INTRODUCTION

Roughness is an integral property of tactile perception. Roughness perception is essential for judging material composition; it informs the perception of important properties like comfort and friction and aids manual dexterity, such as using appropriate grip force for object manipulation (Bilaloglu et al. 2016; Johansson and Westling 1984).

Many studies on roughness perception have been conducted in the past using stimuli such as Braille dots, photo-etched dot arrays, gratings, and natural or manufactured surfaces. However, due to an inability to produce specific and finely controllable stimuli, few of these studies have provided a comprehensive examination of a variety of surfaces or the parametric features that give rise to sensations of roughness.

Physically, the term “roughness” refers to height differences on the surface, which can be described in a number of ways in terms of surface geometry (Tiest 2010). The dimensions of the surface elevations that form textures, called “textons,” are a key feature of textured surfaces. Textons can be uniform in shape, height, and surface area, such as hemispherical Braille dots (Phillips et al. 1990), ridges of rectilinear gratings (Cascio and Sathian 2001; Lederman 1974; Lederman and Taylor 1972; Lederman et al. 1982; Phillips and Johnson 1981; Sathian et al. 1989; Sinclair and Burton 1991; Yoshioka et al. 2001), truncated cones used in dot arrays (Chapman et al. 2002; Connor et al. 1990; Connor and Johnson 1992; Dépeault et al. 2009; Eck et al. 2013; Hollins et al. 2001; Klatzky and Lederman 1999; Meftah et al. 2000; Phillips et al. 1992; Smith et al. 2002), or the threads of textiles (Manfredi et al. 2014; Weber et al. 2013). Irregular textons include many natural materials, animal skins, and sandpapers (Bergmann Tiest and Kappers 2007; Bilaloglu et al. 2016; Hollins et al. 1993; Hollins and Risner 2000). The physical dimensions of individual textons define the “microstructure” of a textured surface.

Similarly, the density and arrangement of textons define texture “macrostructure.” Textons can be arranged in regular patterns characterized by specific spacings (anisotropic arrays) or in seemingly random arrangements that can be defined by a characteristic mean spacing between textons (isotropic arrays). The macrostructure of regular arrays is easily seen in geometric patterns such as rectangular or hexagonal grids of specific size. In this manner, textures can be treated mathematically in terms of texton area, spacing, and arrangement on the surface (Fig. 1).

Perceptually, the term roughness is somewhat imprecise. Generally, a rough surface causes uneven pressure on the skin when touched statically and elicits vibrations when stroked (Connor et al. 1990; Hollins et al. 1993; Hollins and Risner 2000; Manfredi et al. 2014; Tiest 2010). However, the underlying physiological mechanisms are complex. The skin of the

Tymms C, Zorin D, Gardner EP. Tactile perception of the roughness of 3D-printed textures. J Neurophysiol 119: 862–876, 2018.—Surface roughness is one of the most important qualities in haptic perception. Roughness is a major identifier for judgments of material composition, comfort, and friction and is tied closely to manual dexterity. Some attention has been given to the study of roughness perception in the past, but it has typically focused on noncontrollable natural materials or on a narrow range of artificial materials. The advent of high-resolution three-dimensional (3D) printing technology provides the ability to fabricate arbitrary 3D textures with precise surface geometry to be used in tactile studies. We used parametric modeling and 3D printing to manufacture a set of textured plates with defined element spacing, shape, and arrangement. Using active touch and two-alternative forced-choice protocols, we investigated the contributions of these surface parameters to roughness perception in human subjects. Results indicate that large spatial periods produce higher estimations of roughness (with Weber fraction = 0.19), small texture elements are perceived as rougher than large texture elements of the same wavelength, perceptual differences exist between textures with the same spacing but different arrangements, and roughness equivalencies exist between textures differing along different parameters. We posit that papillary ridges serve as tactile processing units, and neural ensembles encode the spatial profiles of the texture contact area to produce roughness estimates. The stimuli and the manufacturing process may be used in further studies of tactile roughness perception and in related neurophysiological applications.

NEW & NOTEWORTHY Surface roughness is an integral quality of texture perception. We manufactured textures using high-resolution 3D printing, which allows precise specification of the surface topographical. In human psychophysical experiments we investigated the contributions of specific surface parameters to roughness perception. We found that textures with large spatial periods, small texture elements, and irregular, isotropic arrangements elicit the highest estimations of roughness. We propose that roughness correlates inversely with the total contacted surface area.
human hand is non-uniform in thickness and contains four
different types of mechanoreceptors that mediate tactile sensa-
tions of spatial distribution, vibration, and skin stretch; this
low-level processing is followed by higher level neural coding
in the central nervous system. Furthermore, texture perception
has three distinct dimensions (rough/smooth, hard/soft, and
slippery/sticky) that interact in complex ways (Callier et al.
Picard et al. 2003; Yoshioka et al. 2007).

In this study we use three-dimensional (3D) printing to
create textures with investigator-defined surface properties.
3D printing provides the ability to rapidly fabricate objects
with user-defined shape and surface features at low cost with
high resolution and accuracy. We created a range of finely
textured surfaces with varying surface properties: surface
textons differ in spacing (0.6 –1.4 mm), diameter (0.1– 0.5
mm), shape (rounded or flat-topped), and alignment (aniso-
tropic or isotropic). We conducted four psychophysical
studies exploring the contribution of these parameters to
roughness perception. We report that
1) large wavelengths
and small texton sizes produce higher estimates of rough-
ness; 2) regularly arranged anisotropic textures are per-
ceived as slightly smoother than isotropic textures of the
same wavelength; and 3) the area or density of texton skin
contact is correlated with surface smoothness.

