

Central mechanisms of tactile shape perception

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Studies show that while the cortical mechanisms of two-dimensional (2D) form and motion processing are similar in touch and vision, the mechanisms of three-dimensional (3D) shape processing are different. 2D form and motion are processed in areas 3b and 1 of SI cortex by neurons with receptive fields (RFs) composed of excitatory and inhibitory subregions. 3D shape is processed in area 2 and SII and relies on the integration of cutaneous and proprioceptive inputs. The RFs of SII neurons vary in size and shape with heterogeneous structures consisting of orientation-tuned fingerpads mixed with untuned excitatory or inhibitory fingerpads. Furthermore, the sensitivity of the neurons to cutaneous inputs changes with hand conformation. We hypothesize that these RFs are the kernels underlying tactile object recognition.

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Introduction

Our understanding of the central neural mechanisms of tactile perception is still in its infancy. Combined psychophysical and neurophysiological studies over the past half century or so have demonstrated that there are four kinds of peripheral afferent fibers that are selectively sensitive to different aspects of cutaneous stimuli and more importantly those studies showed that each afferent type plays a different functional role in tactile perception. However, it is unknown how the informations from these afferents systems are integrated and processed in cortex. Briefly, the peripheral studies showed that the slowly adapting type 1 afferents (SA1) are responsible for the perception of two-dimensional (2D) form and texture, the rapidly adapting afferents (RA) for low frequency vibrations and motion across the skin, the Pacinian afferents (PC) for high frequency vibrations and the slowly adapting type 2 (SA2) afferents for skin stretch and are the

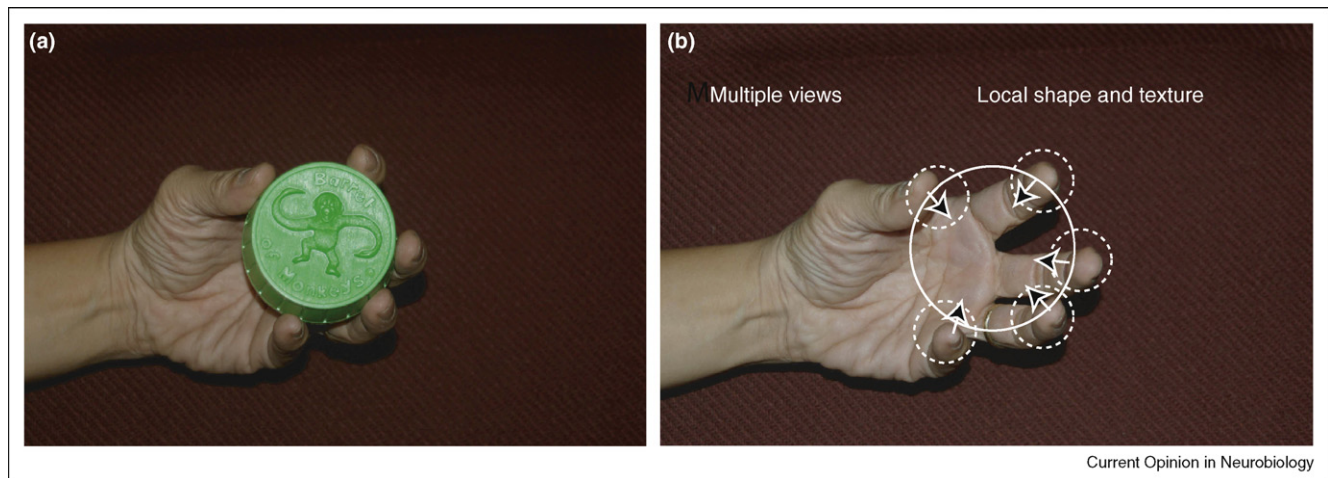
afferents that most probably encode information about hand conformation (see Johnson [1[•]] for a review). This clear segregation of function, however, appears to be lost as the information flows centrally and is replaced by a central representation that is integrative and closely tied to hand conformation.

