

THE UNIVERSITY OF CHICAGO

THE NEURAL BASIS OF TACTILE TEXTURE PERCEPTION

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BY

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PREVIEW

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ABSTRACT

The objective of my program of research is to shed light on how texture is encoded in the nerve, to investigate texture representations in somatosensory cortex – including Brodmann’s areas 3b, 1 and 2 –, and to assess how these neural representations give rise to percepts of texture. To this end, we combine psychophysical experiments with human observers and neurophysiological recordings, both from first-order somatosensory afferents and from somatosensory cortical neurons of Rhesus macaques. First, we show that, in the peripheral nerve, the neural code for roughness – the dominant perceptual dimension of texture – relies on the integration of signals from all three major classes of tactile fibers, and that roughness information is encoded in spatial patterns of activation in one population of nerve fibers and in temporal patterns of activation in two others. Second, we show that these two streams of information – spatial and temporal – are integrated in somatosensory cortex resulting in a representation of texture that is distributed over a large population of cells with heterogeneous response properties. Combining data from our peripheral and cortical recordings, we determine which tactile submodalities drive the responses of individual cortical neurons, and show that neurons driven by afferents that specialize in spatial signaling more effectively encode coarse textural features, and neurons driven by afferents that specialize in temporal signaling more effectively encode fine textural features. Third, we show that, while texture signals at the periphery are highly dependent on the speed at which the surface moves across the finger, texture signals in cortex are nearly independent of speed and can account for the documented speed-invariance of texture perception.

INTRODUCTION

We can identify objects by the way they feel. As we move our fingers over objects in our pocket or purse, we can easily pick out our keys or our phone from an assortment of other items. When we manipulate an object, the skin is deformed, which in turn results in stresses and strains in the tissue, ultimately driving electrical activity in several populations of mechanoreceptors (Sripati et al., 2006a; Saal et al., 2017). Tactile nerve fibers then carry the resulting signals to the brain, where they are integrated and transformed through successive stages of neural processing to ultimately culminate in a tactile percept. Like its visual and auditory counterparts, the somatosensory neuraxis works to extract object-specific, behaviorally relevant information about objects, a process about which much remains to be discovered.

The study of tactile texture perception – the sensory experience associated with surface microstructure – is a fruitful paradigm to interrogate these neural mechanisms for several reasons. First, texture perception is a domain in which touch is the most sensitive sensory modality, far surpassing vision and hearing (Lederman, 1979; Heller, 1989; Klatzky et al., 1993; Guest and Spence, 2003; Klatzky and Lederman, 2010). Second, texture perception operates over six orders of magnitude of spatial scales, ranging from tens of nanometers to tens to millimeters (Skedung et al., 2013). Third, the sensory space of texture is complex, comprising at least four main perceptual axes – roughness, hardness, stickiness, and warmth –, which only partially define it (Hollins et al., 2000a). Fourth, texture exploration typically involves movement between skin and surface (Katz, 1925; Lederman and Klatzky, 1987; Callier et al., 2015). As a result, instantaneous spatial patterns of skin deformation engage spatial encoding mechanisms that draw compelling analogies with vision (Pack and Bensmaia, 2015), and texture-elicited vibrations engage temporal encoding mechanisms that draw analogies to audition (Hollins and Risner, 2000; Bensmaia and Hollins, 2003; Bensmaia and Hollins, 2005; Yau et al., 2009; Saal et al., 2016). Fifth,

stimulation paradigms have been developed and honed to achieve precise experimental control on the speed and force of texture presentation (Johnson and Phillips, 1988; Weber et al., 2013), a necessary precondition to understand tactile processing given the exquisite sensitivity of this sense to submicron skin deformations.

Much of the early work on texture perception was carried out using Braille-like dot patterns which have the merit of being defined by a small set of parameters (dot height, dot width, inter-dot distance, dot configuration). Studies using these stimuli arrived at the conclusion that information about tactile texture is mediated entirely by one population of tactile fibers (Blake et al., 1997). Later studies, however, showed that this conclusion was partially an artifact of the stimulus set, which only spanned a narrow range of spatial scales, measured in the millimeters. The processing and perception of more naturalistic textures, like fabrics or sandpapers, which comprise textural elements over a wider range of spatial scales, rely on the integration of signals from all three main afferent classes (Weber et al., 2013). Interestingly, texture information at different scales is encoded in different ways: Coarse textural features are encoded in spatial patterns of afferent activation and fine features are encoded in temporal patterns evoked as the skin moves across the surface.

In this chapter, we first discuss the phenomenology of texture perception with a review of the psychophysical literature. We then discuss what is known about the neural basis of texture perception, first in the nerve then in cortex. This prior knowledge forms the basis for my dissertation project. In our discussion of the neural basis of texture processing, we omit two interposed neural structures – the cuneate nucleus and thalamus – as the texture responses in these structures have not been explored.

WHAT IS TEXTURE?