MATERIALS AND METHODS

Texture Stimuli

The textures used for the experiments were created using 3D
modeling and fabricated from plastic using a 3D printer. They consist
of flat plates with raised dot-like textons shaped as truncated cones
with flat or spherical caps. The patterns vary in element spacing, size,
shape, and alignment. These types of stimuli are common in texture
experiments and were chosen because the parameters can be easily
and consistently manipulated to create a variety of textures.

3D modeling. Texture patterns were created as height maps with
specified spatial periods or wavelengths (λ), arrangement, and texton
shape. The texture wavelength specifies the center-to-center distance
between neighboring textons and defines the texture macrostructure.
The textures used in this study varied in wavelength from 0.6 to 1.4 mm.
In isotropic arrays, such as those illustrated in Figs. 1 and 2, the
wavelength specifies the mean distance between textons in all directions.
In a rectangular grid anisotropic texture, as illustrated in Fig. 7
A, the
spacing between textons is uniform along the horizontal and vertical axes,
and when rotated 45° to a tetragonal diamond array, the wavelength along
the horizontal and vertical axes is larger by a factor of \sqrt{2}.

The texture microstructure is defined by the texton geometry. In
this study we created textons shaped as truncated cones, with either
flat tops of diameter \( d = 0.1 \) to 0.5 mm or round hemispheres of
\( d = 0.3 \) or 0.5 mm. All textons on an individual surface had uniform
dimensions (tip shape and diameter). All textons had a height \( h = 1.0
\) mm above the base plate.

Fig. 1. Modeling process for isotropic textures. A: Fouriers
magnitude (inverted). B: inverse Fourier transform. C: height map. D: final 3D model, where
\( \lambda \) is the wavelength of texture and \( d \) is the texton
diameter at the tip. The empty space between textons
is equal to the difference \( \lambda - d \). The modeling
process allows for manipulation of texton spacing,
arrangement, and shape.
The 3D modeling procedure used to specify isotropic textures is schematized in Fig. 1. First, a Fourier magnitude spectrum was created for each texture. This matrix represents the magnitude component of the Fourier transform of the image. For a random texture, the final surface has one dominant wavelength over all directions; this magnitude spectrum is visualized as the outline of a circle with a radius given by \( s/\lambda \), where \( s \) is the pixel size of the image and \( \lambda \) is the dominant wavelength (Fig. 1A).

We then take the 2D inverse Fourier transform using the magnitude and a random phase matrix. For an isotropic texture, the resulting pattern (Fig. 1B) has a random noise-like appearance with maxima spaced according to the dominant wavelength. We then create an analogous bump texture by inserting texture elements, e.g., truncated cones, at the relative maxima of the inverse Fourier transform (Fig. 1C). The resulting textured surface has textons arranged with an average spacing of the specified wavelength (Fig. 1D). Isotropic textures of this sort served as the comparison stimuli in most of the experiments described below.

**Texture fabrication.** The textures we specified were produced as square plates measuring 25 mm on each side. They were fabricated in plastic using a digital light processing stereolithography 3D printer with 50-\( \mu \)m pixel resolution (B9Creator v1.2). Textures were created in MATLAB as height maps and exported as 3D model files (.stl), which were processed and sliced for printing using the B9Creator printer software.

The first experiment used isotropic (random) textures with sphere-capped textons of \( d = 0.3 \) mm, arranged with different spatial periods. Three spatial periods were chosen as reference wavelengths: \( \lambda = 0.75 \), 1.0, and 1.25 mm. These three wavelengths were compared with other isotropic textures ranging from wavelength \( \lambda = 0.625 \) to 1.375 mm. In subsequent experiments, the comparison isotropic textures were tested against anisotropic textures (regularly aligned texton grids) of wavelengths \( \lambda = 0.75 \), 1.0, and 1.25 mm and to textures with textons of various tip sizes and shapes.

**Subjects**

The study was approved by the New York University Committee on Activities Involving Human Subjects (IRB). All subjects signed informed consent forms before the study. Sixteen paid subjects (8 men and 8 women, 21–35 yr old) participated in the experiments. All subjects self-identified as strongly right-handed according to the survey used in Chapman and Chapman (1987), and all reported normal sensory and motor ability of their hands and fingers. Each subject participated for up to 4 h of trials spread over at least 2 sessions, which resulted in a total of 600–800 pair comparisons. Each subject was free to terminate a session or withdraw from the study at will. Subjects were also asked to provide fingerprints after completing the trials.

**Psychophysical Procedures**

The experiments conducted followed two-alternative forced-choice discrimination protocols using free, active touch. Subjects were instructed to scan the surfaces using natural exploratory movements to discern their surface properties (Callier et al. 2015). Because surface texture plays an important role in haptic identification of objects, and humans generally move their hands over the surface of test objects during exploratory procedures (Lederman and Taylor 1972; Lederman and Klatzky 1987), we concluded that free, active touch is an appropriate manner for subjects to rate the smoothness of textures.

In each trial, a subject was presented with a reference texture and a comparison (test) texture. The two texture plates were placed inside a 3D-printed plastic case designed to fit the texture plates, as shown in Fig. 3. The case was appended firmly to a table to prevent any motion. The subject sat in a chair facing the table and was instructed to feel the two stimuli using a stroking motion in the proximal direction (toward the body) with the index and middle fingers (digits D2 and D3) of the right hand. Subjects were free to orient their body at the angle that was most comfortable for stroking in a proximal direction. The ordering of the trials was randomized, and the positions of the two stimuli were switched equally to avoid bias in positioning.

