Review

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Neural mechanisms of selective attention in the somatosensory system

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[1]*Department of Neuroscience, Brown University, Providence, Rhode Island;* [2]*The Zanvyl Krieger Mind/Brain Institute, The Johns Hopkins University, Baltimore, Maryland; and* [3]*The Solomon H. Snyder Department of Neuroscience, The Johns Hopkins School of Medicine, Baltimore, Maryland*

Gomez-Ramirez M, Hysaj K, Niebur E. Neural mechanisms of selective attention in the somatosensory system. *J Neurophysiol* 116: 1218–1231, 2016. First published June 22, 2016; doi:10.1152/jn.00637.2015.—Selective attention allows organisms to extract behaviorally relevant information while ignoring distracting stimuli that compete for the limited resources of their central nervous systems. Attention is highly flexible, and it can be harnessed to select information based on sensory modality, within-modality feature(s), spatial location, object identity, and/or temporal properties. In this review, we discuss the body of work devoted to understanding mechanisms of selective attention in the somatosensory system. In particular, we describe the effects of attention on tactile behavior and corresponding neural activity in somatosensory cortex. Our focus is on neural mechanisms that select tactile stimuli based on their location on the body (somatotopic-based attention) or their sensory feature (feature-based attention). We highlight parallels between selection mechanisms in touch and other sensory systems and discuss several putative neural coding schemes employed by cortical populations to signal the behavioral relevance of sensory inputs. Specifically, we contrast the advantages and disadvantages of using a gain vs. spike-spike correlation code for representing attended sensory stimuli. We favor a neural network model of tactile attention that is composed of frontal, parietal, and subcortical areas that controls somatosensory cells encoding the relevant stimulus features to enable preferential processing throughout the somatosensory hierarchy. Our review is based on data from noninvasive electrophysiological and imaging data in humans as well as single-unit recordings in nonhuman primates.

cross-modal; noise correlations; somatosensation; spike-count correlations; spike synchrony

THE NATURAL ENVIRONMENT GENERATES myriads of stimuli that constantly bombard our sensory systems. To effectively function in this environment we employ a set of neural mechanisms that extract the sensory inputs most relevant to our current goals. These mechanisms, which form our selective attention system, are highly flexible and can be harnessed to select information based on the location in space (absolute or relative to the body), sensory modality (e.g., tactile), stimulus features (e.g., motion), object identity, and/or temporal characteristics (e.g., stimulus onset or temporal position in a stream of stimuli). The goal of this manuscript is to provide an ample account of the neural mechanisms mediating stimulus selection in the somatosensory system. While there have been several

review articles on tactile attention (Burton and Sinclair 2000a; Eimer and Driver 2001; Johansen-Berg and Lloyd 2000; Kida and Kakigi 2008, 2015; Sambo and Forster 2011; Spence and Gallace 2007), this review provides a more recent and detailed description of the neural correlates of attention in the somatosensory system and its effects on perceptual functions. In particular, we discuss and, where appropriate, bridge many of the findings observed across species (in particular, human and nonhuman primates) and methodologies [e.g., single-unit recordings, electroencephalography (EEG), and functional magnetic resonance imaging (fMRI)]. We focus on somatotopic- and feature-based attention mechanisms (i.e., selection based on stimulus location on the body surface and stimulus properties, respectively) and the commonalities of attention mechanisms in touch with those in the auditory and visual systems. Our review is based on data from psychophysics, EEG, magnetoencephalography (MEG), and neuroimaging experiments

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(e.g., fMRI) in humans. EEG and MEG activity provides exquisite temporal resolution (≤1 ms level) of neural activity measured at a macroscopic level, whereas imaging methods such as fMRI offer superior spatial localization (≤1 mm^3 resolution), albeit with lower temporal resolution. We also review intracranial neurophysiological studies in humans and nonhuman primates, which combine the strengths of noninvasive neurophysiological and imaging methods. We center on describing the effects of attention in primary and secondary somatosensory (SI, SII) cortexes and the neural mechanisms that mediate these effects. However, we also briefly discuss how attention modulates activity of subcortical and higher-order somatosensory neurons. We begin by providing a short description of the typical experimental paradigms used for controlling the focus of attention and behavioral state of participants in a laboratory setting.