Classically, the term “texture” refers to the feel or appearance of an object’s surface. And yet, not every aspect of a surface is necessarily considered texture – for example, buttons on a video game console are

shapes rather than features. So what are the qualities that separate a shape from a texture? One distinction is that textural features are generally distributed across the extent of a surface, and their precise pattern is meaningless, while shape features tend to be more discrete and their configuration is typically meaningful. In touch, another distinction is the relevant spatial scale: a feature that extends beyond a fingerpad is likely not a textural one.

One way to define a distribution of textural features is to characterize what aspects of this distribution vary between samples and which do not. In other words, we are looking for a set of “generative” statistics that produce non-identical stimuli that are perceptually equivalent, known as metamers (Julesz, 1962, 1981). This approach has been quite successful for visual textures: a generative model can compute a small set of statistics based on early visual representations of natural images, and use those statistics to produce new images that appear to have the same texture (Portilla and Simoncelli, 2000). A similar approach has been fruitfully applied to generate auditory textures, such as the sound of a bubbling stream or crackling fire (McDermott and Simoncelli, 2011). This approach cannot straightforwardly be applied to tactile texture, however, because early processing – well established for vision and audition and crucial for the generation of metamers – has not been established for touch. Furthermore, biomechanical interactions between skin and surface complicate the relationship between stimulus and neural response and thus further thwart the application of the generative approach to tactile texture.

TACTILE TEXTURE PERCEPTION

Texture is a key component of our ability to quickly identify everyday objects through touch (Klatzky et al., 1985) and provides information beyond that available visually (Fishkin et al., 1975; Lederman and Abbott, 1981; Heller, 1982; Lederman et al., 1986). However, because perceived texture is determined in part by complex biomechanical interactions between skin and surface, the link between physical

features of a surface and the evoked percept has been elusive except for highly contrived stimuli, such as gratings and embossed dot patterns.

Nonetheless, examination of the perceptual space of texture has revealed distinct structure. For example, multidimensional scaling based texture dissimilarity judgments consistently yields a space with a few well defined dimensions that approximately map onto qualitative textural continua, including rough/smooth, hard/soft, sticky/slippery, and warm/cool (Figure I.1) (Hollins et al., 2000a; Picard et al., 2003; Okamoto et al., 2013).

The dominant and most studied perceptual dimension of texture is roughness (Hollins et al., 2000a). Perceived roughness maps systematically onto surface microstructure as evidenced by the fact that human observers overwhelmingly agree on the relative roughness of textured surfaces (Stevens and Harris, 1962; Lederman, 1983; Sathian et al., 1989; Connor et al., 1990; Connor and Johnson, 1992; Blake et al., 1997). However, this relationship is not always straightforward. For example, while the roughness of sandpaper increases systematically with decreases in grit, the roughness of embossed dot patterns increases then decreases as inter-dot spacing increases (Connor et al., 1990), except for tall dots (Sutu et al., 2013). In fact, unlike most other sensory continua, there is no established physical determinant of

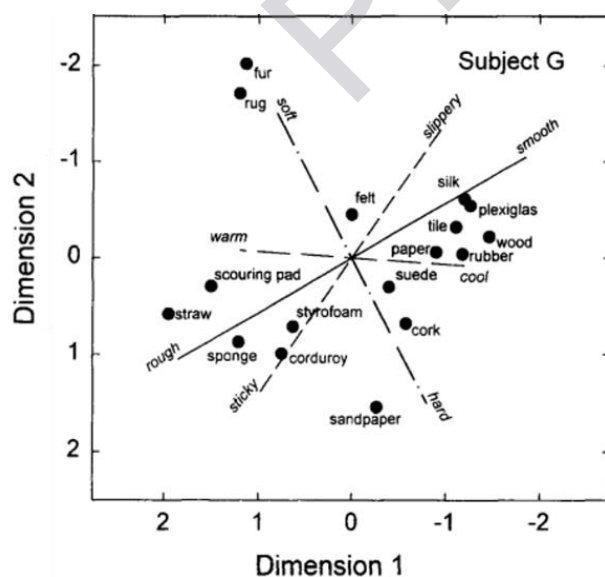


Figure I.1. **The sensory space of texture is multidimensional.** Projection of the multidimensional space of texture, estimated from ratings of dissimilarity, onto two dimensions for an example subject. Textures are further apart to the extent that they are perceived as more dissimilar. The axes of the space map approximately onto subjective dimensions, including rough/smooth and hard/soft. Adapted from Hollins et. al. 2000.

perceived roughness. In contrast, the neural basis of roughness in the nerve has been well established (see below), suggesting that the subjective experience of roughness is largely shaped by our peripheral apparatus.