Before each trial, an audio tone was played to indicate to the subject that the pair of stimuli was ready for the trial to begin. Trials were self-initiated: the subject pressed the right and left arrow keys on a provided keyboard with their left hand to record when they began touching the stimuli. The subject was asked to indicate which texture (left or right) felt smoother by releasing the left or right arrow key. The subject could take as long as needed, and the time taken to palpate the texture and make a decision (i.e., the time between pressing down the two arrow keys and releasing one arrow key) was recorded. Subjects typically stroked the textures repeatedly before making a decision. We did not provide feedback to subjects about performance, because the goal of this study was to determine the physical parameters of textures underlying percepts of smoothness. We assumed that texture pairs were perceptually equivalent if one was rated smoother in 50% of trials; pairs were perceptually distinct if one was rated smoother in 75% or more of trials.

We included a set of practice trials as the beginning of each session to familiarize subjects with the mechanics of the task and to ensure that they understood the task instructions. Subjects were asked to...
close their eyes during the trials, and white noise was played for the duration of the experiment to mask auditory cues.

A preliminary report of this work was reported as an abstract (Tymms et al. 2016).

Data Analyses

Paired *t*-tests (ttest, MATLAB r2014a) were used for the data of experiment 1 to assess the differences in tactile sensitivity and ridge size between the fingers. For the anisotropic textures used in experiment 2, an *N*-way analysis of variance (anovan, MATLAB r2014a) was applied to the data across all subjects for each reference texture. Analysis was applied for two different types of pairs of groups: isotropic vs. anisotropic references and anisotropic vertically aligned vs. anisotropic diagonally aligned reference textures. The test texture was used as additional grouping variable, with the proportion judged vs. anisotropic diagonally aligned reference textures. The test texture is isotropic vs. anisotropic references and anisotropic vertically aligned analysis was applied for two different types of pairs of groups: isotropic vs. anisotropic references and anisotropic vertically aligned vs. anisotropic diagonally aligned reference textures. The test texture was used as additional grouping variable, with the proportion judged smoother as the *Y*-value to determine whether groups were significantly different across the test wavelengths. The level of significance was set at *P* < 0.05 for these analyses.

RESULTS

Experiment 1: Variable Wavelength of Isotropic Textures, Constant Texton Size and Shape

The first experiment addressed the question of how the spatial period of randomly arranged texture elements affects the texture’s perceived roughness or smoothness. Stimuli were pairs of isotropic (random) textures with sphere-capped texture elements of diameter 0.3 mm arranged with different spatial periods. Three spatial periods were chosen as reference wavelengths: 0.75, 1.0, and 1.25 mm. The three reference wavelengths were compared against all other test isotropic textures ranging from wavelength 0.625 to 1.375 mm in 0.0625-mm intervals (see Fig. 2 for examples). To maximize meaningful data, more comparisons were performed between more similar textures and fewer comparisons between more easily distinguishable stimuli. Sixteen subjects participated in this experiment, and each performed between 4 and 20 trials for each texture pair.

The cumulative results from all subjects with respect to the three reference stimuli are shown in Fig. 4A. This figure shows the mean proportion of trials in which the reference texture was judged smoother than the test texture. For each reference texture, a psychometric curve was fit to the data using the Wichmann and Hill psychometric function (Wichmann and Hill 2001), which is a cumulative Gaussian function with additional parameters for guess and lapse rates. The function is of the form

\[
y = g + (1 - g - l) \times \frac{1}{2} \left(1 + \text{erf}\left(\frac{x-u}{\sqrt{2}v}\right)\right),
\]

where *g* is the guess rate, *l* is the lapse rate, *u* is the mean, and *v* is the standard deviation. The threshold of discrimination (*σ*) for each psychometric curve is defined as the difference in wavelength at which the psychometric function crosses the 75% choice interval (see Fig. 4A).

For all pairs of textures, subjects typically rated the surface with the smaller wavelength (and greater density of textons) as smoother than the surface with the larger wavelength, although the proportion varied according to the compared wavelengths. For example, the reference wavelength 0.75 mm was judged as smoother in 99% of trials when compared with the test wavelength 1.25 mm, and it was judged smoother in 86% of trials when compared with test wavelength 1.0 mm; when compared with the smaller test wavelength 0.625 mm, it was judged smoother in only 23% of trials. Likewise, the 0.75-mm reference was always rated smoother than the other references for each comparison, the 1.0-mm reference was judged intermediate in smoothness, and the 1.25-mm reference was rated as least smooth.

The smoothness of surfaces is proportional to the density of the texture elements; when more textons contacted the skin, the surfaces felt smoother to subjects. By analogy, roughness seems to be correlated with greater texton spacing or wavelength within our range of spacings (less than 1.4 mm), suggesting that the extra distance enables each texton to more effectively indent the skin and elicit an abrasive sensation. These observations are consistent with previous studies modeling receptor responses of tactile afferents (Vega-Bermudez and Johnson 1999b).