The Cueing Paradigm: The Study of Attention in a Laboratory Setting

Experimental studies in laboratories employ cues to exogenously or endogenously control the focus of attention of participants. Exogenous attention is typically induced by presenting an abrupt stimulus (e.g., tap, sound, or light flash) that directs attention to the location of that stimulus in the absence of a volitional attention shift (Mayer et al. 2004a, 2004b; McCormick 1997; Turatto et al. 2000, 2004a, 2004b). In contrast, endogenous control of attention can be elicited with symbolic cues (e.g., visually presented arrows or sinusoidal tones) that instruct participants to direct attention to a particular sensory modality or physical characteristic of a stimulus, such as its spatial position, location on the body, or sensory feature (e.g., texture, motion direction, orientation), just to name a few examples (Forster and Eimer 2005; Fu et al. 2001; Gomez-Ramirez et al. 2014; Posner et al. 1982; Thut et al. 2006; van Velzen et al. 2002; Worden et al. 2000). Frequently, participants are cued on a trial-by-trial basis, which promotes deployments of attention that are akin to those made in natural environments (Posner et al. 1980). Attention can also be deployed on a sustained basis by instructing participants to maintain attention to the same location, feature, or sensory modality for an entire block of trials (Bradshaw et al. 1992; Eimer and Forster 2003a; Gomez-Ramirez et al. 2011; Hsiao et al. 1993; Martinez et al. 1999; Michie et al. 1987; Steinmetz et al. 2000). The validity of the symbolic cue can be manipulated such that on most trials the cue predicts the relevant discriminative property of the target (i.e., an informative cue). Cues that on most trials do not provide accurate information of the target's relevant property are termed noninformative or "neutral" cues. In this review, we focus on studying the mechanisms underlying endogenous attention in the somatosensory system.

Effects of Attention on Detection and Discrimination Functions of the Somatosensory System

The effects of attention are measured by comparing responses to a sensory stimulus when it is attended vs. unattended. One of the main functions of our selective attention system is to facilitate perceptual judgments by enabling processing of task-relevant inputs. Indeed, studies show that detection of tactile stimuli is faster and more accurate when attention is preallocated to the body location that is stimulated

(Burton and Sinclair 2000a; Johansen-Berg and Lloyd 2000; Spence and Gallace 2007). Likewise, attention improves performance when directed toward sensory features relevant to the task, such as texture (Sinclair et al. 2000), vibration (Sinclair et al. 2000), orientation (Schweisfurth et al. 2014), and intensity (Burton and Sinclair 2000b; Burton et al. 1997).

The behavioral effects of attention comprise both costs and benefits. This was shown in a somatotopic (tactile spatial) attention study that used informative (80% valid) and neutral (50% valid) cues in separate blocks (Forster and Eimer 2005). The authors presented ~60 Hz vibrating stimuli, which likely activated the rapidly adapting (RA) and Pacinian Corpuscles (PC) peripheral systems preferentially (Freeman and Johnson 1982; Mountcastle et al. 1972). Benefits and costs were assayed by comparing the reaction time (RT) between trials with valid vs. neutral cues and invalid vs. neutral cues, respectively. The RT data revealed behavioral benefits in the first case but behavioral costs in the second. The data also showed that RT costs were significantly larger than RT benefits (104 vs. 40 ms). Based on these findings it was suggested that somatotopic attention is mediated by facilitation of neural processing at attended body locations in combination with suppression of somatosensory stimuli at unattended locations (Forster and Eimer 2005).

The limited capacity of tactile attention. The effects of attention on behavior are generally beneficial. This does not mean, however, that attention always decreases the RT and/or improves stimulus detection or discrimination. There are specific (and rare) instances in which deploying attention to a particular location impairs performance. One example is the "inhibition of return" (IOR) effect, which refers to the increase in RT to target stimuli that are presented in the same location as a preceding peripheral stimulus (Klein 2000; Posner and Cohen 1984; Posner et al. 1985). This effect, originally demonstrated in the visual modality, is typically observed during exogenous attention (Posner et al. 1985), and it is an integral part of computational models of attention (Itti et al. 1998; Koch and Ullman 1985). The IOR is believed to foster exploration of previously unattended stimuli by preventing the focus of attention to return to previously attended locations. The IOR is time dependent in that it is generally manifested when the target stimulus is preceded by the cue by at least 300 ms. Furthermore, studies show that the IOR is long lasting, occurring over a period of ~1,500–2,000 ms after an active deployment of attention (Posner and Cohen 1984). Although the IOR is believed to be mediated by mechanisms of attention, some studies have suggested that the IOR may also be caused by deficits in motor pathways (Hunt and Kingstone 2003; Rafal et al. 1989). However, further investigation is needed, since recent studies have failed to find consistent and supporting evidence for this hypothesis (Chica et al. 2010; Smith et al. 2012).