The second major axis of texture perception is hardness/softness (Klatzky et al., 1989; Hollins et al., 2000a), which closely tracks surface compliance (Harper and Stevens, 1964; Yoshioka et al., 2007; Friedman et al., 2008). When touching a surface, differences in surface compliance lead to different distributions of force across the surface of the finger, both during initial contact and static grip. These forces provide multiple cues – in their spatial distribution and temporal progression – which can be used to extract information about compliance. Indeed, we reliably perceive hardness during static grip, a mode that minimizes temporal cues, (though these are still present at the onset of grip)(Friedman et al., 2008) but we can also perceive the hardness of a surface explored through a rigid probe, an ability that relies on temporal cues from vibrations transmitted through the probe (LaMotte, 2000). When tactile cues are eliminated altogether through digital anesthesia, we can still under certain circumstances perceive hardness using only kinesthetic cues, signaling the movement of the fingers into the object (Srinivasan and LaMotte, 1995).

The third axis of texture is stickiness, which tracks the friction between skin and surface (Smith and Scott, 1996; Yoshioka et al., 2007). For natural textures, perceptual judgments of stickiness are often correlated with judgments of roughness (Hollins et al., 2000a), but this relationship can be broken if friction is controlled (Taylor and Lederman, 1975). While stickiness is a far weaker determinant of perceived texture, the perception of stickiness is critical to the determination of the force required to grasp an object (Cadoret and Smith, 1996).

A fourth, modest axis of texture is warmth (Hollins et al., 2000a), associated with the thermal conductivity of the surface material. Indeed, at room temperature, objects are colder than is the body,

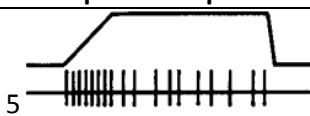
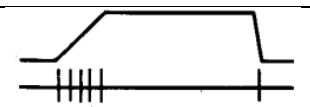
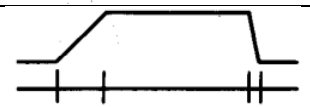
Nerve fiber	End organ	RF size	Optimal Stimulus	Response Properties
Slowly adapting type 1 (SA1)	Merkel cell	Small	Indentation	
Rapidly adapting (RA)	Meissner corpuscle	Small	Flutter, slip	
Pacinian corpuscle-associated (PC)	Pacinian corpuscle	Large	Vibration	

Table I.1. **Cutaneous Mechanoreceptors.** Typical response properties of the three main mechanoreceptors in the glabrous skin. While different afferent types respond differently to skin deformations, they are typically all activated during every day interactions with objects. Table adapted from Ginty et. al. 2013 and Johansson and Vallbo 1983.

so heat will tend to flow out of the skin and into the object. The rate of this heat transfer depends on the thermal conductivity of the material and determines the warmth of the surface, with higher heat transfer leading to cooler surfaces (Ho and Jones, 2006). The thermal properties of a surface are likely encoded by thermoreceptive afferents (Johnson et al., 1973, 1979, Darian-Smith et al., 1979a, 1979b).

Remarkably, the perception of texture is stable whether textures are actively explored or passively scanned over the finger (Lederman, 1981; Lamb, 1983; Friedman et al., 2008; Yoshioka et al., 2011). Furthermore, perceived texture is regardless of how fast the texture moves across the skin (Lederman, 1974, 1983; Yoshioka et al., 2011; Boundy-Singer et al., 2017). Texture invariance across scanning speeds is especially surprising given the strong dependence of skin responses (Manfredi et al., 2014) and afferent responses (Weber et al., 2013) on speed.

THE INNERVATION OF THE SKIN

Fine discriminative touch with the palmar surface of the hand relies on three main mechanoreceptors: slowly adapting type-1 (SA1) fibers, rapidly adapting (RA) afferents, and Pacinian-associated (PC) fibers (Table I.1). A fourth type of nerve fiber, slowly adapting type-2 fibers, which innervate Ruffini end-

organs, only sparsely innervate the glabrous skin of humans and are absent in non-human primates (Paré et al., 2002, 2003) so will not be further discussed here.

SA1 fibers

SA1 fibers are characterized by two main features: 1) small receptive fields (2-3 mm diameter, (Vega-Bermudez and Johnson, 1999)), and 2) a sustained response to a static indentation into the skin (Pei et al., 2009). SA1 afferents innervate Merkel cells (Abraira and Ginty, 2013) and densely innervate the skin,

