J Neurophysiol 118: 2371–2377, 2017.
First published July 19, 2017; doi:10.1152/jn.00161.2017.

RESEARCH ARTICLE | *Sensory Processing*

Speed invariance of tactile texture perception

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Submitted 6 March 2017; accepted in final form 18 July 2017

Boundy-Singer ZM, Saal HP, Bensmaia SJ. Speed invariance of tactile texture perception. *J Neurophysiol* 118: 2371–2377, 2017. First published July 19, 2017; doi:10.1152/jn.00161.2017.—The nervous system achieves stable perceptual representations of objects despite large variations in the activity patterns of sensory receptors. Here, we explore perceptual constancy in the sense of touch. Specifically, we investigate the invariance of tactile texture perception across changes in scanning speed. Texture signals in the nerve have been shown to be highly dependent on speed: temporal spiking patterns in nerve fibers that encode fine textural features contract or dilate systematically with increases or decreases in scanning speed, respectively, resulting in concomitant changes in response rate. Nevertheless, texture perception has been shown, albeit with restricted stimulus sets and limited perceptual assays, to be independent of scanning speed. Indeed, previous studies investigated the effect of scanning speed on perceived roughness, only one aspect of texture, often with impoverished stimuli, namely gratings and embossed dot patterns. To fill this gap, we probe the perceptual constancy of a wide range of textures using two different paradigms: one that probes texture perception along well-established sensory dimensions independently and one that probes texture perception as a whole. We find that texture perception is highly stable across scanning speeds, irrespective of the texture or the perceptual assay. Any speed-related effects are dwarfed by differences in percepts evoked by different textures. This remarkable speed invariance of texture perception stands in stark contrast to the strong dependence of the texture responses of nerve fibers on scanning speed. Our results imply neural mechanisms that compensate for scanning speed to achieve stable representations of surface texture.

NEW & NOTEWORTHY Our brain forms stable representations of objects regardless of viewpoint, a phenomenon known as invariance that has been described in several sensory modalities. Here, we explore invariance in the sense of touch and show that the tactile perception of texture does not depend on scanning speed. This perceptual constancy implies neural mechanisms that extract information about texture from the response of nerve fibers such that the resulting neural representation is stable across speeds.

constancy; psychophysics; touch

OUR NERVOUS SYSTEM effectively extracts invariant information about the environment despite large variations in the patterns of activation across our receptor sheets. For example, we can recognize objects from a variety of different viewpoints (Biederman and Gerhardstein 1993; Booth and Rolls 1998) or identify musical instruments based on their timbre regardless of the note played (Grey and Gordon 1978). In each case, the neural representation at the periphery changes dramatically (with changes in viewpoint or in fundamental frequency) but our perception of the object's attributes (shape, timbre) remains stable.

Some form of invariance also seems to exist in the sense of touch and, specifically, in the perception of texture. Indeed, different materials (denim, silk, and cotton, for example) can be recognized regardless of how these are probed, that is, irrespective of the precise hand movements used to explore them, despite the strong dependence of texture responses of nerve fibers on exploratory movements (Weber et al. 2013, Yoshioka et al. 2011).

Previous studies of invariance in texture perception have focused on the most salient sensory dimension of texture, namely roughness (Lederman and Klatzky 1987). The general conclusion from these studies is that roughness perception is not strongly affected by scanning speed (Cascio and Sathian 2001; Lederman 1974; Yoshioka et al. 2011). In other studies, roughness ratings were found to be essentially identical whether textures are explored actively or scanned across an immobile finger, providing further evidence that exploratory conditions do not influence texture perception (Lederman 1981; Yoshioka et al. 2007).

In these previous studies, however, either coarse gratings or otherwise restricted sets of textures were used to test texture constancy, thereby limiting the generalizability of these findings. Indeed, we have shown that texture perception relies on the following two mechanisms (Fig. 1): coarse textural features, such as those that form a grating, are encoded in the spatial pattern of activation in two populations of afferents, namely slowly adapting type 1 or SA1 fibers and, to a lesser extent, rapidly adapting or RA fibers (see Fig. 1*A* for an illustration of spatial coding) (Johnson and Lamb 1981). Because spatial representations in the nerve are relatively stable across scanning speeds (Bochereau et al. 2015; Connor et al. 1990; DiCarlo and Johnson 1999), perceptual attributes encoded spatially are expected to be stable across speeds. However, both SA1 and RA receptive fields are too big to resolve fine textural features (see Fig. 1*B*), and these afferents do not respond well to textures with small elements (Weber et al. 2013). Instead, fine textural features, on the order of tens to hundreds of microns in size, are encoded in temporal spiking patterns in RA and Pacinian (PC) fibers (Weber et al. 2013). The temporal patterns evoked in these two populations when fine textures are scanned across the skin contract or dilate systematically with increases or decreases in scanning speed,

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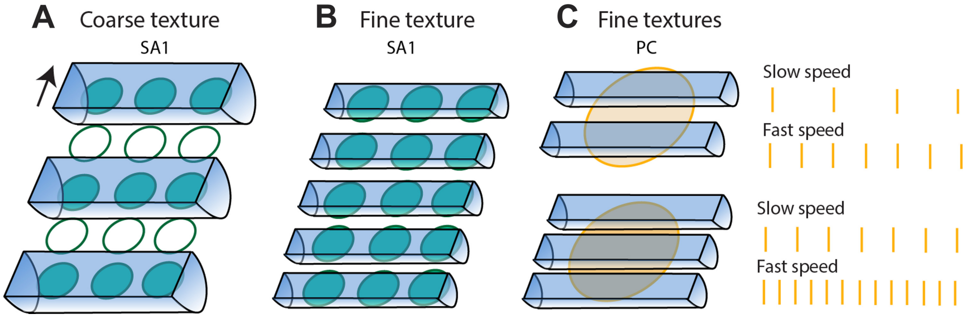