Psychophysical studies demonstrate that tactile perception from the hand is highly integrative and rapid. Without visual input we can effortlessly recognize and manipulate nearly an infinite number of objects with our hands. In one study, for example, Klatzky [2] showed that humans can recognize 100 common objects with an accuracy of 96% with a mean response time of less than 5 s. Further they showed that subjects use a variety of perceptual dimensions (average of about 2), such as information about texture, size, and shape to identify the objects. The results suggest that accurate object recognition is multidimensional and that inputs from the different afferent types are integrated in the cortex. In an older study, Davidson [3] showed that the accuracy of humans to identify objects increases rapidly as the number of fingers used to contact the object increases. That study and more recently studies by Pont [4[•]] showed that the central representation of form involves the integration of inputs across multiple fingers.

Our working hypothesis is that haptic recognition of objects is on the basis of the tight integration of inputs from the cutaneous afferents described above with inputs from proprioceptive afferents from the muscles, joints, and skin (i.e. SA2 receptors). These afferent systems work closely together to produce central representations of objects that contain information about both the local properties of objects and global properties such as their size and shape. The basis for this hypothesis is illustrated in [Figure 1](#). The inputs from the cutaneous SA1 and RA systems provide information about the local form, texture, and motion at each location or ‘view’ where the skin contacts the object. Multiple points of contact, as shown in [Figure 1](#), produce multiple independent views of the object. The global properties are determined by matching a composite of these ‘three-dimensional’ views with previously stored representations of objects.

A simple demonstration shows that this is likely to be the mechanism that is used in the central nervous system. First, consider the case illustrated in [Figure 1b](#) which shows the hand in the same conformation as in [Figure 1a](#) without the object. Clearly proprioceptive inputs alone cannot convey or support the perception of an object.

Figure 1



Working hypothesis of tactile object recognition. (a) Hand holding an object. (b) Hand in the same conformation without the object. Dashed circles represent multiple views of the object. At each view the cutaneous input provide information about local shape and texture.

Conversely if the same cutaneous inputs from Figure 1a are presented to the skin except with the hand held flat, one would perceive a flat wavy surface (because of the local curvature on the skin) and not a round object. Note that multiple views of the object are also produced when the fingers scan the object. This explains why recognition improves with scanning.

In a recent study we showed that indeed the perception of object size relies on inputs from both cutaneous and proprioceptive inputs. In that study [5•] we reported that cutaneous inputs provide information about the compliance of the surface of the objects and proprioceptive inputs provide information about the spread between the fingers. We showed that the size of an object is determined by the spread between the fingers at initial contact. Thus increasing contact force, which greatly decreases the spacing between the fingers for compliant objects, does not affect size perception and size perception is greatly distorted in subjects that have lost cutaneous perception.

In this review I discuss studies over the past 10 years aimed at understanding of how information related to 2D and three-dimensional (3D) form is integrated and processed in somatosensory cortex.

Ascending pathways

The two main synaptic stages that take the peripheral input from the hand to the cortex are the dorsal column nuclei (DCN) and the ventral posterior lateral nucleus of the thalamus (VPL). Although there have been relatively few neurophysiological studies of how spatial form is coded in the responses of neurons in either of these areas, present evidence suggests there is minimal convergence

of sensory inputs in both of these ascending stages. In the DCN there is a tight correspondence between the firing of neurons and their peripheral counterparts [6,7]; single impulses evoked in peripheral afferent fibers appear to directly generate single spikes in target DCN neurons. This suggests that afferent information is faithfully reproduced in DCN neurons. How information is represented in VPL is also not known; however, it appears as if there is little convergence in thalamic neurons with neurons appearing to have small receptive fields (RFs)-like peripheral afferent fibers [8]. This is not to say that these processing stages do not play a significant role in somatosensory processing. Other studies, particularly from the rodent have shown that neurons in the DCN and VP receive large feedback projections from cortex and projections from other subcortical nuclei; which suggests that the ascending inputs are heavily modulated. Our present hypothesis is that the DCN and VPL nuclei do not play a significant role in sensory integration. This is clearly an area that needs further study.