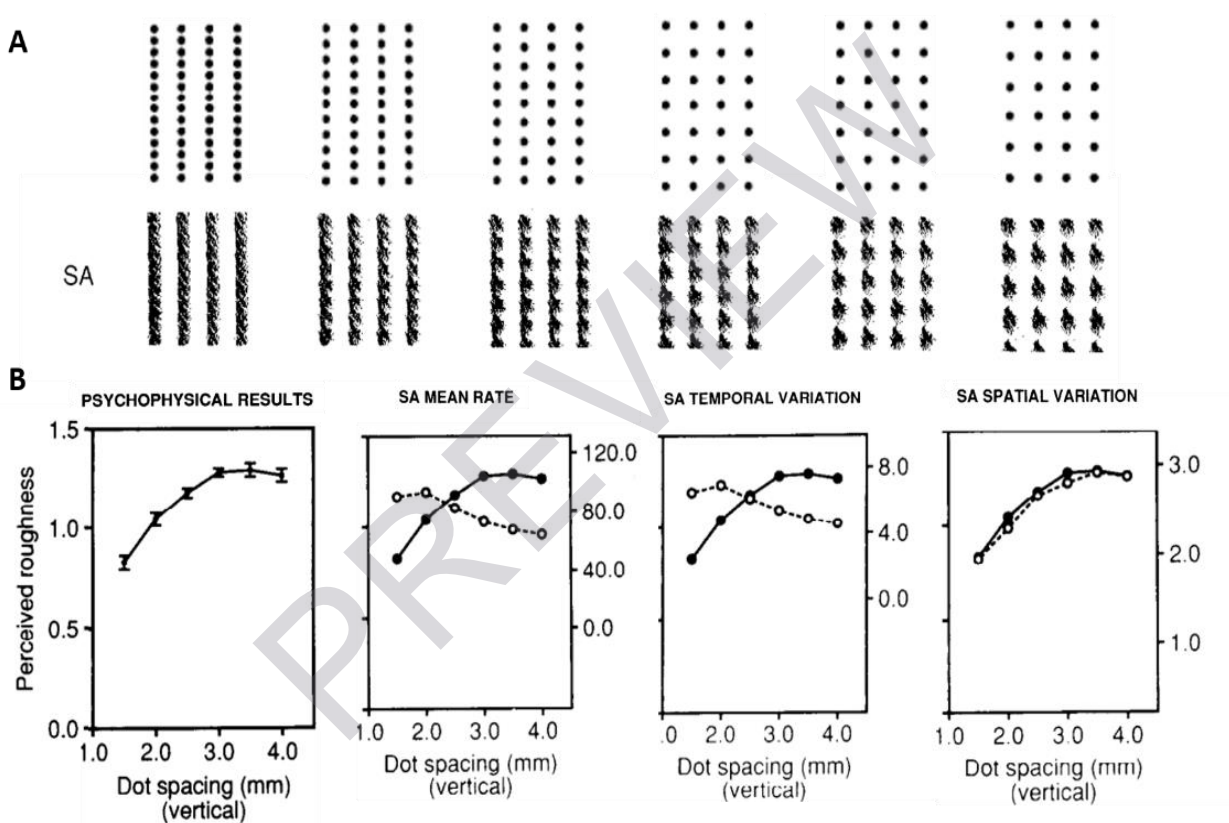


Figure 1.2. **Spatial variation code for perceived roughness.** A| Reconstructed pattern of activation that would be elicited in a population of identical SA1 fibers (bottom row) by a series of dot patterns (shown above). Each line of action potentials corresponds to a single scan of the texture over the skin. Successive lines represent a 200 micron shift of the pattern, perpendicular to the scanning direction. B| Human subjects rated the roughness of each of the dot patterns (left). Neither the firing rate nor the temporal variation of SA1 responses can account how rough the surfaces feel. Rather, perceived roughness mirrors the spatial variability across the SA1 fibers. Adapted from Connor et. al. 1992.

with as many as 1.4 / mm² in the fingertip (Darian-Smith and Kenins, 1980). Populations of SA1 afferents faithfully reproduce the shape of objects that are statically indented into the skin (Phillips and Johnson, 1981) or scanned over the skin (Johnson and Lamb, 1981; Phillips et al., 1988; Connor et al., 1990; LaMotte et al., 1996). That is, SA1 afferents encode spatial patterns in a manner analogous to photoreceptors in the retina and their spatial resolution (around 0.5 - 1 mm, (Phillips and Johnson, 1981)) sets the limits of human tactile acuity (Johnson and Phillips, 1981). On the other hand, SA1 fibers resolve temporally varying stimuli only poorly: they respond best to slowly varying stimuli and the temporal precision of their spiking tends to be lower than that of other classes of tactile afferents (Talbot et al., 1968; Bensmaia et al., 2005; Mackevicius et al., 2012).

RA afferents

RA afferent fibers are characterized by two main features: 1) small receptive fields (3-5 mm diameter, (Vega-Bermudez and Johnson, 1999)), and 2) responses to the transient phases of a skin indentation (onset and offset) but not to the sustained phase (Pei et al., 2009). RA afferents innervate Meissner corpuscles located in dermal papillae densely (1.7 / mm² on the fingertips, (Darian-Smith and Kenins, 1980)). The neural image carried by RA fibers is blurrier than its SA1 counterparts (Phillips and Johnson, 1981) because each fiber branches widely to innervate multiple corpuscles (~30-80, (Paré et al., 2002)). RA fibers are sensitive to skin vibration over the so-called flutter range (5-40 Hz) and tend to produce entrained responses at these frequencies (Talbot et al., 1968). RA responses also tend to be highly precise in their temporal structure and RA spiking sequences can carry information about skin vibrations or textured surfaces (Mackevicius et al., 2012; Weber et al., 2013). An important role for RA fibers may be to signal slip events to trigger short-latency adjustments of grip force during grasp (Johansson and Westling, 1987; Macefield et al., 1996).