Fig. 1. Texture coding and speed dependence in the nerve. *A*: coarse textural features are encoded in the spatial pattern of activation in slowly adapting type 1 (SA1) fibers. Spatial representations are stable with respect to scanning speed. *B* and *C*: fine textural features are not encoded spatially as they are below the spatial resolution of the receptor sheet of SA1 (*B*), rapidly adapting (PC, *C*, *left*) and Pacinian (RA, data not shown, but with bigger receptive fields than their SA1 counterparts) fibers. Instead, different textures elicit different temporal spiking patterns (*C*, *right*). At different speeds, these temporal representations dilate or contract with decreases or increases in scanning speed. Because the spatial properties of the texture and the scanning speed are conflated in such a representation, it is unclear how to decode speed and thus correct for it to achieve a speed-invariant representation of texture. Note that, while afferent receptive fields are not circular, homogenous, nor organized in a periodic grid, the critical factor is the relative size of the RF with respect to the elements (Goodwin and Wheat 2002). Texture perception operates over spatial scales orders of magnitude finer than what can be resolved spatially.

respectively (Fig. 1*C*). Because the texture information for these fibers is hypothesized to be extracted independently from different nerve fibers, information about scanning speed and surface microgeometry is inextricably conflated in these responses. Accordingly, one might expect that the perception of fine textures (e.g., fabrics) would be more susceptible to changes in scanning speed than that of coarse textures (e.g., gratings).

In this view, gratings and embossed dot patterns are not ideal to study the speed invariance of texture perception because the perception of these stimuli relies almost exclusively on a spatial representation at the exclusion of the temporal one so the perception of gratings is in principle less susceptible to the effects of scanning speed than is that of finely textured surfaces (Fig. 1*A*).

With these considerations in mind, we investigate the degree to which the tactile perception of a large number of everyday materials is invariant with respect to scanning speed using two psychophysical paradigms. In the first paradigm, we investigate speed invariance of texture perception along each of the three main perceptual dimensions of texture, namely roughness, stickiness, and hardness (Hollins et al. 2000a), extending previous results that focused exclusively on roughness (Lederman 1981). In the second paradigm, we probe constancy beyond textural dimensions using a dissimilarity scaling approach. We find that the perception of texture is almost completely independent of scanning speed, regardless of texture or perceptual assay, and discuss neural mechanisms that may mediate this observed invariance.

MATERIALS AND METHODS

Experimental Paradigms

We investigated perceptual constancy of tactile texture using two different experimental paradigms.

Magnitude estimation. We implemented a free magnitude estimation paradigm to investigate the dependence on scanning speed of texture perception along well-established textural continua. Subjects rated tactile textures along each of the three major perceptual dimensions, namely roughness, stickiness, or hardness (Hollins et al. 2000a), while textures were presented passively at each of four scanning speeds. To the extent that judgments for each texture were equivalent across speeds, we could infer that the perception along that continuum was invariant with respect to scanning speed.

Dissimilarity scaling. We wished to probe the dependence of texture on speed across all the perceptual dimensions of texture. To this end, we had subjects rate the perceptual dissimilarity between pairs of textures, where both textures could be presented at the same or at different speeds. To the extent that dissimilarity judgments were equivalent whether the two textures were presented at the same speed or different speeds, we could infer that the perceived difference between both textures was invariant with respect to scanning speed.

Stimuli

Materials were chosen to span the range of textures experienced in everyday life, including fabrics, fur, and sandpapers, and also included a small number of stimuli that have been extensively used in texture coding experiments, such as embossed dot patterns and gratings. Fifteen textures were used in each of the three conditions in the magnitude estimation experiment; each set was selected to span the perceptual range of the dimension tested, i.e., roughness, stickiness, or hardness. Of the 15 textures, 10 were common across experiments, and 5 were used to extend the range along the relevant dimension. Seventeen textures were used in the dissimilarity scaling experiment. Seven textures were used in target pairs, and 10 textures were used in random speed-texture pairings to prevent subjects from becoming familiar with particular texture pairs (see Tables 1 and 2 for the full list of textures and pairs, respectively).

Textures were presented to the right index fingertip pad of human subjects using a custom-built rotating drum stimulator (Manfredi et al. 2014) (Fig. 2). Individual textured strips, 25 mm wide and 160 mm long along the scanning direction, were fixed to magnetic tape with adhesive spray and attached to an acrylic drum (258 mm diameter, 312 mm length), itself covered in magnetic tape. Textures were presented with a force of 0.3 N at four speeds that span the range observed during spontaneous texture exploration, namely 40, 80, 120, and 160 mm/s (Callier et al. 2015). Because textures varied in thickness and compliance, the indentation depth required to achieve the desired contact force varied across textures. To take into consideration differences in compliance, we used an automatic calibration routine where each texture was lowered on a scale at different indentation depths until the scale reported a force of 0.3 N. Measurements of indentation depth were repeated three times at each of three locations per texture strip. These nine measurements of indentation depth were then averaged. To set the indentation depth for each participant, we lowered a load cell that was attached to the drum on the subject's fingertip until 0.3 N was registered. This offset and the calibration described above were then used as the basis for calculating the indentation depth for each texture on the drum such that all textures applied the desired contact force on the finger.