Role of primary S1 cortex in tactile perception of form

Although primary somatosensory cortex (S1) is composed of four separate areas in the primate, there is only a single body map in the rodent. This suggests that the processing of somatosensory information in the two species may be different and as such I only reviewed here studies related to coding mechanisms in primates. The fact that SI cortex is composed of four areas (3a, 3b, 1, and 2) is based on evidence from cytoarchitectural studies [9], studies showing differences in somatotopic maps, studies showing differences in responses to proprioceptive (3a and 2) and cutaneous input (3b and 1) [10–12], studies showing differential effects of ablation on animal behavior [13], and by numerous anatomical studies showing that these

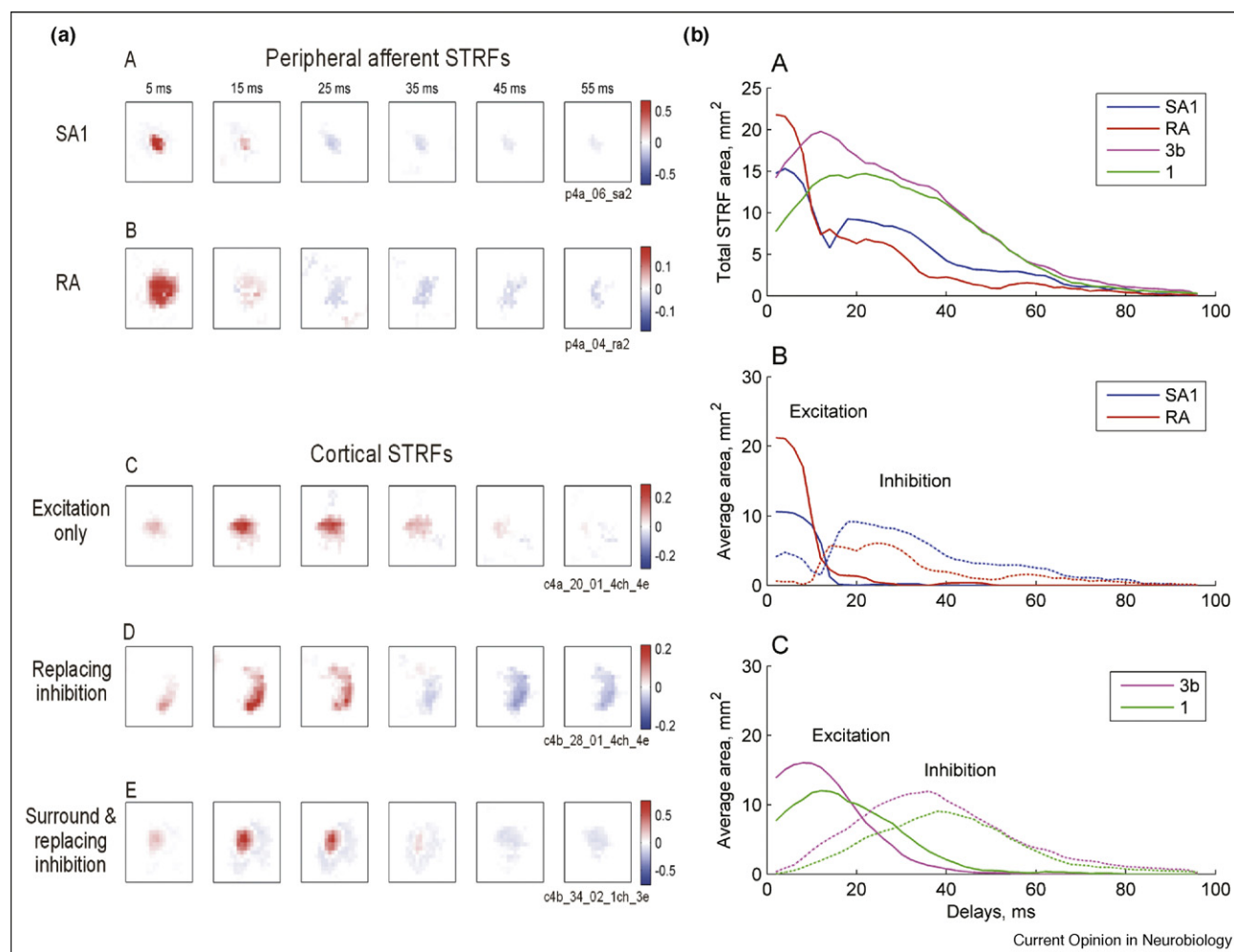
areas have different input/output patterns of connections with cortical and subcortical structures [14]. Only recently have we started to understand how information related to spatial form is processed in these areas.