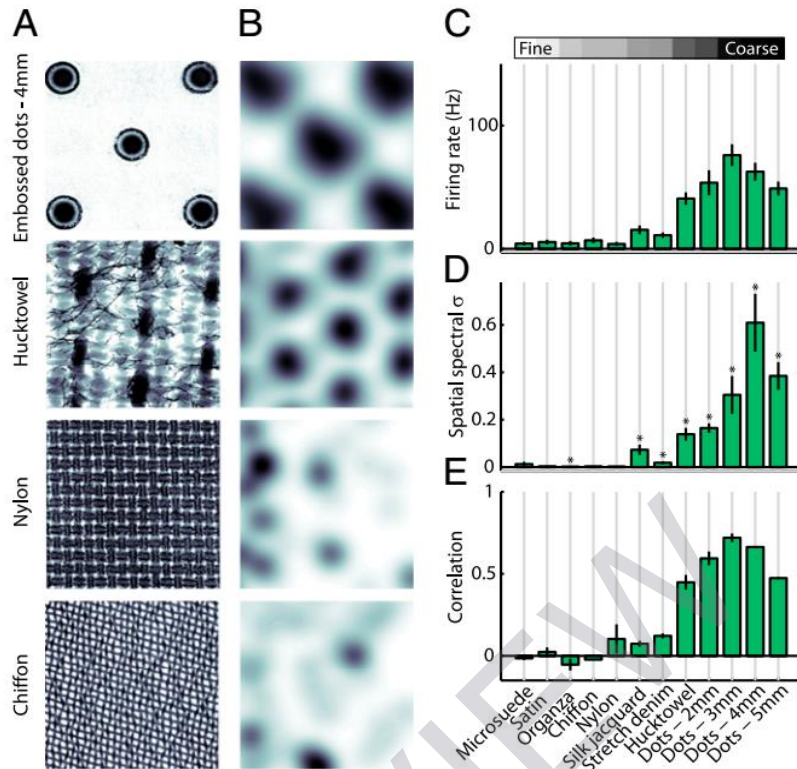


Figure I.3. Spatial coding cannot explain fine texture perception. A| Surface profiles of four different textures, two with coarse spatial features (dots and hucktowel) and two with fine spatial features (nylon and chiffon). B| Spatial patterns of activation (spatial event plots) averaged over 15 SA1 afferents, in response to the four textures. While the coarse textures evoke patterns of activity that preserve the spatial structure in the stimulus, the fine textures do not. C| Average firing rate evoked by twelve different textures, average across the SA1 afferent population. These textures are ordered from least rough (left) to most rough (right). Finer textures do not evoke significant spiking in SA1 afferents. D| Standard deviation across all frequencies the SEP spatial power spectrum (a measure of spatial patterning), plotted for all 12 textures. Responses to coarse textures show more spatial patterning than fine textures. E| Correlation between the surface profiles and the SEPs, plotted for all 12 textures. The structure of coarse textures are faithfully reconstructed in the SA1 population response, while features of fine textures are not. Adapted from Weber et. al .2013.

PC afferent

PC afferent fibers are characterized by three main features: 1) large receptive fields that sometimes encompass the entire hand (Johnson, 2001), 2) responses to the transient phases of a skin indentation but not to the sustained phase, and 3) sensitivity to high frequency vibrations. Due to their large receptive fields and low density in the glabrous skin ($1/7.5 \text{ mm}^2$ (Darian-Smith and Kenins, 1980)), PC

afferents are poorly suited for spatial processing, failing to resolve features spaced 5 mm apart (Phillips and Johnson, 1981). On the other hand, PC fibers are exquisitely sensitive to high-frequency skin vibrations, peaking in sensitivity at around 250-300 Hz, which corresponds to the resonance frequency of the skin (Sherrick, 1953; Manfredi et al., 2012). Indeed, this population of tactile fibers primarily accounts for the perception of skin vibrations above 100-150 Hz (Talbot et al., 1968) and conveys information about fine surface microstructure and about distal contact events from vibrations transmitted through an object grasped in the hand (Brisben et al., 1999; Johnson, 2001).

TEXTURE SIGNALS IN THE NERVE

As we run our hand across a surface, spatiotemporal patterns of activation in all three populations of nerve fibers convey detailed information about the microstructure of that surface, ultimately giving rise to a rich textural percept. Information about surface texture is conveyed in different aspects of afferent responses, with spatial patterns of activation encoding coarse features and temporal patterns encoding fine features. The spatial code for coarse textures, originally hypothesized based on the results of psychophysical experiments with gratings (Taylor and Lederman, 1975; Lederman, 1983), was first established by comparing judgments of roughness of embossed dot patterns, obtained from human observers, to the responses evoked by these textures in the three populations of tactile fibers. In an elegant series of experiments, Johnson and colleagues tested a series of hypotheses as to the neural determinants for roughness and eliminated all but one (Connor et al., 1990; Connor and Johnson, 1992; Blake et al., 1997): Across all conditions tested, the variation (or degree of inhomogeneity) across the responses of SA1 fibers could account, with remarkable precision, for roughness judgments (Figure I.2). This roughness computation could be well approximated by a Gabor filter convolved across the spatial pattern of activation in this population of fibers. That SA1 fibers carry a faithful neural image of embossed dot patterns and that this image accounts for roughness judgments was taken as evidence that SA1 fibers mediate tactile perception of texture across the tangible range (Yoshioka et al., 2001).