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Table 1. *List of textures used in the roughness, stickiness, hardness, and dissimilarity experiments*

Texture No.	Experiment R	S	H	D	Texture Name
1	●	●	●		Embossed dots 4 mm*
2	●	●		●	Corduroy (thick stripes)*
3	●				1 mm Grating*
4				●	5 mm Grating*
5	●				5 mm Sine grating/0.5 mm grating*
6	●	●	●		Neoprene (3/32 in. thick)
7	●	●	●		Silicone (1/16 in. thick)
8	●	●	●		Sandpaper (320 grit)
9	●	●	●		Metallic silk
10	●	●	●		20-Gauge vinyl
11	●	●	●		Chiffon
12	●	●	●	●	Stretch denim
13	●	●	●		Craft foam
14		●			Balloon
15		●	●	●	Empire velveteen
16			●		Rabbit fur
17			●		Butcher paper
18			●		Snowflake fleece (fuzzy side)
19	●	●	●		Wool blend
20				●	Suede cuddle (suede side)
21				●	Hucktowel
22			●		Careerwear flannel
23	●	●		●	Microsuede
24	●	●			Wool gabardine

R, roughness experiment; S, stickiness experiment; H, hardness experiment; D, dissimilarity experiment. *Textures 1–5 are periodic.

On each trial, the drum began to rotate until the desired scanning speed was reached before contact was made with the finger. Textures were presented for 0.7 s in the magnitude estimation experiments and for 0.8 s in the dissimilarity scaling experiments.

Subjects

Five subjects (2 males, 3 females, 18–24 yr old) participated in the roughness estimation experiment, six subjects (3 males, 3 females, 19–23 yr old) participated in the stickiness estimation experiment, five subjects (2 males, 3 females, 18–21 yr old) participated in the hardness estimation experiment, and six subjects (4 males, 2 females, 18–26 yr old) participated in the dissimilarity scaling experiment. All subjects were naïve and only participated in one experiment. Subjects, all University of Chicago students, were paid for their participation and provided informed consent. All procedures were approved by the Institutional Review Board of the University of Chicago.

Psychophysics

Subjects sat with their right arm supinated and resting on a support such that the hand was situated under the drum. A curtain blocked view of the textures. White noise was played through computer speakers, and subjects wore sound-blocking headphones to mask movement sounds from the drum. Because white noise was constant throughout the experiment, any modulating effect auditory stimuli may have had on perceived texture affected all conditions equally and were not expected to impact the results. Roughness, stickiness, and hardness were not defined for the subjects. Subjects were told to rate the stimuli on a scale of their choosing. In each experiment, a small subset of stimuli or stimulus pairs was presented before archival data collection for practice.

In the magnitude estimation experiment, 1 of 15 textures was presented on each trial, and subjects rated the texture according to its perceived roughness, where zero indicated a perfectly smooth surface; its perceived stickiness, where zero indicated a perfectly slippery texture; or its perceived hardness, where zero indicated a perfectly soft surface (softness does not have a clear extremum as do smoothness or slipperiness). Using roughness as an example, if one texture was perceived to be two times as rough as another, it was to be ascribed a rating that was two times as high. Subjects were encouraged to use fractions or decimals if these better reflected perceived roughness. Each texture-speed pair (out of 60 in total) was presented to each subject four times over the course of two blocks, yielding 240 trials per experimental session.

In the dissimilarity scaling experiment, two textures were presented on each trial, each for 0.8 s with a 2-s interstimulus interval, and subjects rated the perceived dissimilarity of the pair. If the two textures were perceived as identical, subjects assigned them a zero. If one pair was perceived to be two times as different as another, it was ascribed a number that was two times as high. The textures presented on each trial could be the same (3 unique textures) or different (6 unique pairs), and they could be presented at the same speed (40, 80, or 120 mm/s) or at different speeds (40/80 or 80/120 mm/s and the reverse). This design yielded 105 trials/block. To prevent subjects from becoming familiar with the specific texture pairs, we interleaved 20 pairs of random textures. All stimulus conditions were presented in pseudo-random order in each of three blocks.

Analysis

Because each subject used a scale of their own choosing, the ratings were normalized by standardizing the ratings for each block (subtracting the mean, dividing by the SD).

Because ratings were generally not normally distributed, we applied nonparametric statistics for inference testing. Specifically, we used Friedman tests, a nonparametric analog of repeated-measures ANOVA, to determine whether speed exerted any effect on perceptual ratings. We ran these tests on individual (z-scored) responses. For the magnitude estimation experiment, we treated each of the four trials per texture/speed pair as a replicate. For the dissimilarity scaling experiment, we treated the three same-speed conditions separately and therefore ran the Friedman test over seven conditions.