One of the original reports of a tactile IOR effect was provided by Lloyd and colleagues (1999), who showed RT increases to tactile stimuli matching the body location of an nonpredictive cue (see also Cohen et al. 2005; Jones and Forster 2014, 2012; Roder et al. 2002; Tassinari and Campara 1996). Lloyd et al. (1999) showed the onset of the IOR effect around 100 ms, with the maximum effect occurring between 200 and 700 ms, which is earlier than the IOR observed in visual studies.

The IOR has also been observed in the auditory modality, indicating that it may be driven by mechanisms that are common across the senses (Spence et al. 2000a). With the use of spatially coregistered auditory, visual, and tactile stimuli on the left and right side of the body (left and right hands for tactile stimuli), it was found that RTs were significantly longer for stimuli presented on the same body side as the last target stimulus. This occurred regardless of the sensory modality of the previously presented stimulus. Interestingly, a recent study showed that the IOR in touch is abolished by engaging in a visual discrimination task (Jones and Forster 2013). In this study, participants performed a divided-attention tactile and visual task that required them to respond to a tactile (delivered to the left or right hand) or visual (a number from 2 to 9 centrally presented on a monitor) target stimulus. The tactile target stimulus was always preceded by a tactile "cue" that was presented on the same hand on 50% of the trials. The target visual stimulus was embedded within a stream of serially presented letter stimuli. On a separate set of blocks, participants engaged in the same tactile task but were asked to ignore all visual stimuli (tactile-only task). When participants performed the tactile-only task, the behavioral data revealed slower responses to tactile targets at the cued locations (i.e., the IOR effect). Furthermore, as expected, participants' RT to tactile stimuli substantially increased in the divided-attention vs. the tactile-only task. However, the data showed no difference in RTs between cued or uncued tactile targets (i.e., no IOR effect) for the divided-attention task. These findings are striking because they suggest that engaging in a visual discrimination task can withdraw significant attention resources from the somatosensory system.

Cross-modal effects in the somatosensory system are not restricted to the IOR. Psychophysical studies have reported another interesting cross-modal phenomenon, termed the Colavita visual dominance effect, which refers to the interference of visual stimuli in auditory or tactile discrimination or detection (Colavita 1974). This effect is akin to exogenous attention in that the presentation of a visual stimulus draws attention away from the tactile modality. The Colavita effect is observed in cross-modal studies of attention where participants are instructed to attend to inputs from a nonvisual channel while ignoring visual stimuli. This effect is modulated by the spatial and temporal relationship between the multisensory stimuli (Koppen and Spence 2007a, 2007b) but not by semantic or probability commonality (Koppen et al. 2008). Interestingly, recent studies show that tactile signals are also masked when visual inputs are substituted with auditory stimuli (Occelli et al. 2010). However, these effects are much weaker and depend on the spatial configuration of the multisensory inputs.

The IOR and Colavita effects highlight the commonalities between the mechanisms of attention that facilitate tactile, auditory, and visual perceptual functions. Furthermore, the Colavita effect, in particular, underscores the dominant role of the visual system over the tactile and auditory modalities. Indeed, as previous studies show, the presence of a distracting visual stimulus during a tactile discrimination task can substantially decrease performance, even when the visual stimulus shares no feature relationship with the tactile stimulus or is irrelevant to performing the task. Furthermore, these findings provide compelling evidence that, at least in primates, visual signals have priority over other sensory inputs in the attention

filter that limit perceptual processing capacity. That said, under circumstances where tactile signals provide more reliable information, the sense of touch has been shown to dominate over vision (Ernst and Banks 2002; Guest and Spence 2003; Lederman et al. 1986). Indeed, it would be intriguing to assess whether similar effects hold in other species that rely more heavily on other sensory systems to sample the environment (e.g., the whisker system in rodents).

In the following sections we describe the neural correlates and mechanisms of selective attention in the tactile modality. We start by providing a brief description of the anatomical organization and information flow of neural signals in the somatosensory system.

Neural Circuitry of the Somatosensory System

A thorough understanding of the neural mechanisms mediating tactile stimulus selection requires sound knowledge of the anatomical and functional circuitry of the somatosensory system. Tactile perception begins in the periphery with the processing of individual features of somatosensory stimuli (e.g., edges, texture, vibrations, and temperature). These features are processed by specialized receptors on the glabrous (hairless) and hairy skin, which are innervated by distinct afferents that convey activity to the central nervous system. The signals carried by these afferents can be categorized into distinct functional modalities depending on the type of somatosensory feature they encode. They include: cutaneous or innocuous touch (e.g., light skin indentation), proprioception (e.g., spatial configuration of fingers enclosing an object or positions of limbs), temperature (e.g., coldness), and nociception (e.g., pain-related signals). Here, we focus on how attention modulates responses of neurons encoding cutaneous and proprioceptive inputs.