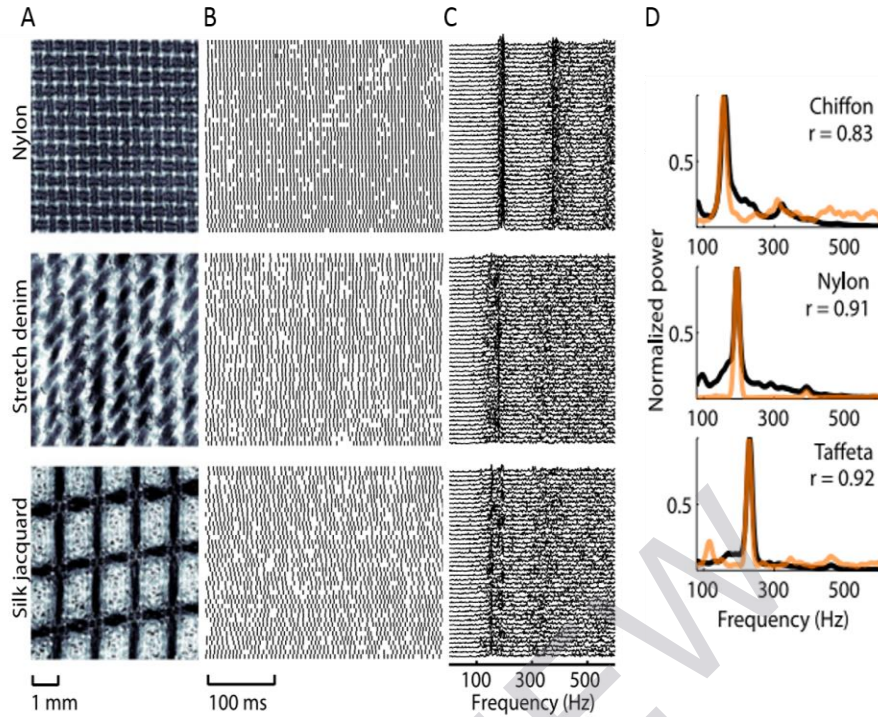


Figure I.4. Fine textures evoke temporally patterned spiking responses. A| Surface profiles for three finely textured materials. B| The spiking responses of a single PC afferent to 42 presentations of each of these three textures. Each texture evokes a consistent pattern of response. C| The power spectrum of each corresponding single trial neural response. PC responses are highly repeatable and afferent responses to texture exhibit consistent spectral signatures. D| The power spectral densities in response to a single texture (averaged across all trials and PC afferents) are plotted in orange, the densities of texture-elicited vibrations are shown in black. The frequency composition of the neural response matches that of the vibrations elicited in the skin (plotted in black). Adapted from Weber et. al. 2013.

However, the spatial image carried by SA1 fibers, while effectively relaying information about coarse textural features, lacks the resolution to encode fine features, given the filtering properties of the skin and its innervation density (Figure I.3) (Phillips and Johnson, 1981; Sripati et al., 2006a). Rather, the perception of finely textured surfaces features requires movement between skin and finger (Katz, 1925; Hollins and Risner, 2000). Indeed, scanning a surface results in the elicitation of characteristic vibrations in the skin whose properties depend on texture (Bensmaïa and Hollins, 2003; Bensmaïa and Hollins, 2005; Delhay et al., 2012; Manfredi et al., 2014): Differences in the texture-elicited vibrations predicts how dissimilar textures feel (Bensmaïa and Hollins, 2005), vibrations imposed onto textures make

textures feel rougher (Hollins et al., 2000b), and adaption of vibration-sensitive nerve fibers impairs subjects' ability to discriminate fine but not coarse textures (Lederman et al., 1982; Hollins et al., 2001). Texture elicited skin vibrations then drive highly precise and repeatable temporal spiking patterns in RA and PC afferents (Figure I.4) which are, in turn, highly texture specific and thus informative about texture, including its fine features (Figure I.5) (Weber et al., 2013). Furthermore, temporal spiking patterns dilate or contract systematically with decreases or increase in scanning speed, but texture information can be extracted from them regardless of speed if they are rescaled to space rather than time (Figure I.6).

In summary, then, coarse textural features are encoded in the spatial pattern of activity evoked in one population of afferents – SA1 fibers – while fine textural features are encoded in the temporal patterns of activity evoked in the other two, RA and PC fibers.