To gauge the degree to which differences in speed could account for variance in the magnitude estimates, a regression analysis was performed. The mean of each presentation of a texture at a given

Table 2. *List of texture pairs analyzed in the dissimilarity experiment*

Texture Pairs Different		Same	
Corduroy (2)	Empire velveteen (15)	Stretch denim (12)	Stretch denim (12)
Corduroy (2)	5 mm Grating (4)	Microsuede (23)	Microsuede (23)
Microsuede (23)	Suede cuddle (20)	Corduroy (2)	Corduroy (2)
5 mm Grating (4)	Hucktowel (21)		
Empire velveteen (15)	Microsuede (23)		
Suede cuddle (20)	Hucktowel (21)		

Numbers refer to Table 1.

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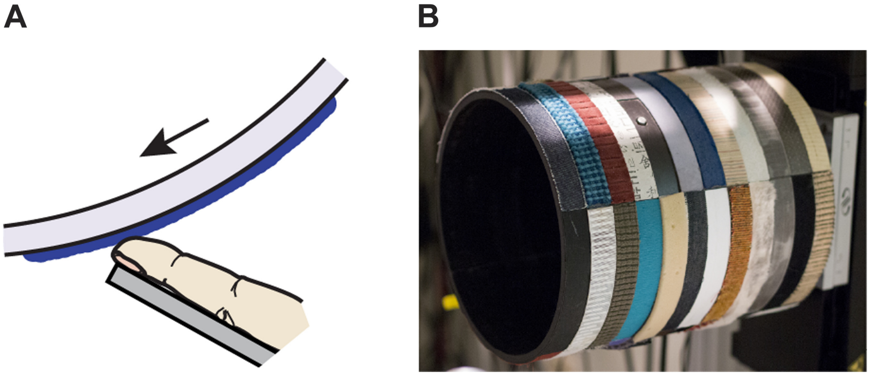

Fig. 2. Experimental setup. *A*: textures were passively scanned over the fingertip at 40, 80, 120, and 160 mm/s. *B*: textures were scanned at a precise speed across the skin with a contact force of 0.3 N using a custom-built drum stimulator.

speed across all subjects was compared with the perceived roughness averaged across all speeds: the coefficient of determination (R^2) of this regression represents the proportion of variance explained by texture identity irrespective of speed.

RESULTS

Constancy of Textural Dimensions

We wished to investigate the degree to which the perceptual rating ascribed to each texture along each of the principal sensory dimensions of texture (roughness, stickiness, and hardness) was dependent on the speed at which the surface was scanned across the finger. To this end, we conducted a series of magnitude estimation experiments in which subjects were presented with 15 textures at 40, 80, 120, and 160 mm/s, spanning the range of scanning speeds adopted spontaneously for texture exploration (Callier et al. 2015), and rated the roughness, stickiness, or hardness of the textures (Fig. 2).

First, we investigated whether perceptual ratings along individual texture dimensions changed with scanning speed. We found that speed exerted a small but significant effect on roughness ratings [Friedman test, $X^2(3,900) = 11.56$, $P = 0.01$]. Post hoc Wilcoxon signed-rank tests with Bonferroni correction revealed that textures were rated as less rough at 40 mm/s when compared with 120 ($P = 0.04$) and 160 ($P = 0.02$) mm/s. When analyzing single-subject data, only one out of five subjects showed a significant difference across scanning speeds [Friedman test, $X^2(3,180) = 12.33$, $P = 0.01$], which again was the result of lower ratings at 40 mm/s compared with 120 and 160 mm/s (Wilcoxon signed-rank tests with Bonferroni correction, $P = 0.04$ and 0.01, respectively). Stickiness ratings did not depend on speed [$X^2(3,1080) = 0.11$, $P = 0.99$], and no significant differences between speeds were found for any of the 6 individual subjects ($P > 0.29$ for all subjects). Finally, hardness ratings were modulated by speed [$X^2(3,900) = 15.40$, $P = 0.002$]. Post hoc Wilcoxon signed-rank tests with Bonferroni correction indicated that hardness ratings were significantly smaller at 40 mm/s compared with 80 ($P = 0.02$) and 160 ($P = 0.01$) mm/s. When analyzing single subjects, only one out of five subjects showed significant differences between speeds [Friedman test, $X^2(3,180) = 12.78$, $P = 0.01$], which again was attributed to lower ratings at 40 mm/s compared with 80 and 160 mm/s (Wilcoxon signed-rank tests with Bonferroni correction, $P = 0.01$ and 0.03, respectively). In summary, then, both on a population and single-subject level, scanning speed exerts little to no effect on perceptual ratings. To the extent that an effect is observed, it always involves the lowest of the four scanning speeds, which is generally associated with smoother and softer ratings.

One might argue that our failure to detect significant effects of speed on texture perception might be attributable to type II error, given the relatively small sample size. To address this concern, we quantified the size of the effect of scanning speed on perceived roughness, stickiness, and hardness. Specifically, we computed how much of the variance in the ratings could be explained simply from differences in texture irrespective of speed. We found that texture accounted for nearly all of the variance in ratings ($R^2 = 0.99$, 0.97, and 0.98 for roughness, stickiness, and hardness, respectively), indicating that any effect that scanning speed might exert on the perceptual ratings is exceedingly small (Fig. 3, *D–F*) and dwarfed by differences in perceptual ratings across different textures.