![Fig. 4. A: psychometric curves plot the mean proportion of trials across all subjects in which the reference texture (0.75 mm (red), 1.0 mm (green), and 1.25 mm (blue)) is judged smoother than the comparison wavelength (±SE). Sigma values for 75% threshold (examplified by the dark arrows for the 0.75-mm reference) are indicated for each reference wavelength. Smaller wavelengths are judged as smoother and have a lower threshold value. B: data points are plotted for each subject, with dot size corresponding to number of trials; data points at the same location are accumulated together. Data show consistent performance across subjects for each reference wavelength.](image-url)
Figure 5A shows the three reference wavelengths plotted against their \( \sigma \) threshold of discrimination values (proportion rated smoother on 75% of trials). The thresholds scale proportionally to the reference wavelengths, indicating that the threshold of discrimination is lower and thus better for smaller wavelengths than for larger wavelengths. The values fit a line with a slope of 0.19. This slope is known in psychophysics as the Weber fraction, and the value is consistent with previous work that found the Weber fraction for roughness discrimination between 0.1 and 0.38 (Hollins and Bensmaïa 2007).

Figure 5A also indicates some variation in the discrimination thresholds of individual subjects (gray traces). Previous studies by Peters et al. (2009) demonstrated that acuity of tactile perception of surface detail corresponds to the distance between the fingerprint ridges, because SA1 afferents are distributed along the centers of the papillary ridges of the finger. To test this hypothesis, we asked subjects to provide samples of their fingerprints after participating in the experiment. The fingerprint images were scanned and analyzed for ridge frequency using the techniques presented in Kovesi (2005) based on methods developed by Hong et al. (1998).

Of the 16 subjects tested, 4 subjects’ fingerprints could not be analyzed reliably according to the algorithm. For the remaining subjects, the median ridge frequency is plotted against the subjects’ mean performance accuracy across all comparison pairs (Fig. 5B). We found that the mean papillary ridge spacing of each subject’s fingerprints (0.398 \( \pm 0.003 \) mm) is inversely correlated with the overall proportion of trials in which they judged the smaller wavelength as smoother (mean spatial sensitivity = 0.833 \( \pm 0.0041 \)). The data fall around a line with a negative slope, meaning that subjects with smaller papillary ridge distance tended to show higher sensitivity in tactile smoothness perception; differences between male and female subjects in this pool were not significant (\( P = 0.48 \)), nor were differences between D2 and D3 (\( P = 0.34 \)). These findings support the idea that smaller papillary ridge spacing is linked to higher tactile sensitivity, possibly due to a greater density of SA1 Merkel cell receptors lying along the center of each papillary ridge, or to amplification of tactile vibrations by papillary ridges (Scheibert et al. 2009; Weber et al. 2013).

Combined with the Weber fraction measurements in Fig. 5A, the data in Fig. 5B indicate that subjects are capable of discriminating pairs of textures spanning adjacent papillary ridges.

**Tactile sensitivity differs between fingers.** We also noted that textures of similar wavelengths were often rated as smoother when tested on D2 than on D3. The heat map in Fig. 6A indicates the mean proportion of trials in which subjects rate the texture presented to D2 as smoother than the texture presented to D3. The vertical axis shows the stimulus wavelength presented to the subject’s D2, and the horizontal axis shows the wavelength presented beneath D3. The values and corresponding colors represent the corresponding proportion of trials in which the D2 stimulus was judged smoother. When textures are similar in wavelength (along the diagonal), it is apparent that subjects were biased toward judging the texture under D2 as smoother, as indicated by the red coloration.

We also found similar biases toward D2 across all of the reference textures tested. The bar graphs in Fig. 6, B and C, illustrate the choice probability on individual trials as a function of the difference in wavelength between the D2 and D3 stimuli. Textures that differ in wavelength by \( \leq 0.5 \) mm are identified as smoother with greater reliability when the smaller wavelength is applied to D2 for the entire range of wavelengths tested.

Not only do the subjects show a tendency to select the D2 stimulus as smoother when the wavelengths differ by \( \leq 0.5 \) mm, but their decision time is shorter, suggesting that they are more certain of the accuracy of the judgment (Fig. 6C). When the texture wavelengths differ by more than 0.5 mm, the subjects’ responses occur at latencies of \( \approx 3 \) s. However, difficult decisions take more than \( \approx 5 \) s and take longer when the smaller wavelength is presented to D3.

Because the reference and comparison stimuli were tested equally often on D2 and D3, the mean smoothness estimates shown in Fig. 4 reflect the discriminability parameter \( d' \) and its performance cognate (PCmax) computed by the method of McFadden (1970) (see Gardner and Johnson 2013).
Experiment 2: Anisotropic vs. Isotropic Textures of Varying Wavelength

Given the correlation of perceived smoothness with texture wavelength, we also examined the relation between perceived smoothness and the irregular spacing of textons in the isotropic textures tested in experiment 1. We fabricated two new sets of anisotropic reference textures with wavelengths $\lambda = 0.75$, 1.0, and 1.25 mm, with the same 0.3-mm sphere-capped textons. Textons were arranged regularly in a rectangular grid with one of two rotations: 1) with textons aligned to the edges of the square, and 2) with the texture pattern rotated diagonally at a 45° angle (Fig. 7A). The new anisotropic stimuli were used as references and compared against the same 13 isotropic textures tested in experiment 1. Seven subjects participated in the experiment, and each performed between 2 and 10 comparisons per stimulus pair, with a greater number of comparisons for more similar stimulus pairs.

Figure 7, B and C, show the data and corresponding psychometric curves for experiments in which anisotropic reference textures oriented in either direction were compared against the isotropic textures used in experiment 1 (dashed lines, open symbols). Both vertically and diagonally aligned anisotropic textures showed similar trends to the isotropic textures: wavelengths with small spacing were judged smoother than those of large wavelengths, and smaller wavelengths had a greater slope and thus a better threshold of discrimination. Anisotropic textures were generally rated smoother than isotropic textures of the same wavelength (Fig. 7B), and the judgments were significant for the two larger wavelengths tested, 1.25 and 1.0 mm ($P = 0.006$ and $P = 0.0304$, with $F = 7.66$ and $F = 4.8$, respectively). When $\lambda = 0.75$ mm, anisotropic and isotropic textures did not differ significantly, suggesting that subjects were unable to distinguish jitter in the position of the textons at such small wavelengths, when textons contacted neighboring papillary ridges.