As discussed above, most work on texture coding has focused on roughness, the most dominant perceptual dimension of texture. However, the neural determinants of other textural continua have also been investigated. The consensus is that perceived hardness, like roughness, depends on both temporal and spatial codes. Surfaces of differing compliance will create different spatiotemporal patterns of activation when they make contact with the skin. For example, at equal contact force, the area of contact between skin and surface is wider for soft than for hard surfaces and forces drop off more

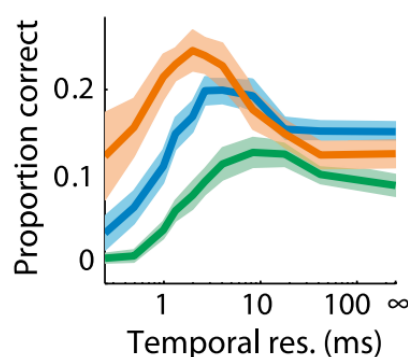


Figure I.5. Temporal spiking patterns convey texture information. The timing of afferent responses (ISI distributions) was used to identify texture identity (55 textures total). Classification performance is plotted for SA1 (green), RA (blue) and PC (orange) afferents against the temporal resolution at which the spike timing is read out. Spike timing in RA and PC responses is most informative about texture identity at a temporal resolution of ~5 and ~2 ms, respectively. Adapted from Weber et. al. 2013.

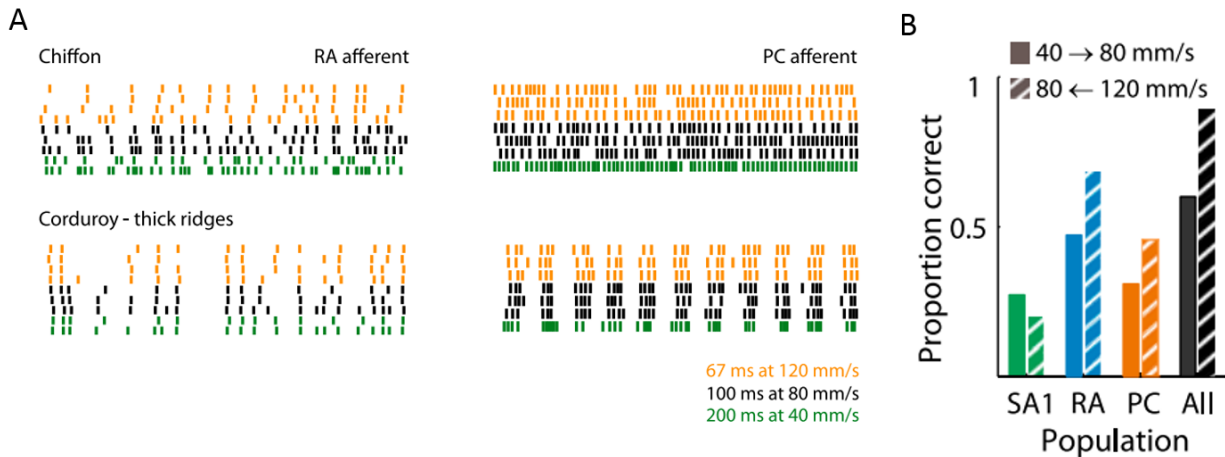


Figure I.6. **Temporal patterns scale proportionally with speed.** A| Spiking responses evoked in an example RA and PC afferent by two textures at three different speeds. Responses at 40 mm/s are compressed (twofold) and responses at 120 mm/s are expanded (by a factor of 1.5 so that they are placed on a common spatial scale). B| Classification performance of small populations of afferents, based on the distance between warped spike trains (using a spike distance metric). The temporal structure of spike trains, when scaled appropriately for speed (to a common spatial frame of reference), contains texture-specific information. Adapted from Weber et. al. 2013.

progressively for soft than hard surfaces. As a result, the distribution of SA1 responses is thus shaped, in part, by surface compliance: SA1 fibers are activated over a wider area and the drop off in their activation is more progressive when contacting a compliant surface (Condon et al., 2014; Hudson et al., 2015). However, hardness can also be perceived through rapid tapping of surface with a probe (LaMotte, 2000), which elicits hardness-dependent vibrations in the probe which are transduced primarily by RA and PC fibers.

Finally, stickiness is correlated with tangential forces that stretch the skin; both SA1 and RA fibers respond to tangential forces (Birznieks et al., 2001, 2010) as do SA2 fibers, but little work has been done to quantitatively link stickiness perception to patterns of afferent activation.

ASCENDING SOMATOSENSORY PATHWAY

Touch signals from the hand are carried by the somatosensory nerves through the spinal cord and into the brainstem, where they synapse (ipsilaterally) onto neurons in the cuneate nucleus. Neurons from

this nucleus send axons across the midline to the contralateral ventral posterolateral nucleus of the thalamus (VPL). The few studies of tactile responses within these two nuclei suggest that their tactile responses look qualitatively similar to those of peripheral afferents (Douglas et al., 1978; Ghosh et al., 1992; Zhang et al., 2001) but texture representations have not been systematically investigated there.