Processing of cutaneous inputs related to local form and texture

The studies of spatial form in cortex show that there is a striking difference between the responses of peripheral afferents and cortical neurons. Figure 2 shows sample RFs of typical SA1 and RA afferents and of neurons in area 3b and 1. Peripheral neurons have small circular excitatory RFs with diameters of about 2–4 mm and provide an isomorphic neural representation of 2D shape [15]. In contrast, neurons in area 3b have larger and more complex RFs. The RFs of 3b neurons are classically

thought to be confined to a single finger; however, recent studies show that the responses are modulated by inputs from adjacent fingers. These results suggest that the integration of information across digits begins early in cortical processing [16]. Using reverse correlation techniques we have found that the RFs of neurons in area 3b are two to three times larger than first-order afferents and consist of an excitatory region, one or more inhibitory subregions that spatially overlap with the excitatory region and an infield inhibitory response that persists longer than the excitatory response (Figure 2b) [17,18]. The structure of the RFs of 3b neurons are like simple cells in primary visual cortex with many neurons showing selective responses to spatial features of stimuli such as orientation [19,20,22]. It is interesting to note that neurons with RFs composed of mixed excitatory and

Figure 2



(a) Spatial temporal receptive fields (STRF) of typical SA1, RA afferents, and typical cortical neurons. Red — excitation, blue — inhibition (from Sripathi *et al.*, 2006 [17]). **(b)** Temporal evolution of peripheral and cortical receptive fields (RFs). **(A)** is the total RF area, **(B)** excitatory and inhibitory areas of peripheral SA1 and RA neurons. The initial inhibitory response in the SA1 neurons is because of skin mechanics. The replacing inhibition is most likely due to the refractory period of the neurons. **(C)** Excitatory and inhibitory areas of cortical neurons in areas 3b and 1. The inhibition evolves slower than the excitatory response. Note that there is a period where there is both excitation and inhibition. This inhibition is related to the surround inhibition (see (a)) both the excitation and inhibition are replaced with a period of infield inhibition (adapted from Sripathi *et al.*, 2006 [17]).

inhibitory subregions are exactly what was predicted by the peripheral coding studies of roughness perception [21] suggesting that roughness is represented in this area of cortex as well.

Recently we showed that the population response of 3b neurons to both scanned and indented oriented bars accounts well with the ability of human subjects to discriminate orientation. We observed neural thresholds, which is an estimate of the minimum orientation difference that is discriminable by the population response, to be about 20° which is nearly identical to psychophysical thresholds of humans [19,22]. This ability is surprisingly poor considering that humans have a high capacity to discriminate complex scanned patterns such as embossed letters of the alphabet [23].

In addition to the spatial component of the response, 3b neurons also have an inhibitory infield component which temporally lags the spatial response. This delayed or replacing inhibition defines a period of integration that allows features to be integrated, prevents temporal smearing of the response and allows the neurons to show invariance to changes in scanning velocity [24]. These results suggest the mechanisms underlying the early stages of 2D form processed from the skin are similar but not identical in vision and touch [25].

The RF properties of neurons in area 1 are more complex, and less well understood. The classical RF of area 1 neurons typically span more than one digit suggesting that they are more integrative and lie at a higher processing stage than 3b neurons. These neurons function less like local feature detectors, are more nonlinear and convey a higher degree of feature selectivity than 3b neurons. Many neurons in area 1 also show strong sensitivity to stimulus movement which suggests that this area plays an important role in motion processing. Recently we showed that humans have a high capacity to perceive tactile motion. In particular we used a 400 probe stimulator to present moving plaids, barber poles, and bar fields like stimuli to the skin and found that the perception of motion in touch and vision is similar [26]. Like in vision, tactile motion perception operates in stages, with motion first being detected by local motion detectors which are then combined to produce a coherent perception of pattern motion (i.e. area 1).