Additionally, vertically aligned textures were generally judged smoother than diagonally aligned textures (Fig. 7C), but the difference was significant only for the 1.25-mm wavelength ($P = 0.005$, $F = 8.46$). This finding supports the suggestion that texture spacing, specifically with respect to the direction of motion, influences estimates of roughness, because textures oriented diagonally have a slightly larger spacing (i.e., $\lambda \sqrt{2}$).
along the path of motion (Connor and Johnson 1992). The difference may be attributable to the different frequency of vibrations elicited by the different arrangements when stroked vertically.

The difference between these textures was more pronounced for the larger wavelengths, suggesting that when texture features are dense, differences in arrangement may become less easily discernable. Dense features may be more difficult to distinguish because mechanoreceptors have a limited ability to resolve spatial detail. In particular, the SA1 afferents can differentiate spatial detail down to 0.5 mm (Johnson 2001), so features arranged near that minimum distance might be more difficult to resolve. Similarly, sensitivity to vibration differs at different frequencies, so the differences in vibrations may be more noticeable for the larger wavelength.

Experiment 3: Isotropic Textures with Constant Wavelength, Variable Texton Size, and Shape

Experiments 1 and 2 assessed the effect of texture wavelength and texton density and orientation on judgments of smoothness. All of the textures were composed of 0.3-mm-diameter rounded textons. In experiment 3, we assessed the effect of texton diameter and shape on perceptions of smoothness by varying these parameters while maintaining a constant wavelength and texton density. We fabricated a new set of textures with flat-topped truncated cone-shaped textons of diameter 0.1, 0.2, 0.3, 0.4, and 0.5 mm and rounded sphere-capped elements with diameter 0.3 or 0.5 mm (Fig. 8A). Wavelengths of 0.75, 1.0, and 1.25 mm were chosen as references for each set of textures. Each texture was compared against all other textures of the same wavelength using our standard two-alternative forced-choice protocol. Eight subjects participated in the experiment, and each performed an average of five comparisons per pair. Results were fit with psychometric curves and are shown in Fig. 8B: the left column shows the comparisons between flat texton shapes of a given wavelength, and the right column shows the comparison between round texton shapes alongside the flat shapes of the same wavelength. At each reference wavelength and at each texton diameter, textures with the larger diameter textons of each pair were judged smoother. The largest diameter textons tested (0.5 mm) were judged smoother than all other sizes tested; likewise, surfaces with the smallest diameter textons (0.1 mm) were perceived as roughest (least smooth).

Fig. 7. A: experiment 2 compared anisotropic textures with textons oriented vertically or parallel to the edges of the texture plate (left), anisotropic textures with textons oriented diagonally (at 45°) to the texture plate (middle), and isotropic textures (right). Yellow arrows indicate the axes of texton alignment. B: anisotropic (regular) textures are generally judged smoother than isotropic textures when compared with the same set of 13 isotropic textures used in experiment 1. Dashed psychometric curves and open symbols plot the mean proportion of trials across all subjects in which an anisotropic reference texture [0.75 mm (red), 1.0 mm (green), and 1.25 mm (blue)] is judged smoother than the comparison isotropic wavelength (±SE). Solid curves and filled symbols replot the data from Fig. 4 in which both reference and comparison textures were isotropic. The preference for anisotropic textures is greatest for the largest wavelengths tested. C: vertically oriented anisotropic textures are judged smoother than diagonally oriented textures of the same wavelength. Iso., isotropic; aniso., anisotropic; vert., vertically oriented; diag., diagonally oriented.
Likewise, textures with rounded caps, as indicated by the dashed lines and empty circles in Fig. 8B, right column, are judged as slightly less smooth than the same diameter texton with a flat cap. This expands on the theory that the sensation of roughness or abrasiveness is caused when textons effectively indent the skin. Thus more sharply pointed elements feel rougher, whereas flatter elements feel smoother.

Experiment 4: Interaction Between Texture Wavelength and Texton Dimensions

Given the investigation of texture element shape and spacing, the next natural question to ask is how combinations of different texture shapes and wavelengths relate to each other perceptually. The stimuli in this experiment were a combination of the stimuli from experiments 1 and 3. The

Fig. 8. A: sample 1.25-mm wavelength textures with flat textons of different sizes. a, Texture with small (0.1-mm diameter) textons; b, texture with 0.3-mm textons; c, texture with large (0.5-mm) textons; d, texture with 0.3-mm round textons for comparison. B: comparisons between textons of different sizes in the 3 reference wavelengths. The smallest textons (such as the 0.1-mm size shown with the magenta solid line) are judged the least smooth; larger diameter textons are judged progressively smoother, with the 0.5-mm size (red solid lines and filled red symbols) perceived as smoothest at all wavelengths. Flat textons feel smoother than rounded ones.
reference stimuli were the flat-texton stimuli from experiment 3 manufactured with three reference wavelengths (0.75, 1.0, and 1.25 mm). The test stimuli were the comparison isotropic textures used in experiments 1 and 2; their wavelengths varied from 0.625 to 1.375 mm, and textons were 0.3-mm diameter-rounded cones. To maximize significant data in this experiment, fewer comparisons were performed between more obviously different textures. Five subjects participated in this experiment, and each performed on average four comparisons per texture pair.