Cutaneous stimuli are predominantly encoded by mechanoreceptors. In particular, Merkel-Neurite Complex receptors, innervated by slowly adapting I (SA-I) fibers, best encode tactile spatial features such as edges, curvature, and texture (Connor et al. 1990; Connor and Johnson 1992; Goodwin et al. 1997; Johnson 1983; Yoshioka et al. 2001). Meissner's corpuscles, which are innervated by RA afferents, process motion and low-frequency vibrations (Johnson et al. 2000). PC, which are innervated by PC afferents, are specialized for high-frequency vibrations (>100 Hz) and fine texture (Harvey et al. 2013).

The sense of proprioception is initially encoded by muscle (Cordo et al. 2002; Houk and Henneman 1967; Proske and Gregory 2002; Roll et al. 1989) and skin mechanoreceptors innervated by slowly adapting II (SA-II) fibers that respond to selective patterns of skin deformation (Edin and Abbs 1991; Hallin et al. 2002; Olausson et al. 2000). As we will discuss later, the effects of attention on cutaneous processing and behavior are modulated by the spatial arrangement of the body parts (i.e., proprioception).

The classical model of somatosensory processing indicates that activity from peripheral afferents is transmitted to the brain via separate channels and then converges in "late-processing" areas (Mountcastle 2005). However, results from recent studies are at odds with this view by showing that cutaneous and proprioceptive signals are integrated at the earliest level of SI (i.e., areas 3a and 3b) and possibly even earlier (Kim et al.

2015). Furthermore, a recent study in nonhuman primates found that cutaneous signals, such as those from SA-I and RA inputs, also converge in area 3b (Pei et al. 2009). In fact, recent work using anatomical and electrophysiological methods in genetically modified animals indicates that peripheral signals are integrated even at the level of the spinal cord (Abraira and Ginty 2013). Thus, given that many submodality (e.g., RA, SA-I, and PC) and modality-specific (e.g., cutaneous and proprioceptive) peripheral afferent signals converge in subcortical and early SI, we deem that tactile selective attention operates by targeting functional, as opposed to anatomical, cell ensembles that have common neural selectivity for the relevant physical properties of sensory stimuli (e.g., spatial, feature, and temporal) (Gomez-Ramirez et al. 2014).

Although, as discussed, some modality-specific signals converge in different neural subareas before reaching cortex, the somatosensory system maintains a topographical organization that is conserved throughout SI and, to a lesser extent, SII cortex. In particular, SI cortex has a detailed topographical representation of the body, whereby neurons located more medially (i.e., toward the interhemispheric fissure) have a receptive field (RF) over the lower part of the body (e.g., toes and lower limbs), whereas neurons located more laterally (toward the lateral sulcus) have a RF over the upper body (Mountcastle 2005). In addition, SI in each hemisphere predominantly responds to inputs from the contralateral side of the body. SII cortex also has a body map. However, this representation is less well defined, and most SII cells have bilateral RFs (Fitzgerald et al. 2006a, 2004, 2006b). A major advantage of having a detailed neural representation of the body is that attention can leverage this topographical organization to select stimuli based on their somatotopic location. We discuss this mechanism in a later section of the manuscript.

Somatosensory activity beyond SII is believed to be processed in two distinct, but interrelated, functional pathways. One pathway, which is related to object grasping and manipulation, includes areas in the posterior parietal cortex (e.g., areas 5 and 7), and it is tightly connected with motor and premotor neural areas. The other pathway, which is involved in tactile object recognition and aesthetics, includes more anterior structures such as the insula and cingulate. These two functional pathways are thought to operate in parallel and in concert during natural object grasping, manipulation, and recognition (Hsiao and Gomez-Ramirez 2011).

