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THE EFFECT OF CONTACT FORCE ON THE RESPONSES OF TACTILE NERVE FIBERS TO SCANNED TEXTURES

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ABSTRACT

The perception of fine textures relies on highly precise and repeatable spiking patterns evoked in tactile afferents. These patterns have been shown to depend not only on the surface microstructure and material but also on the speed at which it moves across the skin. Interestingly, the perception of texture is independent of scanning speed, implying the existence of downstream neural mechanisms that correct for scanning speed in interpreting texture signals from the periphery. What force is applied during texture exploration also has negligible effects on how the surface is perceived, but the consequences of changes in contact force on the neural responses to texture have not been described. In the present study, we measure the signals evoked in tactile afferents of macaques to a diverse set of textures scanned across the skin at two different contact forces and find that responses are largely independent of contact force over the range tested. We conclude that the force invariance of texture perception reflects the force independence of texture representations in the nerve.

INTRODUCTION

Scanning a texture with our fingertip elicits highly precise and repeatable temporal spiking patterns in tactile afferents, and these spike sequences carry information about texture identity (Weber et al., 2013). Temporal spiking patterns mediate our ability to distinguish fine surfaces with different fine microstructure, measured in the tens of microns (Skedung et al., 2013; Weber et al., 2013; Manfredi et al., 2014). Spiking patterns do not simply depend on the textured surface, however; they also depend on the speed at which it moves across the skin: patterns contract and dilate with increases and decreases in scanning speed, respectively (Weber et al., 2013).

While natural texture exploration involves scanning movements that vary widely in speed and in contact force (Morley et al., 1983; Smith et al., 2002a, 2002b; Tanaka et al., 2014; Callier et al., 2015), our perception of texture depends little on these scanning movements: Velvet feels like velvet and sandpaper like sandpaper no matter how we touch them, suggesting that some aspect of the evoked response is invariant with respect to scanning parameters. For example, changes in scanning speed do not affect roughness perception (Lederman, 1974; Meftah el-M et al., 2000), despite its powerful influence on texture responses in tactile afferents (Weber et al., 2013). Similarly, the perceived roughness of textured surfaces is relatively insensitive to huge changes in contact force (Lederman and Taylor, 1972; Lederman, 1981): a five-fold increase in force only leads to a 10% increase in perceived roughness.

In the present study, we examine the degree to which texture-specific spiking sequences evoked during texture scanning depend on contact force. We find that, while firing rates increase slightly at higher forces, the precise temporal patterning is almost completely unaffected and remains highly informative about texture identity across contact forces. Thus, while speed invariance of texture perception likely relies on specialized neural circuits (Saal et al., 2016), force invariance of perception simply reflects the force-independence of texture representations in the nerve.

METHODS

PERIPHERAL NERVE RECORDINGS

Stimuli. A diverse set of 55 textured surfaces (see Manfredi et al., 2014 for complete list) was presented to the fingertips of anesthetized macaques using a custom-built rotating drum stimulator, as described previously in detail (Weber et al., 2013). In brief, textured strips (2.5 cm wide x 16 cm in scanning direction) were wrapped around an acrylic drum (25.4 cm in diameter and 30.5 cm in

length). The texture set included gratings and tetragonal arrays of embossed dots created from a photosensitive polymer (Printight, Toyobo Co., Ltd.), as well as finer, more naturalistic textures such as fabrics and sandpapers. Textures were scanned across the skin at 80 mm/s for 1.2 s at two different normal forces: 50 and 25 g wt. Each individual texture presentation lasted 1.2 s, followed by an inter-trial interval of 3.5 s, designed to be long enough to minimize the effects of afferent adaptation (Bensmaia et al., 2005; Leung et al., 2005). Each texture was presented two or three times.