Next, we wished to further assess the magnitude of any effects of scanning speed on perceived texture by comparing mean ratings with the magnitude of their trial-by-trial variability. Specifically, we first quantified the perceptual noise across trials by computing the SD of the rank of each texture rating along each texture dimension across speeds. This value represents the degree to which the position of each texture along each dimension varies across speeds, with lower values denoting greater consistency. We then quantified the average shift in rank for each texture across speeds as a gauge of consistency across speeds, with lower values again denoting greater consistency. For roughness, we found a noise level of 0.9 ranks (over the 4 speeds) while the average rank only increased by 0.3 across speeds. In fact, in only 39% of cases were textures rated as rougher at 160 than at 40 mm/s; on the remaining trials, they were rated as the same or lower. A similar picture emerged for hardness: the noise levels reached 0.9 ranks compared with a difference of 0.3 ranks between the highest and the lowest speed, and textures were rated as harder on only 40% of comparisons. Thus, the effect of speed was far from consistent from trial to trial. This analysis confirmed that the effect of scanning speed on perceived texture is indeed exceedingly small.

Texture Constancy across Dimensions

Results from the magnitude estimation experiments, then, show that the position of each texture along each of the three major textural dimensions (namely roughness, stickiness, and hardness) (Hollins et al. 2000a) is relatively independent of the speed at which the texture is scanned across the finger. However, not all aspects of texture perception can be reduced to these salient dimensions. One possibility is that our perception

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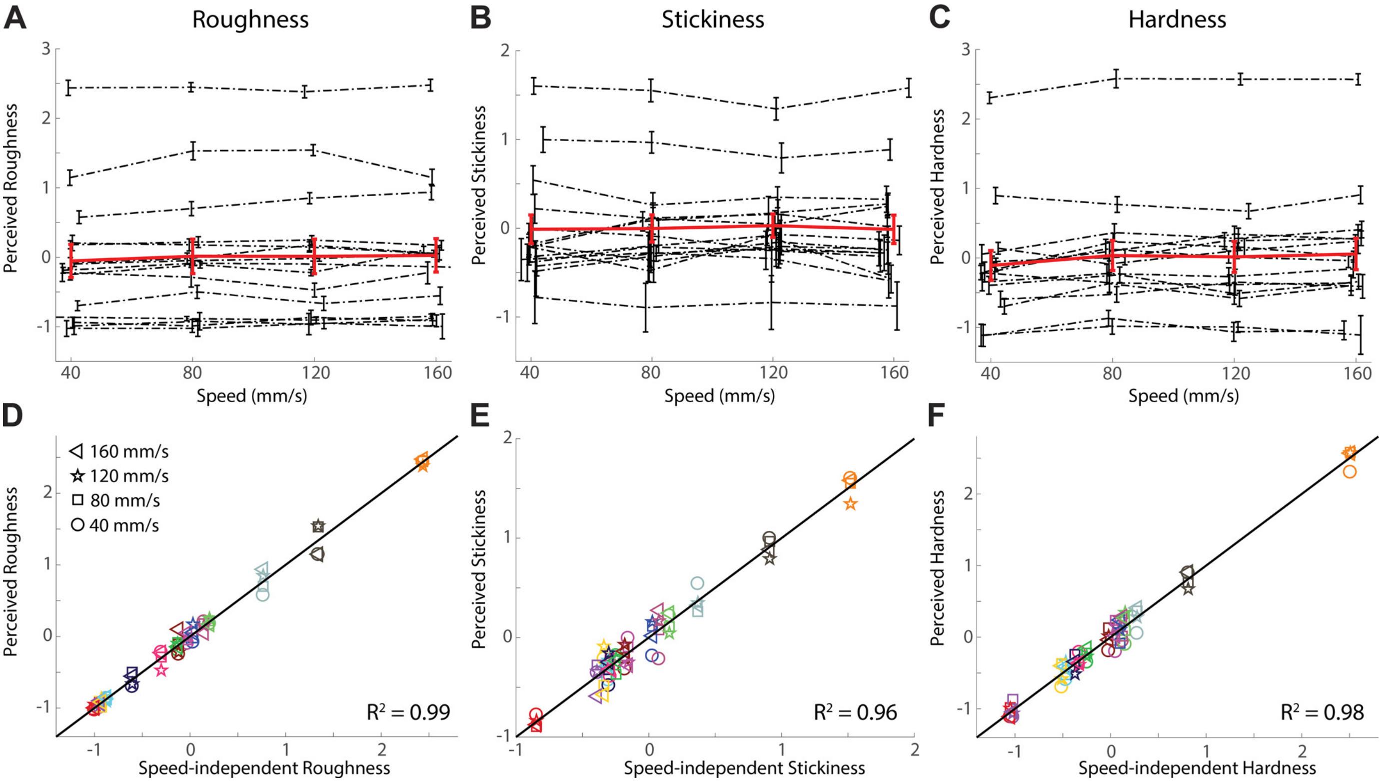

Fig. 3. Perceptual invariance of individual textural dimensions. *A–C*: average roughness (*A*), stickiness (*B*), and hardness (*C*) ratings vs. scanning speed. Gray lines connect individual textures at different scanning speeds. The red line denotes the mean rating of all 15 textures across speeds. Error bars denote the SE of the mean across all trials and subjects (n = 20/speed-texture pair for roughness and hardness, n = 24 for stickiness). *D–F*: measured mean ratings of roughness (*D*), stickiness (*E*), and hardness (*F*) vs. ratings averaged across speeds. Each color represents a unique texture, whereas different symbols denote different scanning speeds. Texture identity, and not speed, explains virtually all of the variance in the magnitude estimates of roughness, stickiness, and hardness.

of texture is speed invariant along any of the major dimensions but is affected by scanning speed in ways that are not captured in these dimensional measurements. To test for this possibility, we had subjects rate the dissimilarity of pairs of textures presented at different speeds relative to each other. The idea is that dissimilarity ratings capture all differences in texture not just those captured within specific dimensional representations. If speed does not influence texture perception at all, a given pair of textures should be perceived as equally similar or dissimilar regardless of the relative speed of the two textures.