Figure 9 shows psychometric curves for the five texton sizes at the three reference wavelengths. Results indicate that textures with larger texton sizes feel smoother at all wavelengths. Surfaces with textons larger than the reference 0.3-mm size were judged smoother than the comparison reference texture regardless of wavelength. Likewise, surfaces with textons smaller than the reference 0.3-mm values were judged less smooth, because the psychometric functions crossed the 75% threshold level at greater wavelengths than the reference values.

To further analyze the interaction of texton spacing (i.e., wavelength) and texton diameter on perceptions of smoothness, we defined the point of subjective equality (PSE) for each psychometric function in Fig. 9 as the wavelength whose roughness is estimated as 0.5. In other words, the PSE is the estimated wavelength judged as most equal to the reference stimulus; the computed PSE values for the whole set of textures compared in this experiment are plotted in Fig. 10. For example, the reference texture with wavelength 0.75 mm and flat texton \( d = 0.1 \) mm has a PSE of 0.855 mm, meaning that the psychometric curve crosses the 50% threshold at \( x = 0.855 \). Therefore, this texture is judged similar in smoothness to a test texture with rounded 0.3-mm elements of wavelength 0.855 mm. Likewise, the 1.25-mm reference texture of flat texton \( d = 0.5 \) mm feels equivalent to the 1.0-mm wavelength comparison texture.

The PSE data indicate that increasing the texton diameter is equivalent to decreasing the texture wavelength, that is, reduc-
Fig. 11. Relative magnitude estimates of smoothness of textures varying in wavelength and texton diameter. The data from each psychometric function in Fig. 9 were averaged to obtain mean smoothness estimates for each wavelength and texton size measured in experiment 4.

To assess the relative contributions of wavelength and texton diameter, we averaged the relative smoothness of each reference surface in experiment 4 and plotted the resulting mean judgments as functions of both parameters in Fig. 11. The resulting curves show common effects of texton diameter regardless of the texture wavelength. The data show that smoothness is influenced by both the size and spacing of textons such that increases in the surface area contacting the skin are perceived as relatively smoother, regardless of whether this results from large individual textons or increased texton proximity, or a from combination of these properties. The smoothest textures we tested are those with the shortest wavelengths and the largest diameter textons ($\lambda = 0.75 \text{ mm}$, $d = 0.5 \text{ mm}$); the ratio of texton diameter to wavelength ($d/\lambda$) = 0.667. The least smooth (i.e., roughest) texture had small-diameter, widely spaced textons ($\lambda = 1.25 \text{ mm}$, $d = 0.1 \text{ mm}$); $d/\lambda$ = 0.08. The combination in the middle ($\lambda = 1.0 \text{ mm}$, $d = 0.3 \text{ mm}$) is judged smoothest on only ~50% of trials.

How do subjects judge surface smoothness? When subjects discriminate the relative smoothness of textures that differ in wavelength, what are they actually detecting? One possibility is that they are measuring the relative mean spacing between textons. Likewise, decreases in texton diameter decrease estimates of smoothness and are therefore perceived as rougher surfaces.

Another possibility is that subjects compare the density of textons contacting the fingertip skin as they scan the pair of surfaces simultaneously. Texton density may be easier to extract as entire surfaces are evaluated rather than a random set of points. For example, a 0.875-mm comparison texture is distinguished as smoother than an 0.75-mm reference texture on 82% of trials (Fig. 4). The wavelengths of this pair differ by 0.125 mm, but the texture with $\lambda = 0.75 \text{ mm}$ contains 178 textons/cm$^2$, whereas the texture with $\lambda = 0.875 \text{ mm}$ contains only 131 textons/cm$^2$.

A further possibility is that subjects compare the total skin area contacted and indented by the two textures. Skin contact area clearly depends on the total density of textons per square centimeter of skin and the diameter of each texton. Note that the contact area is equal for the isotropic and anisotropic surfaces of the same mean wavelength. When analyzed graphically (Fig. 12), judgments of smoothness based on estimates of skin contact area yield similar curves that are superimposed for all of the three reference wavelengths. Note that identical results are obtained when texton density (number of textons/cm$^2$) is compared, suggesting that the underlying neural mechanisms used on individual trials engage the entire surface palpated during motion.

We also found that large-diameter textons with closer spacing produce the greatest sensations of smoothness when total skin contact area is compared (Fig. 13A); the relationship is not as strong when texton density is measured on the skin (Fig. 13B), suggesting that texton shape plays an important part in texture roughness. The proximity of surface elevations appears to impede skin deformation and displacement of papillary ridges into the interstices between textons.

DISCUSSION

In this study, we used 3D printing to create textured surfaces with controlled texton size, spacing, and arrangement. Textons were shaped as flat or rounded truncated cones with diameter 0.1–0.5 mm; they were distributed in anisotropic or isotropic arrays with mean wavelengths of 0.6–1.4 mm. These surfaces allowed us to independently assess the effect of texton spacing and size on human percepts of surface smoothness. Two-alternative forced-choice protocols revealed that both wave-
length and texton dimensions influence human judgments of relative smoothness: the smoothest textures were composed of textons with small wavelengths and large diameters, whereas the least smooth textures comprised large wavelengths and small-diameter textons. Textons arranged in regular, anisotropic patterns were judged slightly smoother than isotropic textures with textons jittered with the same mean wavelength. We concluded that percepts of texture are related not just to the distance between pairs of textons, but rather to the overall skin area contacted by textons and their spatial distribution integrated by the palpating finger.