Neurophysiology. Extracellular single-unit recordings were obtained from the median and ulnar nerves innervating the distal fingertips of 4 Rhesus macaques (*Macaca mulatta*) as described previously (Muniak et al., 2007; Weber et al., 2013). Data were collected from 4 SA1 a, 1 RA, and 2 PC fibers. All procedures complied with the NIH Guide for the Care and Use of Laboratory Animals and were approved by the Animal Care and Use Committee of the University of Chicago. Some of the data obtained from the one RA was compromised, and so the (good) data from this afferent were used for display purposes only (in Figure 1). Responses from two additional RA fibers were obtained in a separate experiment involving recordings from the dorsal root ganglia, described below.

DORSAL ROOT GANGLION RECORDINGS

Stimuli. The stimuli consisted of 10 textured surfaces – Chiffon, City Light, Corduroy, Crocodile Skin, Deck Chair, Denim, Hucktowel, Metallic Silk, Nylon, and Upholstery –, seven of which were also used in the peripheral nerve recordings. Textures were scanned across the fingertips of anesthetized macaques using a custom-built rotating drum stimulator, a smaller version of the previously described one (Weber et al., 2013). Textured strips, each 2.5 cm wide and 16 cm long along the scanning direction, were wrapped around the drum, itself 14 cm long and 6.4 cm in diameter. Textures were scanned at a speed of 80 mm/s and presented at two different normal forces: 10 and 50 g wt. Each texture was scanned across the skin four times, each for 1.2 s, and texture presentations were separated by inter-trial intervals lasting 3.5 s.

Neurophysiology. Extracellular single-unit recordings were obtained from the dorsal root ganglia of 1 Rhesus macaque, as described previously in cats (Gaunt et al., 2009). Animals were anesthetized with ketamine and maintained on isoflurane anaesthesia for the duration of the procedure. The C3 through T2 vertebrae were exposed through a midline incision and retraction of the overlying musculature and a dorsal laminectomy was performed to expose the spinal cord from C5 through T1. The laminectomy was extended laterally through the articular processes past the foramina of the C6-C8 spinal roots to expose the dorsal root ganglia (DRG). Ligaments and other tissue over the DRG were resected to provide a clear view of the DRG enlargement. 32-channel microelectrode arrays (4x8, Blackrock microsystems) were positioned over the C6-C8 DRG and inserted using a pneumatic high-speed inserter.

Extracellular single-unit recordings were obtained from the dorsal root ganglia innervating the distal fingertips (D2 and D4) of 1 Rhesus macaque (*Macaca mulatta*) using a high density microelectrode array (Utah Array, BlackRock Microsystems, Salt Lake City, Utah). Data were collected from 2 RA fibers. All procedures complied with the NIH Guide for the Care and Use of Laboratory Animals and were approved by the Animal Care and Use Committee of the University of Pittsburgh.

TEXTURE CLASSIFICATION FROM NEURAL DATA.

For all analyses, we used 500 ms of steady-state spiking data (after the onset transient and before the texture began to lift off the fingertip). To determine the extent to which textures can be distinguished based on spiking sequences evoked in individual afferents, we implemented a nearest

