuli (Fig. 8). This finding was surprising because peripheral SA1 afferent populations, which densely innervate the skin and project crisp, isomorphic representations of 2D form to cortex, are especially sensitive to sharp corner features (Phillips and Johnson 1981; Sripati et al. 2006a). The apparent scarcity of corner sensitivity in area 2 neurons has many potential explanations. One possibility is that this bias in the tuning of somatosensory cortical neurons reflects the statistics of our haptic interactions with objects: Because we typically contact smooth surfaces rather than sharp corners when we grasp and manipulate objects, cortical representation of corners may be sparse. A second
possibility is that the neural mechanisms underlying the integration of input signals to area 2 impose a spatial filtering cost on area 2 representations. Specifically, area 2 selectivity could reflect the limited spatial sensitivities of its feed-forward inputs from areas 3b and 1 – in these areas, most RFs only partially cover single finger pads and orientation tuning functions can be quite broad (Bensmaia et al. 2008). Spatial filtering through input signal integration could similarly lead to reduced area 2 selectivity for subtense. Area 2 insensitivity to these stimulus characteristics may account for general insensitivity to these properties in SII neurons (Yau et al. 2009). Critically, although subtense and corner information may not be encoded by individual neurons at intermediate stages of cortical processing, this information may still be maintained in the population activity across neural ensembles. Further studies are clearly needed to understand whether and how area 2 curvature representations contribute to tactile perception of sharp angles and corner features.

Curvature tuning patterns in area 2 are comparable to those in SII (Yau et al. 2009) with respect to the prevalence of tuned neurons, position consistency of tuning, and relative insensitivity to subtense. This degree of tuning similarity between the areas is somewhat surprising, although it may reflect the limitations of our experimental paradigm rather than true neurophysiological equivalence. Indeed, in the previous and current experiments we concentrated on identifying contour response selectivity on a single finger pad: More comprehensive sampling of RF locations (area 2 RFs typically cover one or more digits on a single hand (Pons et al. 1985) whereas SII RFs can span multiple digits on one hand or both hands in their entirety (Fitzgerald et al. 2006a; Robinson and Burton 1980)) may reveal clearer response differences. Similarly, probing with larger shape stimuli, rather than those designed to span a single pad, may reveal complex tuning preferences that are more relatable to naturalistic objects we typically
touch and manipulate. However, the response dynamics of area 2 and SII neurons potentially reveal important processing differences. Specifically, while the area 2 PSTH comprises a large initial response peak followed by sustained responses at a relatively diminished level, the distinction between onset and sustained responses in the SII PSTH is much less notable (Fig. 9). These dissociable time courses were evident in the temporal analysis including all neurons and also in the analysis restricted to only the curvature-tuned samples, suggesting that the evolution of area 2 and SII population spiking activity may be generally different. These differences may reflect distinct convergence patterns of rapidly-adapting (RA) and slowly-adapting (SA) inputs in area 2 and SII, although it is important to note that such response distinctions are less obvious in cortex compared to the peripheral afferent system (Pei et al. 2009).

Regardless, the temporal dynamics analysis reveals that area 2 curvature signals do not lag SII signals (Fig. 9). In analyses including all responsive neurons, curvature signals in area 2 preceded SII signals at all latency thresholds, but the offset between area 2 and SII curvature modulation time courses was statistically significant in only a subset of thresholds (75-85% of the modulation range). Similarly, in temporal analyses restricted to only the curvature-tuned neurons the average offset over all latency thresholds indicated earlier area 2 curvature signaling, although no offset between area 2 and SII times achieved statistical significance. Thus, from the fact that curvature modulation in SII never significantly preceded curvature modulation in area 2, we conclude that curvature information is generated in the postcentral gyrus. Critically, our data cannot address the potential dependence of SII curvature responses on SI processing: The temporal analysis results are consistent with both serial and parallel processing models of somatosensory functional organization. Specifically, in a parallel processing somatosensory model, like that proposed for the marmoset monkey (Zhang et al. 2001a;
Zhang et al. 1996; Zhang et al. 2001b), curvature representations could be generated in both SI and SII independently. Indeed, SII neurons could synthesize curvature signals based on cutaneous inputs that bypass SI cortex, received directly from the ventroposterior inferior thalamic nucleus (VPI) (Friedman and Murray 1986).

Alternatively, in a serial processing somatosensory model (Pons et al. 1992; Pons and Kaas 1986), SII curvature tuning could be based on the elaboration of feedforward curvature signals from area 2. Functional organization based on hierarchical or distributed processing may differ between primate species and may be specific for spatial (e.g., contour shape) and temporal (e.g., vibration frequency) information channels, and while our results clearly indicate that contour representations in the postcentral gyrus do not lag those in SII, the specific relationship between area 2 and SII processing in macaque monkeys remains to be clarified in future studies.