Neurophysiological Correlates of Attention in the Somatosensory System

The effects of tactile attention on behavior are thought to be mediated by the enhancement of activity in somatosensory cortical areas with RFs over attended stimuli (Forster and Eimer 2005; Gomez-Ramirez et al. 2014; Hsiao et al. 1993; Michie 1984; Michie et al. 1987; Steinmetz et al. 2000; van Velzen et al. 2002). In a seminal study, Hsiao and his colleagues found that attention modulated activity of neurons in SI and SII cortex when attention was directed to touch vs. vision (Hsiao et al. 1993). In this study, animals switched between performing a tactile letter and visual luminance discrimination task. During attend-visual blocks, animals were presented with the same tactile letter stimuli as in the tactile blocks but were trained to ignore these letters and focus attention on visual

stimuli. The data revealed greater firing rate in SI and SII neurons when performing the tactile vs. visual task. Furthermore, it was found that the firing rates of a subset of cells were additionally enhanced during correct vs. incorrect trials. These findings are shown in Fig. 1A.

In addition to modulating firing rates, attention can also modulate the correlated spiking activity between somatosensory cells. This was originally shown by Steinmetz and colleagues who trained animals to perform a tactile and visual discrimination task and recorded from multiple cells while animals directed attention to tactile or visual stimuli (Steinmetz et al. 2000). It was found that tactile attention increased the synchronized spiking activity (spikes within approximately ±5 ms; see Fig. 1B) between neural pairs in SII cortex. Enhanced spike synchrony was also observed in a more recent attention study in animals trained to discriminate tactile stimuli based on their orientation and/or frequency (Gomez-Ramirez et al. 2014). It was also found that the spike synchrony between feature-selective cells was tightly correlated with animals' performance, whereby greater correlated spiking was associated with higher performance.

Tactile attention can also influence synchronized neural activity measured at macroscopic levels [e.g., EEG, MEG, electrocorticography (ECoG), and local field potentials]. This was originally shown in a delayed-to-match sample task of somatotopic attention (Bauer et al. 2006). Specifically, Bauer and colleagues showed increases in γ-band (30–80 Hz) activity over contralateral somatosensory cortexes when attention was directed to the left vs. right hand that commenced around 100 ms after stimulus onset (Fig. 1C). Similar findings were observed in a cross-modal attention task using ECoG recordings in humans (Ray et al. 2008). Specifically, it was shown that attention toward touch compared with audition increased high γ-band activity (80–150 Hz) over the postcentral gyrus. Conversely, increased high γ-activity was observed over auditory cortexes when attention was deployed to audition. These findings indicate that enhancement of synchronized γ-band oscillations represents a neural correlate of signaling behavioral relevance across all sensory modalities.

Anatomical and temporal distribution of attention effects in the somatosensory system. Attention effects on somatosensory cells can occur early in the neural processing stream. Neural responses of somatosensory neurons can be modulated by behavioral states at the levels of the thalamus (Bushnell and Duncan 1987; Morrow and Casey 2000, 1992; Tremblay et al. 1993) and even the medullary dorsal horn (Dubner et al. 1981; Hayes et al. 1981; Hoffman et al. 1981). Hayes and colleagues (1981) reported that neurons in the dorsal horn increased their responses when animals performed a thermal (innocuous or noxious stimuli) vs. visual discrimination task. Furthermore, they found that neural responses were enhanced already during the initial volley of afferent activity, indicating that attention can modulate the neural activity of dorsal horn neurons in anticipation of peripheral stimulation.