neighbour classifier. This classification analysis gauges whether spike trains evoked by one stimulus (in this case a given texture) are more similar to each other than to those evoked by other stimuli (different textures). Specifically, we applied a leave-one-out approach, in which we computed the dissimilarity between each spike train S_i and every other spike train. The texture was correctly classified when the mean dissimilarity between S_i and spike trains from the same texture was lower than the mean dissimilarity between S_i and spike trains from each of the other textures. This procedure was repeated for every spike train obtained from each afferent. As a measure of dissimilarity, we employed a spike train distance metric (D_{spike}), used in our previous studies, that computes the cost to transform one spike train into another (Victor and Purpura, 1997; Mackevicius et al., 2012; Weber et al., 2013; Suresh et al., 2016). A cost of 1 is incurred for adding and deleting spikes, and a cost per unit time, q , is incurred to move spikes. By varying q , we can assess the contribution of precise spike timing to the distance computation and thus to the classification performance. That is, a q of 0 leads to a distance metric based solely on differences in spike count: Two spike trains will be different to the extent that the number of spikes is different. With non-zero q 's, shifting spikes in time is less expensive than adding or subtracting spikes when the required shifts are less than $2/q$ ms. For each pair of spike trains, we shifted one spike train relative to the other (in 1-ms increments, for up to 100 ms in each direction) and used the minimum distance across all shifts to ensure that the classification analysis could not exploit differences in absolute response phase, which depends on the precise location of the stimulus relative to the receptive field of the nerve fiber. We performed this analysis in two different ways: First, on a subset of the data including only trials at a single contact force (either 25 g wt or 10 g wt, and 50 g wt); second, on the full data set comparing trials from one force to trials from the other. While the former analysis tests whether and at what temporal resolution information about texture identity is encoded in the spiking sequences, the latter analysis tests the robustness of the neural code across different force levels, and therefore how robust the neural code is to changes in force.

RESULTS

We assessed how much varying the level of normal force exerted by the drum during texture scanning affected the neural responses of the three different afferent types implicated in texture perception: slowly-adapting type I (SA1), rapidly-adapting (RA), and Pacinian (PC) afferents (see Figure 1 for examples of neural responses recorded at different force levels). Data were obtained both through single-unit recordings from the peripheral nerve (SA1 and PC fibers) and array recordings from the dorsal root ganglia (RA fibers, see Methods for details).

Effects of force on firing rates

First, we examined the influence of contact force on the firing rates elicited in the three different afferent populations (Figure 2). We found that doubling the force (from 25 to 50 g wt) results in an increase in firing rate of 30% for SA1 fibers and 24% for PC fibers. RA afferents are even less susceptible to changes in force, as evidenced by the fact that a fivefold increase in force (from 10 to 50 g wt) resulted in a 16% increase in firing rate.

Effects of force on precise spike timing

Next, we examined whether the precise spiking sequences evoked during texture scanning were different at different levels of contact force. To test the robustness of the texture signals conveyed through temporal spiking patterns, we classified texture identity from the neural responses at different temporal resolutions. To the extent that temporal spiking sequences evoked by a given texture were consistently more similar to each other across contact forces than they were to

patterns evoked by other textures, then texture identity could be decoded from these patterns by downstream structures, regardless of contact force. The analysis also allows us to determine the optimal temporal resolution to extract texture information.

First, we tested spike sequences at each force level individually and found that classification performance was consistently well above chance at both force levels for all three afferent types (Figure 3, blue and orange traces). Note that classification performance is poor with rates alone and that the optimal resolution is highest for PC responses, lowest for SA1 responses, and intermediate for RA responses, as has been previously shown (Weber et al., 2013).

Second, we gauged whether spiking sequences were sufficiently similar across force levels to support texture classification. We found that, indeed, classification performance achieved by comparing neural responses evoked at high contact force (50g) to those collected at a low one (25 g or 10 g) was also far above chance for each class of nerve fibers at their optimal temporal resolution, albeit lower than that achieved at each level separately (Figure 3, yellow traces). This was also true for the finest textures, the perception of which relies exclusively on these temporal patterns. Indeed, classification performance for the four smoothest textures – chiffon, denim, silk, and upholstery – was 71, 66, and 63% for SA1, RA, and PC fibers, respectively, so performance was better than chance (25%) for those too. In conclusion, then, texture-specific temporal spiking patterns are preserved across changes in force level.

Next, we found that combining responses from a few fibers (4 SA1, 2 RA, and 2 PC fibers), yielded improved classification (except for PC fibers, asterisks in Figure 3), suggesting that a complete afferent population, comprising hundreds of nerve fibers, could convey texture information that is robust across contact forces.