The fact that shape representations are elaborated within the postcentral gyrus is especially important for dual stream models of somatosensory processing in which somatosensory information projects to posterior parietal cortex along a dorsal stream and to SII along a ventral stream (Reed et al. 1996; Reed et al. 2005). Area 2 curvature representations in the parietal stream may be sufficient to guide exploration- and manipulation-related movements that are mediated by areas 5 and 7 in parietal cortex (Kalaska et al. 1983; Mountcastle et al. 1975), and the sensitivity of area 2 neurons for joint manipulations (Hyvarinen and Poranen 1978b; Iwamura and Tanaka 1978) may be crucial for such sensorimotor function. In parallel, form representations synthesized in area 2 may propagate along the ventral stream to SII, presumably increasing in complexity and invariance, before engaging with emotional, memory and decisional regions in insula, hippocampus, and frontal cortex (Augustine 1996; Murray and Mishkin...
1984). Thus, area 2 appears to occupy a critical processing stage in the somatosensory hierarchy, directing shape information along distinct pathways for perception and action.

Transformation of shape information in the somatosensory processing pathway supports structural coding theories that posit component form representations (Biederman 1987). Across the hierarchical levels of somatosensory processing, individual neurons encode shape information that can be understood in terms of the size of object features and neural RF scale. Isomorphic spatial representations in peripheral neuron populations make sense because small punctate afferent RFs can only convey information regarding whether any stimulus was present in a restricted contact region. In areas 3b and 1, RFs partially cover single finger pads (Hyvarinen and Poranen 1978b; Iwamura et al. 1993), and RFs at this scale typically encompass small smooth contours that can be represented optimally in terms of orientation. In area 2 and SII, single- and multi-digit RFs typically encompass larger contour fragments that contain gradual and abrupt changes in orientation. Neurons in these intermediate hierarchical levels thus explicitly represent curvature. Notably, contour representations in the ventral visual pathway undergo a similar series of transformations (Connor et al. 2007). However, despite similarities in visual and somatosensory coding of 2D information, the ultimate representation of three-dimensional (3D) objects may be mediated by distinct neural mechanisms in the two sensory systems: 3D perception in vision relies on integrating disparity cues and inferences based on 2D information like lighting (Yamane et al. 2008), whereas 3D perception in touch relies on combining cutaneous and proprioceptive information (Hsiao 2008). The relationship between these integration mechanisms remains to be tested. Regardless, with respect to simple and intermediate-level shape processing, parallel coding strategies in the somatosensory and visual systems imply
analogous neural mechanisms for shape representation. These common shape codes could serve to facilitate cross-modal information transfer between vision and touch.

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### Table

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<tr>
<th>Tuning classification</th>
<th>Number of neurons</th>
<th>Model performance ($r^2$)</th>
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<td>Total</td>
<td>Position consistent</td>
<td>Curvature model</td>
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<tr>
<td>Orientation</td>
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<td>Responsive, unclassified</td>
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<td>7</td>
<td>0.12 ± 0.02</td>
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Tuning classifications are determined from model-free vector strength metrics of curvature and orientation selectivity. Model performance expressed as average variance explained (± s.e.m.) over all neurons within each tuning classification.

Figure Legends
Figure 1. Embossed contour curvature stimulus and tactile stimulator. A, Example contour curvature stimulus machined onto the surface of a plastic block. Stimuli were indented into the distal finger pad of digits 2, 3, or 4 of an awake, behaving monkey (gray circles). Dashed black circle provides estimate of finger pad area with respect to stimulus. B, Pneumatic gripper (white dashed circle) mounted to rotary and linear motors held stimulus blocks (as in A) and presented blocks to skin contact region (Materials and Methods).

Figure 2. Example neural responses: Curvature-tuned patterns. A, Example cell 1. Embossed contour curvature stimuli were indented into the distal finger pad of an awake, behaving monkey. Background gray-level indicates average response to each stimulus (see scale bar). Marginal plot averages responses across rows of stimuli projecting in the same direction. Error bars indicate s.e.m. The fitted von Mises function explained a substantial fraction of total response variance ($r^2 = 0.47$). B, Raster plots show spike trains sorted by curvature direction (rows in A) and collapsed across curvature acuteness and sharpness. Peri-stimulus time histograms show total spike count in successive 10-ms windows. Central bouquet plot indicates average responses to each direction (dashed circle indicates 0.5 x maximum response). Single-peak distribution indicates preference for contours projecting in the 135-180° direction range. C, Average responses to oriented bar stimuli. See scale bar in A. Responses to bar stimuli were less robust compared to curvature stimuli. D, Example cell 2. Conventions as in A. This neuron is tuned for rightward pointing curvature stimuli ($r^2 = 0.60$). E, Conventions as in B. F, Conventions as in C.
Figure 3. Example neural responses: Orientation-tuned patterns. Two example orientation-tuned neurons. Conventions as in Fig. 2. The curvature model fails to account for the bimodal distribution of responses in the curvature direction domain. Contour response patterns for these neurons can be understood by considering response selectivity based on orientation tuning. The orientation model fitted to contour responses explained a substantial proportion of response variance ($A: r^2 = 0.25; D: r^2 = 0.23$). Preferred orientations derived from contour stimuli matched orientation preferences based on bar stimuli ($C, F$).

