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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.

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Keywords: somatosensory, neurophysiology, monkey, invariance, touch.

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 microstructures, 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,b; 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 fivefold 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.

EXPERIMENTAL PROCEDURES

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 × 16 cm in scanning direction) were wrapped around an acrylic drum (25.4 cm in diameter

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Abbreviations: DRG, dorsal root ganglia; PC, Pacinian; RA, rapidly adapting; SA1, slowly adapting type I.

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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 SA1a, 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 Fig. 1). Responses from two additional RA fibers were obtained in a separate experiment involving recordings from the dorsal root ganglia (DRG), 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 DRG of 1 Rhesus macaque, as described previously in cats (Gaunt et al., 2009). Animals were anesthetized with ketamine and maintained on isoflurane anesthesia 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 to T1. The laminectomy was extended laterally through the articular processes past the foramina of the C6–C8 spinal roots to expose the DRG. Ligaments and other issue over the DRG were resected to provide a clear view of the DRG enlargement. 32-Channel microelectrode arrays (4×8, 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 DRG 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

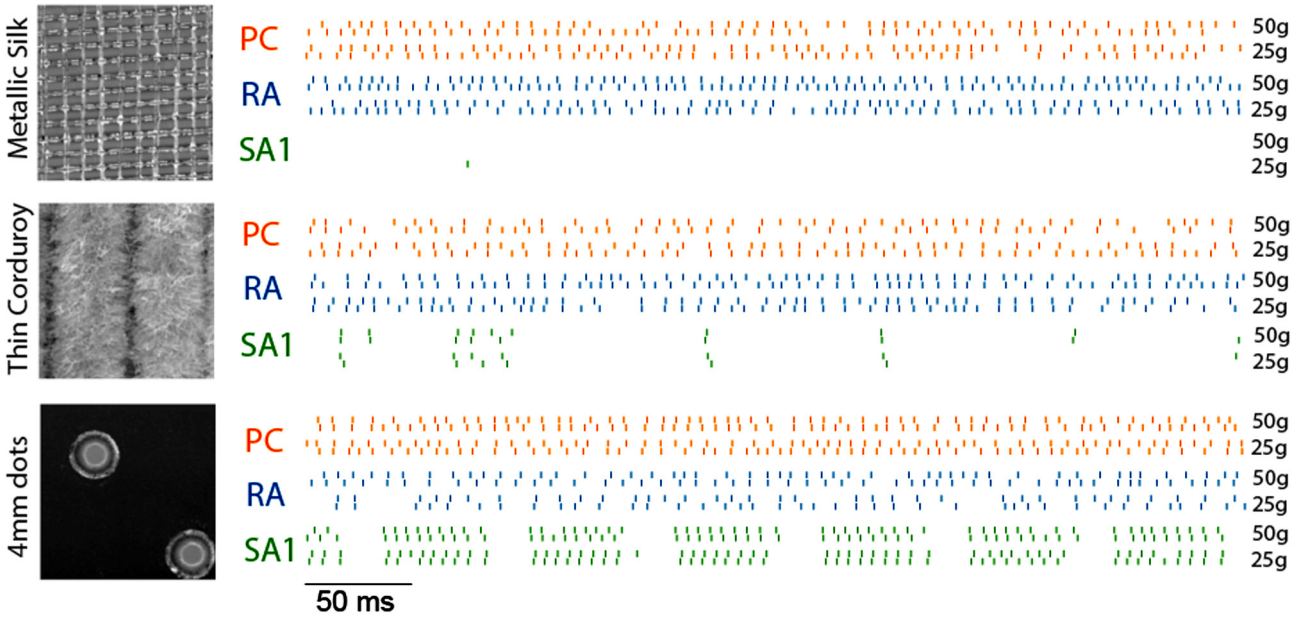

Fig. 1. Sample spike trains evoked in one afferent of each type by three different textures at two different contact forces. Visual inspection suggests that both the strength and temporal patterning in the response are relatively consistent across contact force conditions. These afferent responses were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

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