DISCUSSION

Our ability to discern fine textures is thought to be mediated by the elicitation of precise temporal spiking sequences in somatosensory afferents as the fingertip moves across the surface (Bensmaïa and Hollins, 2003; Weber et al., 2013). For this neural code to be viable, however, these patterns have to remain consistent when the movements used to explore the surface change. Indeed, both scanning speed and contact force vary widely during the natural exploration of textures (Smith et al., 2002b; Callier et al., 2015). If the texture signals from the hand changed in unpredictable ways with changes in scanning parameters, these signals would be impossible to interpret. Instead, our perception of texture is mostly independent of exploratory parameters (Lederman, 1974) (but see Cascio and Sathian, 2001), suggesting that some aspect of these spiking sequences is consistent across changes in scanning speed and contact force.

In previous work, we have shown that changes in scanning speed lead to systematic changes in the neural responses: the spiking patterns dilate and contract as scanning speed decreases or increases, respectively (Weber et al., 2013). Here, we found that the temporal structure of the spiking sequences is relatively consistent across contact force levels so that textures can be reliably classified across different force conditions when spike timing is taken into account. In other words, the neural code for texture is robust across changes in contact force.

Note that the sample size in the present study is small, particularly for RA and PC afferents. The experimental protocol in which we probed the effects of contact force on afferent responses was one of several, and we were often unable to maintain stable recordings from a nerve fiber to run that particular protocol. However, SA1 afferents are the most sensitive to changes in contact force (Knibestöl, 1975) and the other two classes of afferents respond primarily to changes in indentation

rather than absolute levels of indentation (Knibestöl, 1973; Johansson and Vallbo, 1983). We might thus expect the texture signals carried by SA1 fibers to be most sensitive to changes in contact force, and they are not. In fact, SA1 responses have been shown to respond to surface elements that create local deformations within the fingertip in a way that is relatively independent of the overall force exerted on the skin (Vega-Bermudez and Johnson, 1999), consistent with the present findings. Thus, the preservation of spiking sequences across force levels is not only consistent across fiber types, but also observed in the fiber type that should be most sensitive and has the largest sample size. We thus feel that our conclusion – that texture-specific spiking sequences are preserved across force levels and form the basis for perceptual invariance – is justified.

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Figures



Figure 1. Sample spike trains evoked in one afferent of each type by three different textures at two different contact forces. Visual inspection suggests that both the strength and temporal patterning in the response are relatively consistent across contact force conditions. These afferent responses were collected from the nerves.

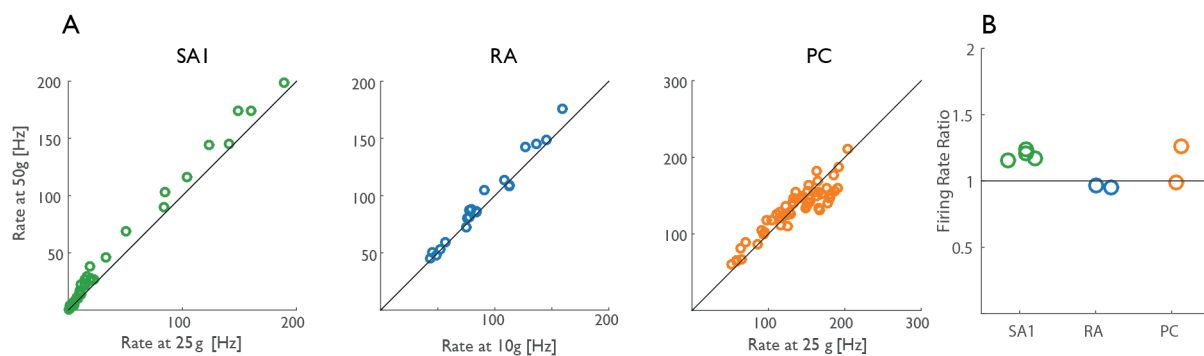


Figure 2. A | Mean firing rate evoked in three individual afferents at a high force (50 g) versus that evoked at a low one (25 g or 10g). **B |** Ratio of the firing rate evoked at a high contact force to that evoked at a low one, averaged across textures, for the three different afferent classes.