We just described that attention can modulate neural activity of somatosensory neurons in the early phases of stimulus processing. However, similar to the visual system (Desimone and Duncan 1995; Luck et al. 1997; Martinez et al. 1999; Reynolds et al. 1999), the magnitude and prevalence of these effects increase throughout the sensory hierarchy. For instance, Hsiao and colleagues (1993) showed that attention modulated
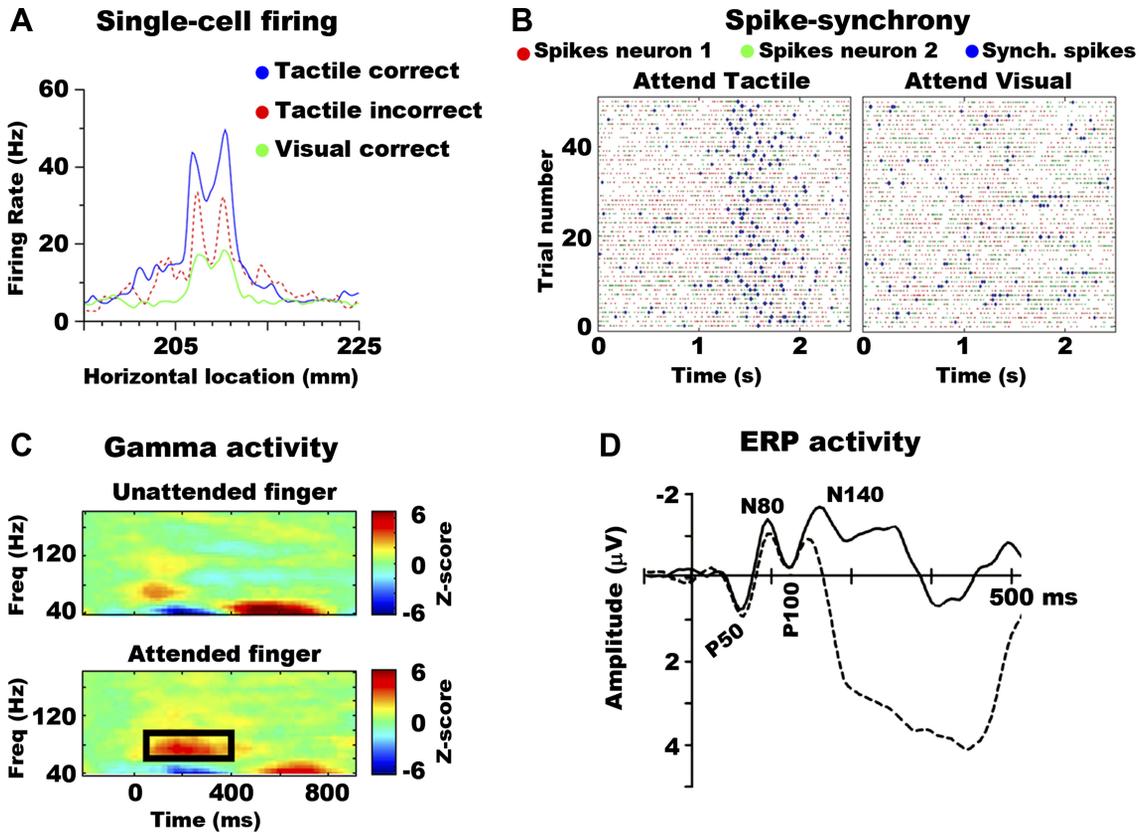
Fig. 1. Attention effects on neural activity. *A*: instantaneous mean firing rate of secondary somatosensory (SII) neurons responding to a tactile stimulus when it was attended and the behavioral response was correct (blue) or incorrect (red) and when the stimulus was unattended (green; in this case attention was to a visual stimulus, and behavioral response to the latter was correct). Firing rate is plotted as a function of time, which is represented here for technical reasons as the location of the drum used to present the tactile stimuli. Because the drum moved with constant velocity, there is a one-to-one mapping between drum location and time, with 1 s corresponding to a distance of 15 mm. Adapted with permission from Hsiao et al. 1993. *B*: raster plots of two neurons in SII cortex when attention was directed to the tactile (*left*) and visual (*right*) modality. Green and red dots indicate individual spikes for each neuron, whereas blue dots are coincident spikes between both neurons within 2.5 ms of each other. There are substantially more coincident spikes between SII neurons when attention is directed to touch (*left*) vs. vision (*right*). Adapted with permission from Steinmetz et al. (2000). *C*: time-frequency plots over somatosensory areas for unattended (*top*) and attended (*bottom*) stimuli. The black frame in the *bottom* highlights the difference in the γ-band between the two conditions. Adapted with permission from Bauer et al. (2006). *D*: event-related potential (ERP) activity to attended (broken line) vs. unattended (solid line) stimuli. The voltage polarity of the evoked potential is indicated by the first letter ("N" for negative, "P" for positive), whereas the timing of the peak activity of the ERP component is indicated by the numbers. Thus, the N80 refers to a negative deflection occurring 80 ms after the onset of the tactile stimulus. Adapted with permission from Forster and Eimer (2004).

the responses of ~50% cells in SI and 80% of neurons SII. A similar percentage difference was observed in a separate study that trained animals to perform a tactile texture and visual discrimination task (Meftah el et al. 2002). Approximately 25% of cells in SI and 62% of SII neurons were modulated by attention. This pattern of attention effects has also been observed in human imaging studies, which show greater attention modulations in hemodynamic responses of SII and insula compared with SI (Burton et al. 1999; Chen et al. 2010, 2008; Hamalainen et al. 2002). However, in the somatosensory system, it is unknown whether attention effects continue to scale across associative areas (e.g., beyond SII cortex), a finding that has been observed in the visual system (Luck et al. 1997).