At the next cortical processing stage, neurons in area 2 have RFs that are even larger than neurons in area 1 with some RF spanning the entire hand. Neurons in area 2 are not sensitive to stimulus motion (personal observation) but instead appear to play a role in combining cutaneous and proprioceptive inputs related to 3D object recognition. The notion that area 2 is involved in the processing 3D shape is supported by ablation studies [13], anatomical studies, imaging studies in humans, and by

neurophysiological studies in nonhuman primates. Anatomical studies show that area 2 neurons receive cutaneous inputs from both areas 3b and 1 and from the shell region of VPL and neurons in area 3a both of which contain neurons that are driven by proprioceptive inputs [14]. fMRI imaging studies in humans show that this area is driven by both cutaneous and proprioceptive input [27]. Neurophysiological studies initially performed by Iwamura and Tanaka [28] reported that area 2 neurons show selective responses when primates grasped objects that varied in shape. Recently we have found that changing hand conformation alters the sensitivity of neurons in area 2 to cutaneous stimulation but not the selectivity of neurons to features such as orientation [29].

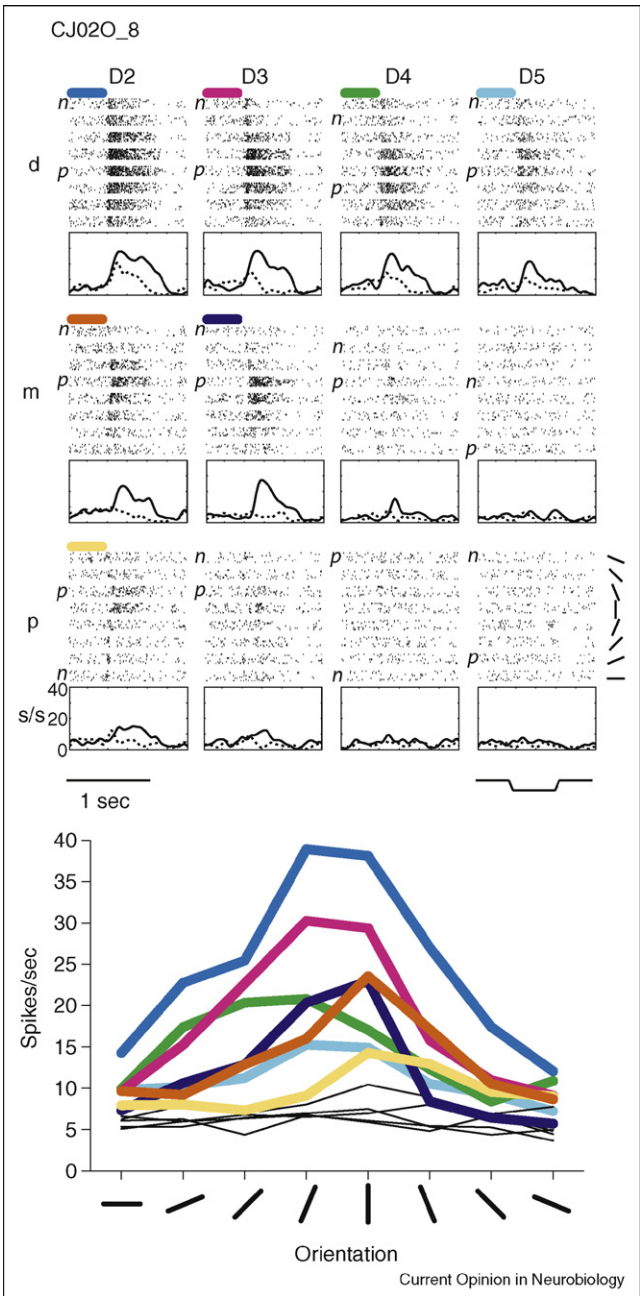
Role of secondary SII cortex in tactile perception of form