Figure 4. Curvature and orientation tuning distributions for 112 area 2 neurons. $A$, Direction index (vector strength) for neurons with (filled circles) and without (open circles) significant curvature direction tuning is plotted with respect to response variance explained by the curvature model (vertical axis). Marginal histograms show numbers of tuned (black) and untuned (white) neurons. Curvature models tended to account for more response variance in neurons with large and significant direction index values. $B$, Orientation index (vector strength) is plotted with respect to orientation model performance. Conventions as in $A$. Orientation models tended to account for more response variance in neurons with large and significant orientation index values. $C$, Bayesian information criterion (BIC) for orientation models is plotted with respect to BIC for curvature models for neurons exhibiting significant tuning for curvature (squares), orientation (circles), and both (asterisks). Optimal model for each neuron is determined by lower BIC value. Curvature models outperformed orientation models for 28 of 38 tuned neurons. $D$, Distribution of tuning strength ratios indicating relative performance for curvature and orientation models. Positive values indicate greater curvature...
preference and negative values indicate greater orientation preference. Across the
sample, neural tuning was significantly biased toward curvature preference.

Figure 5. Distributions of curvature direction tuning peaks. A, Baseline-subtracted
fitted von Mises functions from 26 neurons with significant direction tuning. B, Preferred
curvature directions (μ values of fitted von Mises functions) for neurons with (red) and
without (black) significant direction tuning. Preferred curvature directions were uniformly
distributed over the neural samples.

Figure 6. Position consistency of curvature responses. A, Example neuron from Fig.
2. Embossed tactile stimuli were repeated at multiple contact positions across the finger
pad. Gray-level indicates the average response to each stimulus (see scale bar). B,
Distribution of position consistency values for neurons with (filled) and without (unfilled)
significant direction tuning. Larger values indicate consistent contour curvature
selectivity across the finger pad. Curvature-tuned neurons displayed substantial levels of
position consistency.

Figure 7. Analyses of variance results. A, Distribution of neurons with respect to main
effects of stimulus (angles and arcs), main effects of curvature direction, and interaction
effects (numbers indicate percentage of 112 responsive neurons). B, Distribution of
response variance explained by ANOVA across neurons with (filled histograms) and
without (open histograms) at least one significant effect.

Figure 8. Subtense sensitivity and responsiveness to angles and arcs. Pie segment
size indicates proportion of 57 neurons with significant response modulation (ANOVA
main or interaction effects; see Fig. 7) sorted according to preference for subtense (i.e.,
Inset values indicate total neuron numbers. **A**, Neurons sorted according to maximum average responses for 45° (blue), 90° (black), or 135° (red) subtense values. Filled segments indicate samples with significant response modulation by subtense (one-way ANOVA, \( P < 0.05 \)). **B**, Neurons sorted according to maximum average responses (collapsed across direction and acuteness) for angles (black) and arcs (red). Filled segment indicates sample exhibiting significant response differences to angle and arc stimuli (two-tailed, paired t-test, \( P < 0.05 \)).

**Figure 9. Area 2 and SII population response dynamics.** Data are plotted separately for curvature-tuned neurons (*left column*) and for all responsive neurons (*right column*). **A**, Average PSTH for area 2 curvature-tuned neurons (black trace) and SII curvature-tuned neurons (gray trace). Stimulus reached final indentation position at time 0. Times corresponding to two example latency thresholds defined as a percentage of the baseline-to-peak range along the response trace (dashed vertical line, 60%; solid vertical line, 100%) are indicated for each sample. **B**, Average curvature modulation index for area 2 curvature-tuned neurons (black trace) and SII curvature-tuned neurons (gray trace). Times corresponding to two example latency thresholds defined as a percentage of the baseline-to-peak range along the curvature modulation trace (dashed vertical line, 60%; solid vertical line, 100%) are indicated for each sample. **C**, Temporal offset between area 2 and SII curvature modulation traces in curvature-tuned neurons for a set of latency thresholds (see 60 and 100% thresholds highlighted in **B**). Filled markers indicate significant offsets (Methods). Average offset across all latency thresholds revealed earlier area 2 curvature signals in the curvature-tuned samples. Error bars indicate s.e.m. **D**, Average PSTH for all responsive area 2 neurons (black trace) and SII neurons (gray trace). Conventions as in **A**. **E**, Average curvature
modulation index for all responsive area 2 neurons (black trace) and SII neurons (gray trace). Conventions as in B. F, Temporal offset between area 2 and SII curvature modulation traces in all responsive neurons for a set of latency thresholds. Conventions as in C. Average offset across all latency thresholds revealed earlier area 2 curvature signals across all responsive neurons.
A

Significant Effects (ANOVA)
(% of 112 cells)

Stimulus
Stimulus x Direction
Interaction

Stimulus
12
4

Direction
1

No effect

Stimulus x Direction Interaction

B

Variance explained

Number of neurons

0.15
0.3
0.45
0.6
0.75

0
5
10
15
20
25
30

0.15
0.3
0.45
0.6
0.75

0
5
10
15
20
25
30
A

- 45° pref. (p < 0.05)
- 90° pref. (n.s.)
- 135° pref. (p < 0.05)

B

- Arcs pref. (p < 0.05)
- Arcs pref. (n.s.)
- Angles pref. (n.s.)