To date, there are only a handful of studies that have investigated the effects of tactile attention on neural activity beyond SII cortex. In particular, a study in nonhuman primates showed that most neurons (~60%) in area 7b are enhanced by attention (Burton et al. 1997). The sample size in this study was small (*n* = 22 cells), but these findings are supported by several human imaging studies that show increased responses in higher-order neural areas encoding the attended stimuli

(Burton et al. 1999; Goltz et al. 2013). Studies in humans have also shown that attention increases the functional connectivity between high- and low-order somatosensory areas. In particular, a combined EEG and fMRI study in humans found enhanced coupling between the intraparietal sulcus and somatosensory cortexes during sustained attention to tactile stimuli. These findings indicate that attention synchronizes activity between high- and low-order areas in parietal cortex as a means to enhance the relevant sensory signals (Goltz et al. 2015).

An interesting phenomenon observed in single-unit studies is the heterogeneity of attention effects across somatosensory areas. Hsiao and colleagues (Hsiao et al. 1993) reported that, of those SI neurons that showed attention effects (~50% of the entire SI population), all had greater activity when attention was deployed to touch vs. vision. In contrast, attention effects on SII neurons were found to be variable, with only 73% of attention-modulated cells exhibiting greater responses when attention was directed to touch vs. vision, whereas 27% of the remaining set of cells modulated by attention showed enhanced responses when attention was deployed to vision vs. touch (Hsiao et al. 1993). Such diversity of attention effects in SII has

also been observed in other tactile attention studies (Burton et al. 1997; Gomez-Ramirez et al. 2014). The cause of this heterogeneity is unknown, but one plausible hypothesis is that attention imposes different selection filters across neural areas. That is, it is possible that attention effects on SI cells are driven by spatial selection mechanisms that operate by solely enhancing cells' responses when the RF is aligned with the spatial focus of attention, regardless of their selectivity for the attended stimulus feature. In contrast, because of the diversity of feature encoding of SII neurons (Gomez-Ramirez et al. 2014), attention might impose feature selection filters in SII (or a composite of features and spatial selection filters) such that a cell's response is further modulated according to its affinity for the attended stimulus features. Thus, neurons that are selective for attended features are enhanced, whereas neurons that encode task-irrelevant features are suppressed.

The temporal incidence of tactile attention effects has been extensively investigated in human studies using event-related potential (ERP) and MEG methods. These techniques afford exquisite temporal resolution of neural activity albeit at a macroscopic spatial scale. Studies show that attention can modulate the amplitude of early and midlatency tactile ERP components (e.g., P55, N80, P100, N140 where "N" indicates negative, "P" indicates positive, and the numbers indicate the timing of the peak activity of the ERP component in ms) as well as later-occurring components (see, e.g., Fig. 1D) (Eimer and Forster 2003a; Eimer et al. 2004b; Forster and Eimer 2004, 2005; Garcia-Larrea et al. 1995; Kennett et al. 2001; Kida et al. 2011, 2004; Michie 1984; Michie et al. 1987). With the use of inverse source modeling, EEG and MEG studies report that the N80 component arises from contralateral neural ensembles in SI cortex, whereas the P100 response emerges bilaterally in SII (Allison et al. 1992, 1989; Inui et al. 2004; Mauguiere et al. 1997; Mima et al. 1998). These data confirm single-unit findings in nonhuman primates that tactile attention modulates responses during early phases of stimulus processing.

Most ERP studies in humans also indicate that feature-based attention effects (e.g., effects related to deploying attention to oriented or textural features) are observed after spatial selection of somatosensory stimuli. However, the evidence is not unequivocal. An example where spatial and feature attention effects occurred at the same time was published previously (Forster and Eimer 2004). In this study, human participants were instructed to perform frequency and intensity discrimination tasks with stimuli delivered to the right or left hand. Participants were told to attend to specific combinations of stimulus location (left or right hand) and nonspatial feature (frequency or intensity) on different blocks. The data showed that the onset of spatial attention effects occurred around 140 ms (i.e., in the period related to the N140 component). Furthermore, it was shown that ERP attention effects on nonspatial features modulated activity around the same latency range and that these feature attention effects did not vary as a function of the spatial focus of attention. This pattern of effects led the authors to conclude that feature and spatial selection in the somatosensory system are neural processes that occur in parallel and are independent from each other (Forster and Eimer 2004). However, as noted earlier, several studies found that somatotopic (spatial) attention modulates neural activity at ~100 ms posttactile stimulus (Eimer and Forster 2003a, 2003b), and even earlier (~55 and 80 ms) (Eimer and Forster

2003a; Michie et al. 1987) (see also Fig. 1D). The range of differences in the onsets of spatial attention effects between the Forster and Eimer (2004) study and the aforementioned studies is quite substantial (~40 and 85 ms). The reasons for these dramatically different time courses are unclear and not addressed in the literature. Thus, further studies are needed to bridge the discrepancies between these datasets. However, as it stands right now, the aggregated evidence supports the thesis that somatotopic (or spatial) selection is a neural process that precedes the effects of feature attention by at least ~40 ms.