Anatomical evidence suggests that haptic sensory information is processed beyond SI along two main pathways; a dorsal stream that projects from SI to areas 5 and 7 and a ventral stream that projects from SI to secondary somatosensory cortex (SII). Neurons in the dorsal stream appear to play a role in multisensory integration and directing attention and are not important for processing information about object shape [30–32]. In particular, areas 5 and 7 interact closely with motor areas and are part of the ‘how’ system that determines how to position the hand to perform different grasping tasks. Recent imaging studies in humans suggest that an area in the posteromedial parietal sulcus (pIPS) in humans is important for tactile spatial acuity and object perception [33,34]. Whether this area is part of the dorsal or ventral stream, which I discuss next, in nonhuman primates is not known.

In nonhuman primates the ventral stream flows from the four areas of SI cortex to SII. The organization of SII has been contentious. Initially it was considered to be a single area, then it was thought to consist of two separate body maps [35,36] which Krubitzer termed SII and PV (parietal ventral). More recent studies, however, suggest that SII is composed of at least three distinct areas [37]. Two of the areas [anterior field of SII (SIIa) and posterior field of SII (SIIp)] in nonhuman primates have responses that appear to be similar to responses seen in area 2 in that neurons in these areas respond well to both cutaneous and proprioceptive input. These areas flank a central field (SIIc) that contains neurons that respond mainly to cutaneous inputs. The representation of touch in the lateral sulcus in humans is even more elaborate with Hinkley *et al.* [38] identifying a new area called parietal rostral (PR) that responds to proprioceptive inputs and Eickhoff and his colleagues reporting that there are at least four distinct areas in the upper bank of the lateral sulcus related to somatosensory input [39].

Neurons in the areas that make up SII have both small and large RFs and respond to more complex stimuli than

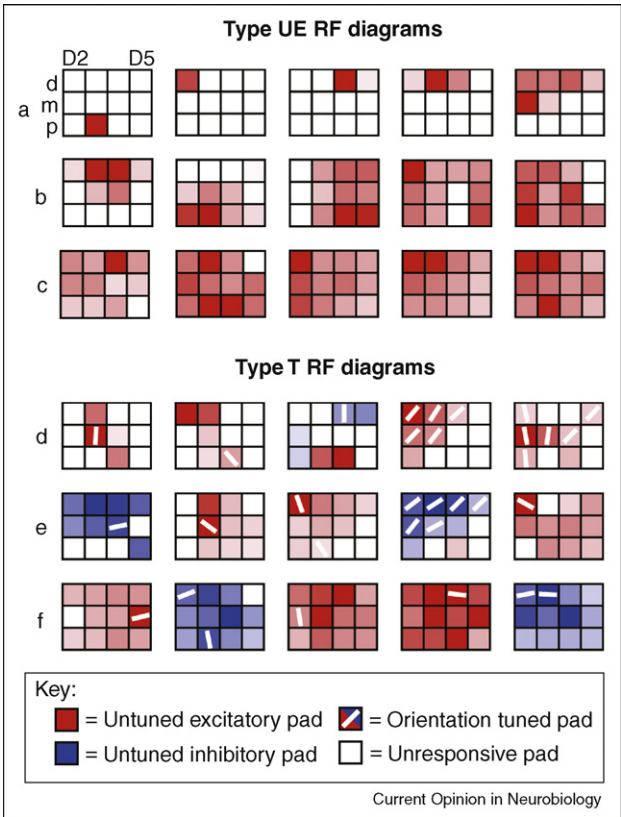
Figure 3



Sample receptive field (RF) for an SII neuron. The 12 large raster plots represent the responses from the distal, middle, and proximal finger pads of the index (D2), middle (D3), ring (D4), and pinky (D5). Within each block are rasters representing the responses to oriented bars that were indented into the skin (see bottom right raster). The graphs below each block are the mean firing rate at the most sensitive and least sensitive orientation. Pads that were significantly driven by the stimulus are highlighted with a colored line above the block. Below the rasters are the mean firing rates at the most sensitive orientation for each of the 12 blocks. The colors are the same as the block. Pads that were not driven by the bar are shown as a thin black line (adapted from Fitzgerald *et al.* [42*,43*]).