When comparing textures of varying wavelengths and texton diameters in experiment 4, we found perceptual equivalencies between surfaces that differed in both dimensions, suggesting that textures of differing geometries may evoke the same overall perceptual roughness. These results are in agreement with Sathian et al. (1989), Cascio and Sathian (2001), and Yoshioka et al. (2001), who found that the perceived roughness of gratings is...
of the first stimulus when sampling the second one. Although textures, and subjects did not need to remember the properties measured nearly identical force and speed was used for both discrimination. The simultaneous movement of both fingers ensured nearly identical force or speed; this protocol allowed them to choose report which of them felt smoother. We did not specify the simultaneous with digits D2 and D3 using active touch and tent results. Subjects were instructed to stroke two textures the task is objective and simple for subjects and yields consistent data. Moreover, our finding of greater spatial sensitivity on D2 confirms previous observations of differential spatial acuity between digits reported by Vega-Bermudez and Johnson (2001).

Models of Neural Representation of Textures

Although Meissner corpuscle (RA1), Merkel cell (SA1), and Pacinian (PC) afferents respond to textured surfaces scanned over their receptive fields, SA1 fibers are considered the principal class responsible for sensations of roughness, because their firing patterns directly mirror the pattern of skin contact area and thereby provide an isomorphic image of the texture (Blake et al. 1997a, 1997b; Connor et al. 1990; Connor and Johnson 1992; Johnson and Hsiao 1992; Phillips et al. 1990, 1992; Sripati et al. 2006; Yoshioka et al. 2001, 2007). The spatial variation hypothesis posits that the population of SA1 fibers is responsible for texture roughness integration via variations of bursts and silences as textures are scanned over the skin. This hypothesis rejects temporal patterning of spike trains as a coding mechanism for texture representation, and instead proposes that differences in mean firing rates between neighboring SA1 receptive fields yield a spatial derivative that accounts for sensations of perceived roughness.

An alternative, more subtle mechanism proposed by Katz (1925) and Hollins and Risner (2000) invoked a duplex theory of roughness as two separate qualities: large-scale roughness of large (>0.2 mm) features detected spatially without hand motion, and small-scale roughness eliciting vibrational cues during hand motion over surfaces. Large-scale roughness is mediated primarily by Merkel cell afferents responding to static pressure (SA1 fibers) that have small receptive fields (Connor et al. 1990; Connor and Johnson 1992; Goodwin and Wheat 2004; Johansson 1978; Phillips and Johnson 1981, Phillips et al. 1990, 1992; Sripati et al. 2006; Vega-Bermudez and Johnson 1999a). Smaller features are encoded during dynamic touch by temporal codes in the spike trains of rapidly adapting motion sensors (RA1 and PC afferents) that innervate Meissner and Pacinian corpuscles, respectively (Bensmaïa and Hollins 2003; Bensmaïa et al. 2006; Hollins and Bensmaïa 2007; Manfredi et al. 2012, 2014; Weber et al. 2013).

Strong experimental support exists for the vibrational model for coding fine textures such as fabrics (Harvey et al. 2013; Manfredi et al. 2014; Saal et al. 2016; Weber et al. 2013). When scanning natural textures over the fingers, Weber et al. (2013) demonstrated that SA1 fibers responded to coarse textures such as embossed dot arrays or fabrics with large protuberances (hucktowel) but not to fine textures such as silk, satin, or chiffon. RA and PC fibers responded to most of these fabrics. Moreover, the frequency composition of PC and RA1 spike trains reflect the oscillations evoked in the skin as measured by vibrometry, rather than the surface profile of the texture itself. Using this same measurement technique, Mackevicius et al. (2012) demonstrated that the spike trains evoked in cortical neurons by vibratory stimuli applied perpendicularly to the skin surface (sinusoids, diharmonic, and noise trains)
mirrored the temporal precision of the skin oscillations at millisecond resolution. Texture-evoked spike patterns, particularly in PC afferents, scale with the scanning speed, suggesting that they do not simply reflect the spatial structure of the stimulus, but rather the skin response to the texture. Likewise, Harvey et al. (2013) used information theoretic analyses to show that the timing of spikes in S1 cortex plays a crucial role in encoding the frequency content of skin vibrations, while the mean firing rate of these same neurons encodes the vibratory amplitude.

In a follow-up study, Manfredi et al. (2014) examined the frequency composition of spike trains evoked by a large set of natural textures. When testing nonperiodic materials, they found peaks in the frequency spectra mirroring the product of the scanning velocity and the spatial period of the papillary ridges of the individual subjects. These findings suggest that the papillary ridges of the glabrous skin play an important role in tactile perception of texture.

Papillary Ridges as Tactile Processing Units for Textures

All of the textures used in this study had spacing larger than the experimentally derived papillary ridge span of 0.4 mm in the subjects tested. Thus neighboring textons in our basis set of textures (isotropic with 0.3-mm-diameter textons and wavelengths of 0.75, 1.0, or 1.25 mm) typically stimulated mechanoreceptors in different papillary ridges. Our data, and those of other investigators, suggest that the papillary ridge might serve as the basic computational unit of glabrous skin. Merkel cells are located in clusters at the central base of the dermal ridges; each Merkel cell is innervated by a single axon with multiple branches that innervate several Merkel cells. Each cluster of Merkel cells in glabrous skin is innervated by several afferent fibers (type SA1), yielding substantial overlap of receptive fields. Meissner corpuscles are located in dermal papillae arrayed along both sides of the epidermal ridges (Cauna 1956; Nolano et al. 2003; Paré et al. 2002). Each papillary ridge is innervated by a unique combination of sensory afferents, and the ridges in each finger are fairly uniform in width, thereby providing an anatomical grid structure for localizing tactile stimuli on the fingertips. Furthermore, Peters et al. (2009) reported that the ability of humans to distinguish grating orientation correlates significantly with papillary ridge dimensions and finger size; the expected higher density of Merkel cells in small fingers correlates with better spatial acuity.