SOMATOSENSORY CORTEX

Anterior parietal cortex (APC), located on the posterior bank of the central sulcus and on the postcentral gyrus, comprises four cortical modules, namely Brodmann's areas 3a, 3b, 1, and 2, progressing posteriorly (Geyer et al., 1999). All of these areas receive direct projections from thalamus (Jones, 1975, 1983; Jones and Burton, 1976; Jones and Friedman, 1982; Padberg et al., 2009), though cutaneous neurons in thalamus project to areas 3b, 1, and 2, while proprioceptive ones project to areas 3a and 2 (Friedman and Jones, 1981). Only area 3b receives thalamocortical input that is characteristic of primary sensory areas, and so this area is considered to be primary somatosensory cortex proper (Kaas, 1983).

Texture coding in APC

Little is known about the neural representation of texture in APC. In studies using dot patterns and gratings as stimuli, neurons in APC have been shown to depend on the spatial period of the stimulus as it is scanned across the skin (Darian-Smith et al., 1982; Sinclair and Burton, 1991; Burton and Sinclair, 1994; Tremblay et al., 1996). Furthermore, some APC neurons respond more strongly to textures that are perceived as rougher (Figure I.7) (Chapman et al., 2002; Bourgeon et al., 2016), however the stimulus space in these studies is very narrow and, as discussed above, yields an incomplete view of texture processing. Lesions to area 1 seem to lead to specific deficits in texture perception (Randolph and Semmes, 1974; Carlson, 1981) but results from aforementioned electrophysiological studies suggest that this area does not carry a more elaborate representation of texture than do its neighbors.

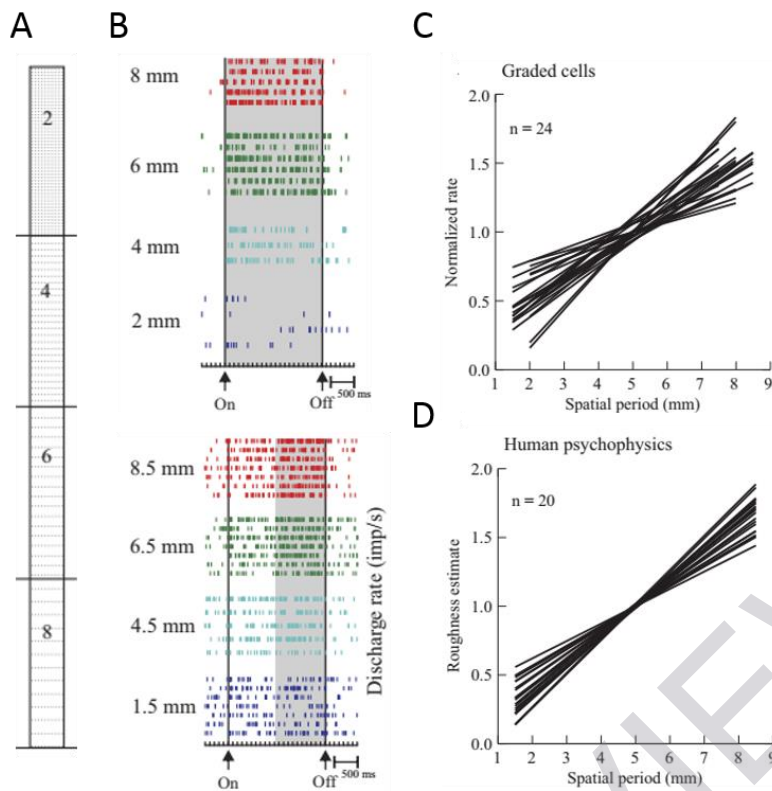


Figure 1.7. Firing rates in APC predict perceived roughness. A| Four dot patterns whose interdot spacing varies from 2 to 8 mm. B| Spiking responses of two example APC neurons to the four stimuli. C| Responses of a subset of APC neurons ("graded cells") that show a steady increase in firing rate with spatial period. D| Human judgments of roughness increase with spatial period over the range tested. Responses of graded cells in APC mirror human judgments of roughness. Adapted from Bourgeon et. al. 2016.

While few studies have directly investigated texture representations in APC, a much broader body of work investigating neural coding in APC yields insights about texture processing in these cortical modules.

Spatial processing in APC

As tactile information propagates through APC from area 3b to 1, the selectivity of neurons for spatial features grows increasingly complex. In area 3b, neurons have elongated spatial receptive fields comprising both excitatory and inhibitory subfields (Figure 1.8A) (DiCarlo et al., 1998; Sripathi et al., 2006b), a receptive field structure that conveys to these neurons a selectivity for orientation (DiCarlo and Johnson, 2000; Bensmaia et al., 2008), drawing obvious analogies with neurons in primary visual cortex. The receptive fields of neurons in area 3b can be well approximated by a (linear) Gabor function (Bensmaia et al., 2008), which matches the computation that has been hypothesized to underlie the computation of roughness (see above). In contrast, neurons in areas 1 and 2 have larger, more complex