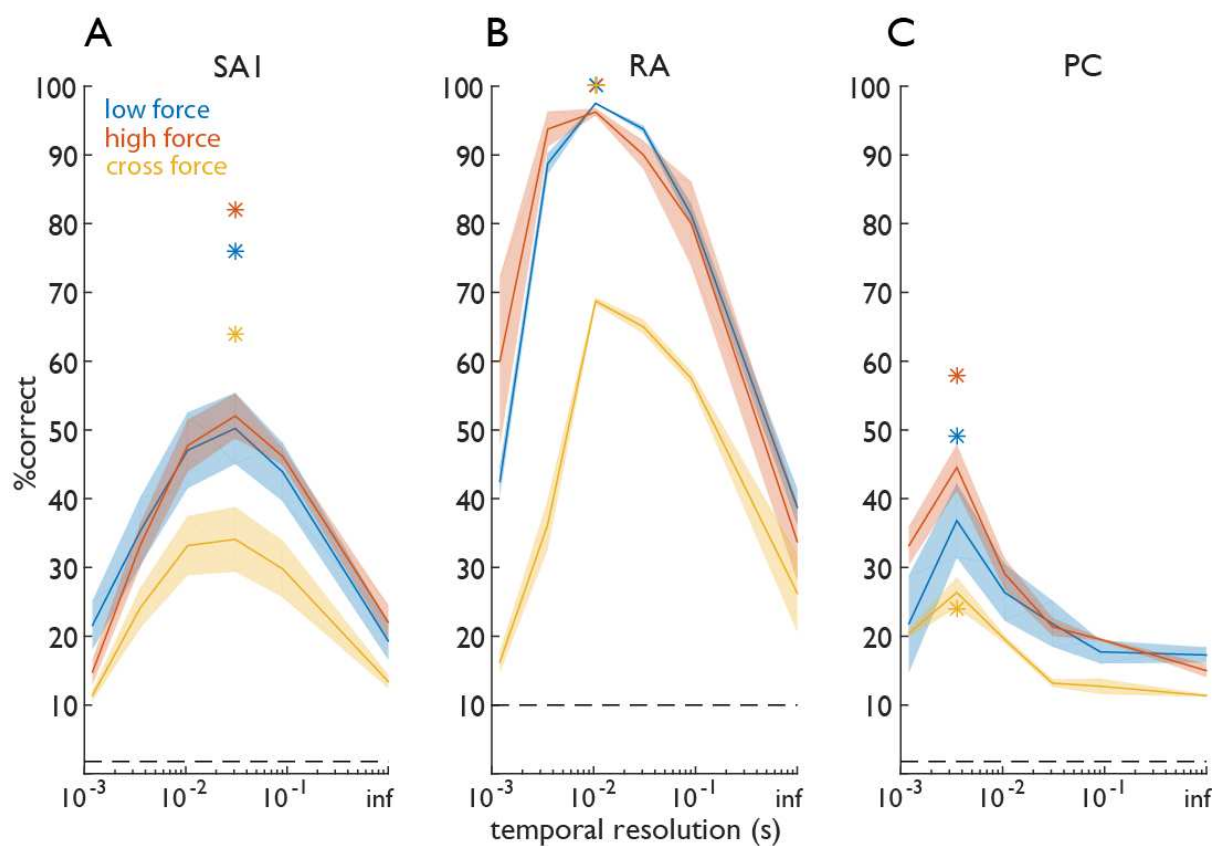


Figure 3. Percentage of correctly classified textures at different temporal resolutions for SA1 (A), RA (B), and PC (C) afferents within force condition (blue and red) or across force conditions (yellow). Asterisks represent performance of a small sample of nerve fibers at their peak temporal resolution (n=4, 2, and 2 for SA1, RA, and PC fibers, respectively).