We found that dissimilarity ratings were not significantly modulated by speed ratio [Friedman test, $X^2(6,1614) = 10.49$, $P = 0.11$], suggesting that texture identity drove the judgments rather than the relative speed at which textures in the pair were scanned across the skin (Fig. 4*A*). To further investigate the impact of relative speed on perceived dissimilarity, we split the data into "same" and "different" pairs, i.e., pairs in which a texture was compared against itself (presented at the same or a different speed) and pairs where two different textures were presented. First, we found that ratings for same pairs were significantly lower than those for different pairs, as expected (Wilcoxon rank-sum test, $z = -22.27$, $P < 0.001$). Second, although speed ratio exerted a small but significant effect on the perceived dissimilarity of same pairs (Wilcoxon rank-sum text, $z = 3.83$, $P < 0.001$), it had no effect on the ratings of different pairs ($z = 0.91$, $P = 0.36$) (Fig. 4*B*). In other words, if the same texture is scanned two times at different speeds, it will feel slightly more different than if it is scanned two times at the same speed. In contrast, if two textures are scanned at different speeds, they will feel as dissimilar as if the two textures are scanned at the same speed.

Finally, to examine the extent to which speed could explain the dissimilarity ratings, we tested the extent to which we could predict dissimilarity ratings based on the texture pair identity alone and found that pair identity explained 95% of the variance (Fig. 4*C*). These results suggest that scanning speed only exerts a very minor, if any, influence on the tactile perception of texture, even when perception is gauged across all aspects of texture.

DISCUSSION

The brain forms representations of objects that are invariant with respect to how we explore them, a phenomenon that has been well documented in several sensory modalities. Here, we investigated this phenomenon in touch, focusing on the perceptual constancy of tactile texture perception across different scanning speeds. Our results are unequivocal: under all conditions tested, we found that scanning speed exerted either no effect on the perception of tactile texture or only a very minor one.

Texture Constancy for Coarse vs. Fine Textures

The fact that tactile texture perception is invariant with respect to scanning speed for fine textures is surprising. Coarse textural features are encoded spatially, a representation that has been shown to be largely unaffected by changes in scanning speed (Bochereau et al. 2015; DiCarlo and Johnson 1999). In

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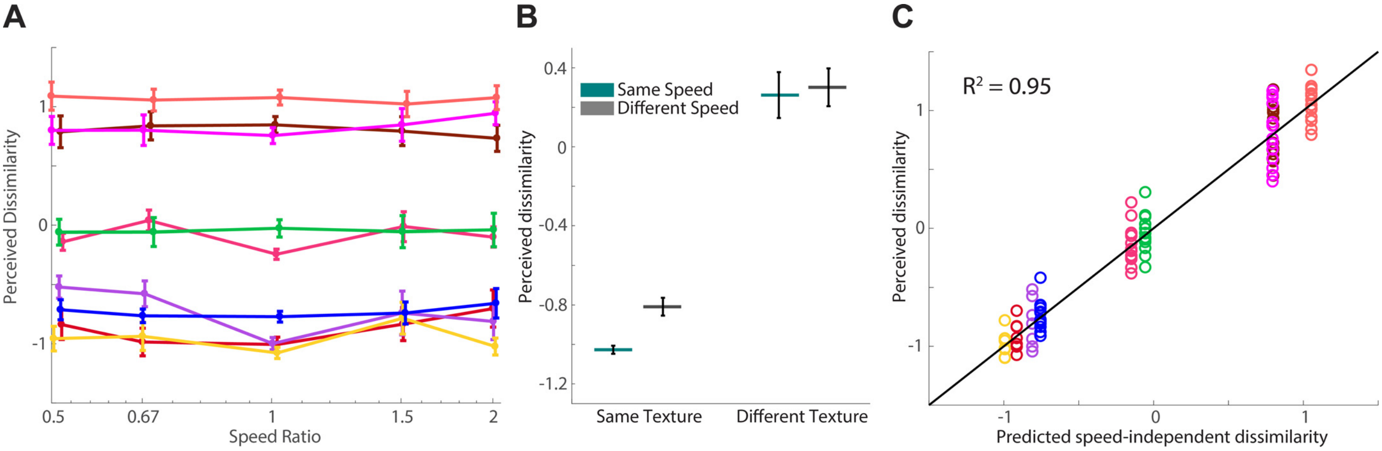

Fig. 4. Perceptual invariance of perceived texture. *A*: dissimilarity ratings for 9 texture pairs plotted at 5 different speed ratios. Colors denote different texture pairs. Error bars denote the SE of the mean across all trials and subjects ($n = 54$ for same-texture pairs at speed ratio = 1, $n = 18$ otherwise; $n = 108$ for different-texture pairs at speed ratio = 1, $n = 36$ otherwise; see MATERIALS AND METHODS for details). *B*: average dissimilarity ratings when the same texture was presented two times (*left*) and when two different textures were presented (*right*). Dissimilarity ratings are lower for same-texture same-speed pairs than for same-texture different-speed pairs, but the perceived dissimilarity of different-texture pairs is the same whether the two textures are presented at the same or different speeds. Error bars as in *A* (same sample sizes as in *A* averaged over 3 same-texture pairs and 6 different-texture pairs, respectively, see MATERIALS AND METHODS for detailed breakdown of the different conditions). *C*: texture identity alone predicts 95% of the variance in the mean dissimilarity ratings, suggesting that the effects of scanning speed are small. Each circle represents the mean rating of a texture pair at a specific speed ratio, and different colors denote different texture pairs.