SI neurons with many neurons responding to both cutaneous and proprioceptive input [37*,40,41]. The RFs vary greatly in size with many neurons having RF that cover much of the contralateral hand and a majority of SII neurons (as many as 90%) exhibiting bilateral responses [37*]. Figure 3 shows a sample RF for a SII neuron. This neuron had a RF that spanned the distal pads of digits 2–5, the middle pad of digits 2 and 3 and was weakly responsive on the proximal pad of digit 2. What is striking about this neuron is that the different pads show similar orientation selectivity. This similar orientation tuning across pads is characteristic of SII neurons and it is highly probable that these neurons may play an important role in integrating information about edges that span across multiple fingers. Example RFs of a population of SII neurons are shown in Figure 4. As can be seen, the RFs of SII neurons vary in size and shape. Further, they often exhibit heterogeneous responses from the different finger pads with some

Figure 4



Sample receptive fields (RFs) for SII neurons. Each set of 12 blocks represents the response from a single finger pad (see top left block for labels, distal (d), middle (m), proximal (p), D2 represents digit 2, etc.). The top set of blocks (a, b, and c) represent neurons with only untuned excitatory pad (UE). The bottom set of blocks represent neurons that had one or more tuned pads, combined with untuned excitatory and untuned inhibitory pads (d, e, and f). The tuned pad is denoted by an oriented bar in the small block (adapted from Fitzgerald *et al.* [42*,43*]).

neurons having RFs with only untuned excitatory pads (a, b, and c), and others having RFs with one or more tuned pads that are mixed with untuned excitatory pads and untuned inhibitory pads (d, e, and f). A few neurons have RFs with only inhibitory pads (not shown). We believe that these RF structures represent the processing kernels that underlie tactile object recognition [42*,43*].

As stated earlier, the orientation selectivity of area 3b neurons is based on neurons with oriented excitatory and inhibitory regions-like simple cells in visual cortex. By contrast, many neurons in SII show position invariant responses with the tuning being the same regardless of where the bar is positioned on a single finger pad [44]. These results in addition to other studies showing that neurons in SII cortex are affected by selective attention support the notion that SII cortex lies further along the processing pathway and is the key site for integrating the inputs for haptic size and shape perception [45–47].

Conclusions

As stated in 'Introduction', our working hypothesis is that form processing involves the integration of proprioceptive and cutaneous inputs from the hand. We believe that cutaneous inputs related to local 2D stimulus form, texture, and possibly motion are initially processed in area 3b of SI cortex. These neurons have small RFs and as such have a limited view of stimuli on the skin. Area 1 neurons have larger RF and combines inputs from area 3b to extract information about more complex features and plays a key role in processing tactile motion. Neurons in both of these areas are only minimally affected by changes in hand conformation. Information from the proprioceptive and cutaneous afferents are integrated in area 2. Neurons in area 2 change their sensitivity to cutaneous inputs depending on hand conformation. We hypothesize that as hand conformation changes, different sets of neurons become sensitive to different combinations of cutaneous inputs. Neurons in the four areas of SI then send their projections to SII where they are integrated to form representations of the global features of objects. In SII, neurons have RFs that are highly sensitive to hand conformation. As the hand contacts and explores objects, different combinations of SII neurons like those shown in Figure 4 are activated. Object recognition occurs as these 3D spatial views of the object are matched against previously stored representations of objects.

Although it is not understood how the cutaneous responses are modulated by proprioceptive input, recent studies from our lab may provide a clue [48]. In that study we showed that, while the hand has 22 degrees of freedom, the positions, and movements of the hand during object exploration can be explained by seven to nine movement synergies. These synergies are highly similar between humans and capture more than 90% of

the variance of the movements. Future studies are needed to investigate whether these synergies are related to the cutaneous responses of cortical somatosensory neurons.

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