The relationship of the papillary ridges to spatial features on surfaces was explored previously by LaMotte and Whitehouse (1986). They found that humans were able to detect a dot as small as 1.3 μm in amplitude on a smooth (glass) surface. When similar dots were scanned tangentially across the fingertips of macaques, RA afferents responded when the dot contacted the edge of the fingerprint ridges, in a very localized region of the digit. The interspike interval of RA spike trains directed correlated with the distance between adjacent ridges; the spatial pattern of the papillary ridges was thereby reflected in the impulse rate of these RA fibers. Firing rates were highest when the dot was scanned across the ridges; lower rates were measured when the dot moved along the ridges or diagonally to them. The leading edge of the dot appeared to compress the ridge as far as the neighboring one when larger dots were tested.

A study by Srinivasan et al. (1990) provided further evidence for the role of tactile receptors in detection of minute surface features. Using glass microscope slides with a fine grating etched on one half, they found that when the smooth end was slid over the fingertips of macaques, it elicited a weak contact burst but no further activity from all three types of cutaneous mechanoreceptors regardless of the direction of scan (see their Fig. 6). The textured portion of the surface did not activate RA or SA1 fibers, but PC afferents responded robustly to this stimulus, confirming the role of vibratory stimuli for sensing fine, textured surfaces.

Indeed, models of the papillary ridges suggest that these structures enhance the transmission of vibration to the subcutaneous tissue where most PCs are located (Adams et al. 2012; Dahiya and Gori 2010; Prevost et al. 2009; Scheibert et al. 2009). Furthermore, Bilaloglu et al. (2016) found that covering the fingertips with a thin layer of adhesive plastic (Tegaderm), and thereby impeding papillary ridge mobility, impaired the adaptation of fingertip grip forces to surface friction and grip force efficiency, suggesting that textured surfaces appeared smoother than when sensed with bare hands.

Neural Ensembles Encode the Spatial Properties of Textures

The evidence cited above and found in our studies suggests that texture information is transmitted by a “combinatorial code” in which all three classes of mechanoreceptors are important for giving rise to sensations of surface irregularity (Saal and Bensmaia 2014). All three classes of touch receptors respond to textures (Muniak et al. 2007; Phillips et al. 1990, 1992; Saal et al. 2017; Yoshioka et al. 2007) but at different rates; their inputs are weighted differently depending upon the fine structure of the material palpated. Though a strong argument can be made for the role of SA1 afferents in coarse texture percepts, it is well known that hand motion across textures enhances the percept of an irregular surface and produces prominent vibration of the skin. Although PCs have very large receptive fields and can integrate vibrations from distant parts of the hand, PCs are capable of summating the output of multiple papillary ridges as they are contacted by the individual textons comprising the textured surface. The small, localized receptive fields of SA1 and RA1 fibers may serve to localize the precise position of the texture on the hand. Indeed the lower fidelity spatial inputs from RA1 and PC fibers may enhance sensations of surface irregularity through skin vibration or displacement of the papillary ridges, much as the diverse instruments of a symphony orchestra contribute to the complexity of sound expressed in the music of Beethoven and Mahler (Saal et al. 2016).

Rather than considering texture perception as a simple representation of individual textons, we propose that hand motion across textured surfaces activates unique ensembles of afferents that fire together as the fingers traverse the surface. In regular, anisotropic surfaces, the textons contact the same groups of afferents repeatedly so that each afferent fires concurrently with a set of equally spaced fibers according to the texture wavelength regardless of the speed of motion. Different wavelengths activate different partners in the ensemble. Anisotropic textures stimulate different groups of afferents because the textons are scattered in a random fashion on the surface, and so each afferent couples with different touch receptors.
during the passage of the finger over the texture. The alteration in partners may explain why the isotropic surfaces feel less smooth than the anisotropic regular arrays: anisotropic textures stimulate the same groupings of afferent fibers synchronously in a regular pattern, and the brain may integrate this consistent pattern of active and silent afferents as smooth; meanwhile, isotropic textures are random and therefore not encoded in this manner.

Future studies will require direct recordings of cutaneous mechanoreceptive afferents to determine the precise neural activity generated by the 3D textures introduced in this report. We note, however, that other textures described in the literature activate all three types of afferents innervating the glabrous skin of primates, including humans. There is no evidence that activity in RA1 and PC fibers is erased or otherwise extinguished at higher brain centers; indeed, spatial coding mechanisms are less prevalent in higher brain areas than are temporal and intensive coding properties (Harvey et al. 2013; Kops and Gardner 1996; Rossi-Pool et al. 2016). We conclude by why the nervous system expend energy to activate specific receptor populations in the skin, if the information is then erased later in sensory pathways?

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

C.T., D.Z., and E.P.G. conceived and designed research; C.T. performed experiments; C.T. and E.P.G. analyzed data; C.T., D.Z., and E.P.G. interpreted results of experiments; C.T. and E.P.G. prepared figures; C.T. and E.P.G. analyzed data; C.T., D.Z., and E.P.G. interpreted results of experiments; C.T., D.Z., and E.P.G. edited and revised manuscript; C.T. and E.P.G. approved final version of manuscript.

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