light of this, perceptual constancy is expected for this class of textures. In contrast, the neural code for fine textures relies on the transduction of small high-frequency oscillations in the skin, which are strongly affected by changes in scanning speed (Delhaye et al. 2012; Manfredi et al. 2014). Indeed, the frequency composition of the vibrations translates up or down the frequency axis with increases or decreases in scanning speed, respectively. Consequently, the aspect of the neural response that encodes fine textures is also dependent on scanning speed (Weber et al. 2013). The texture-specific spike patterns contract or dilate with increases or decreases in speed. Not only do the temporal patterns change, then, but the overall firing rates increase with speed. Thus, the signals that the hand sends the brain about fine textures are highly dependent on scanning speed. To achieve speed invariance for these textures thus requires that these speed-related changes be compensated for. Most of the textures used in the present study comprised some fine textural features so the perception thereof might have been expected to be speed dependent.

Comparison with a Previous Study

While most previous studies reached the conclusion that texture perception is relatively invariant with respect to scanning speed, one study came to the opposite conclusion (Yoshioka et al. 2011). In that study, a small but significant increase in perceived roughness was observed with increases in scanning speed. One possibility is that textures were perceived as rougher because the rotational motor induced vibrations in the finger. Indeed, the drum stimulator had been reported to induce unwanted skin vibrations that strongly activate PC fibers (Johnson and Phillips 1988). As the stimulator rotated faster, vibrations induced by the rotational motor and transmitted to the finger through the drum likely became stronger: the superposition of vibration on texture has been shown to cause an increase in perceived roughness, and this effect depends on the power of the imposed vibrations (Asano et al. 2015; Hollins et al. 2000b). The magnitude of the effect of imposed vibration on perceived roughness is consistent with that observed in the study by Yoshioka et al.

We should note, however, that the discrepancy between the studies is minimal. Indeed, we too find a small but significant effect of speed on roughness, an effect that is likely somewhat amplified by the drum-induced vibrations in the previous study. Regardless, the effect of speed on roughness (even confounded by motor-induced vibrations) is far stronger when textures are explored with a probe and information about speed is unavailable, perhaps providing an indication of how strong the effect would be were it not corrected for when the surface is sensed directly through the skin.

Neural Mechanisms of Texture Constancy

The speed invariance of the perception of fine surface features could theoretically be achieved by integrating texture-evoked temporal spiking patterns with the available cutaneous information about scanning speed. Indeed, as mentioned above, fine textural features are reflected in high-frequency components in the evoked skin vibrations (Bensmaïa and Hollins 2003; Bensmaïa and Hollins 2005; Manfredi et al. 2014) and, ultimately, in the spiking responses of nerve fibers (Weber et al. 2013). These frequency components shift to lower or higher frequencies with decreases or increases in scanning speed, respectively. Correcting for scanning speed, by dividing the frequency of each component by the speed, yielding a representation in spatial coordinates, results in a representation of texture that is invariant with respect to speed. However, this hypothesis assumes that the tactile speed signal is precise and robust enough to achieve this correction, which has yet to be demonstrated for fine textures (but see Dépeault et al. 2008 for coarse ones).

Another possibility is that the speed invariance of texture is achieved using a mechanism akin to auditory timbre invariance: while the frequency composition of the spiking responses to texture shifts to lower or higher frequencies with decreases or increases in scanning speed, their harmonic structure re-

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mains relatively consistent across speeds (Manfredi et al. 2014). Speed-independent representations of texture might be achieved by extracting this harmonic structure in a way that is independent of the speed (Yau et al. 2009; Saal et al. 2016). How the auditory system achieves timbre invariance is unknown, so investigation of timbre and texture may lead to the discovery of a general neural mechanism to extract invariances in waveforms across time warps.

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

Z.M.B.-S. performed experiments; Z.M.B.-S. analyzed data; Z.M.B.-S., H.P.S., and S.J.B. interpreted results of experiments; Z.M.B.-S. prepared figures; Z.M.B.-S., H.P.S., and S.J.B. drafted manuscript; Z.M.B.-S., H.P.S., and S.J.B. edited and revised manuscript; Z.M.B.-S., H.P.S., and S.J.B. approved final version of manuscript; H.P.S. and S.J.B. conceived and designed research.

REFERENCES

Asano S, Okamoto S, Yamada Y. Vibrotactile stimulation to increase and decrease texture roughness. *IEEE Trans Hum Mach Syst* 45: 393–398, 2015. doi:10.1109/THMS.2014.2376519.

Bensmaïa S, Hollins M. Pacinian representations of fine surface texture. *Percept Psychophys* 67: 842–854, 2005. doi:10.3758/BF03193537.

Bensmaïa SJ, Hollins M. The vibrations of texture. *Somatosens Mot Res* 20: 33–43, 2003. doi:10.1080/0899022031000083825.

Biederman I, Gerhardstein PC. Recognizing depth-rotated objects: evidence and conditions for three-dimensional viewpoint invariance. *J Exp Psychol Hum Percept Perform* 19: 1162–1182, 1993. doi:10.1037/0096-1523.19.6.1162.

Bochereau S, Sinclair S, Hayward V. Looking for Physical Invariants in the Mechanical Response of a Tactually Scanned Braille Dot. Evanston, IL: IEEE World Haptics Conf., June 22–26, 2015. doi:10.1109/WHC.2015.7177701.

Booth MC, Rolls ET. View-invariant representations of familiar objects by neurons in the inferior temporal visual cortex. *Cereb Cortex* 8: 510–523, 1998. doi:10.1093/cercor/8.6.510.

Callier T, Saal HP, Davis-Berg EC, Bensmaia SJ. Kinematics of unconstrained tactile texture exploration. *J Neurophysiol* 113: 3013–3020, 2015. doi:10.1152/jn.00703.2014.

Cascio CJ, Sathian K. Temporal cues contribute to tactile perception of roughness. *J Neurosci* 21: 5289–5296, 2001. https://www.ncbi.nlm.nih.gov/pubmed/11438604.

Connor CE, Hsiao SS, Phillips JR, Johnson KO. Tactile roughness: neural codes that account for psychophysical magnitude estimates. *J Neurosci* 10: 3823–3836, 1990.

Delhaye B, Hayward V, Lefèvre P, Thonnard J-L. Texture-induced vibrations in the forearm during tactile exploration. *Front Behav Neurosci* 6: 37, 2012. doi:10.3389/fnbeh.2012.00037.

Dépeault A, Meftah M, Chapman CE. Tactile speed scaling: contributions of time and space. *J Neurophysiol* 99: 1422–1434, 2008. doi:10.1152/jn.01209.2007.

DiCarlo JJ, Johnson KO. Velocity invariance of receptive field structure in somatosensory cortical area 3b of the alert monkey. *J Neurosci* 19: 401–419, 1999.

Goodwin AW, Wheat HE. How is tactile information affected by parameters of the population such as non-uniform fiber sensitivity, innervation geometry and response variability? *Behav Brain Res* 135: 5–10, 2002.

Grey JM, Gordon JW. Perceptual effects of spectral modifications on musical timbres. *J Acoust Soc Am* 63: 1493–1500, 1978. doi:10.1121/1.381843.

Hollins M, Bensmaïa S, Karlof K, Young F. Individual differences in perceptual space for tactile textures: evidence from multidimensional scaling. *Percept Psychophys* 62: 1534–1544, 2000a. doi:10.3758/BF03212154.

Hollins M, Fox A, Bishop C. Imposed vibration influences perceived tactile smoothness. *Perception* 29: 1455–1465, 2000b. doi:10.1068/p3044.

Johnson KO, Lamb GD. Neural mechanisms of spatial tactile discrimination: neural patterns evoked by braille-like dot patterns in the monkey. *J Physiol* 310: 117–144, 1981. doi:10.1113/jphysiol.1981.sp013540.

Johnson KO, Phillips JR. A rotating drum stimulator for scanning embossed patterns and textures across the skin. *J Neurosci Methods* 22: 221–231, 1988. doi:10.1016/0165-0270(88)90043-X.

Lederman S. The perception of surface roughness by active and passive touch. *Bull Psychon Soc* 18: 253–255, 1981. doi:10.3758/BF03333619.

Lederman SJ. Tactile roughness of grooved surfaces: the touching process and effects of macro- and microsurface structure. *Percept Psychophys* 16: 385–395, 1974. doi:10.3758/BF03203958.

Lederman SJ, Klatzky RL. Hand movements: a window into haptic object recognition. *Cognit Psychol* 19: 342–368, 1987. doi:10.1016/0010-0285(87)90008-9.

Manfredi LR, Saal HP, Brown KJ, Zielinski MC, Dammann JF III, Polashock VS, Bensmaia SJ. Natural scenes in tactile texture. *J Neurophysiol* 111: 1792–1802, 2014. doi:10.1152/jn.00680.2013.

Saal HP, Wang X, Bensmaia SJ. Importance of spike timing in touch: an analogy with hearing? *Curr Opin Neurobiol* 40: 142–149, 2016. doi:10.1016/j.conb.2016.07.013.

Weber AI, Saal HP, Lieber JD, Cheng J-W, Manfredi LR, Dammann JF III, Bensmaia SJ. Spatial and temporal codes mediate the tactile perception of natural textures. *Proc Natl Acad Sci USA* 110: 17107–17112, 2013. doi:10.1073/pnas.1305509110.

Yau JM, Hollins M, Bensmaia SJ. Textural timbre: the perception of surface microtexture depends in part on multimodal spectral cues. *Commun Integr Biol* 2: 344–346, 2009. doi:10.4161/cib.2.4.8551.

Yoshioka T, Bensmaïa SJ, Craig JC, Hsiao SS. Texture perception through direct and indirect touch: an analysis of perceptual space for tactile textures in two modes of exploration. *Somatosens Mot Res* 24: 53–70, 2007. doi:10.1080/08990220701318163.

Yoshioka T, Craig JC, Beck GC, Hsiao SS. Perceptual constancy of texture roughness in the tactile system. *J Neurosci* 31: 17603–17611, 2011. doi:10.1523/JNEUROSCI.3907-11.2011.

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