Neural Mechanisms Mediating Selection of Tactile Sensory Stimuli

The attentional system is highly flexible and involves separable mechanisms of both enhancement and suppression. As noted earlier, γ-band oscillations are associated with enhancement of neural activity encoding attended stimuli (see Fig. 1C) (Bauer et al. 2006; Fries et al. 2001; Karns and Knight 2009; Ray et al. 2008; van Ede et al. 2014). In contrast, α-band (8–14 Hz) oscillations are linked to suppression of activity encoding stimuli outside the focus of attention, a phenomenon that is commonly referred to as the α-suppression effect (Foxe and Snyder 2011). However, unlike γ-band oscillations, which have been shown to arise from local recurrent excitatory/ inhibitory effects (Cardin et al. 2009; Siegle et al. 2014; Whittington and Traub 2003; Whittington et al. 1995), the mechanisms driving α-oscillations are not fully determined (but see Contreras et al. 1992, 1996, 1997a, 1997b; Destexhe et al. 1998; Sherman 2001, 2005; Sherman and Guillery 2002 for putative models). In the next section, we describe in more detail the role of this α-oscillatory effect in the somatosensory system. In what follows we provide a description of the mechanisms mediating spatial selection of somatosensory stimuli. Particularly, we focus on describing the neural mechanisms that establish and maintain the spatial focus of attention and how proprioceptive inputs can influence neural representations of cutaneous sensory signals.

Somatotopic (spatial) selection in the somatosensory system. In vision, attention has been proposed to function like a "spotlight" by enhancing all relevant information within its focus and changing its size (Eriksen and Hoffman 1972; Eriksen and St. James 1986). Furthermore, fMRI data show that tasks requiring attention to multiple spatial locations, at the same time, lead to multiple peaks in the hemodynamic response of areas selective for those spatial locations. This finding led to the suggestion that the spotlight of attention can be simultaneously split across different spatial locations to maximize the likelihood that only relevant stimuli receive preferential processing (McMains and Somers 2004; Morawetz et al. 2007). Indeed, a similar phenomenon has been described in the tactile modality (Eimer and Forster 2003b).

In vision, there is also evidence of a limited degree of autonomy of the cerebral hemispheres in the control of selective attention. The classical multiobject tracking results by Pylyshyn and Storm (1988) showed that humans can track about four independent objects. Later it was shown that this number is actually two plus two, with two objects being tracked in each visual hemifield (Alvarez and Cavanagh 2005; Cavanagh and Alvarez 2005).

In touch, discrimination of spatial patterns diminishes when distracters and targets are presented to the same hand as compared when they are presented to different hands (Craig 1985). For stimuli presented on the same hand, this interference effect increases as the distance between targets and distracters decreases. Specifically, discrimination of stimuli presented to the little finger (digit 5) diminished when distracter stimuli were presented on the ring finger vs. the index finger (digit 4 vs. digit 2). However, this interference effect decreased when distracters were presented on the opposite hand, and it was not further modulated by the spatial distance between the hands (Evans et al. 1992). These psychophysical data indicate that distracters presented on the same hand may not be fully suppressed. This effect was confirmed by ERP studies that also showed that there is no clear modulation of attention when deployed to either whole fingers or individual phalanxes (Eimer and Forster 2003b). Whereas ERP attention modulations generally decayed with distance from the focus of attention, the decay was gradual, and no discrete jumps were observed at the boundaries of phalanxes or fingers. Whether there are any other categorical distinctions in the spread of tactile attention merits further examination.

A related question is whether the focus of attention can be split in two noncontiguous regions separated by an unattended region. This question was investigated in a human ERP study that compared ERP responses with tactile stimuli when attention was directed to two adjacent fingers vs. two nonneighboring stimuli (e.g., attention to digit 3 and digit 4 vs. digit 2 and digit 5) (Eimer and Forster 2003b). It was hypothesized that, if two separate attention foci are maintained, one would expect a difference in ERP signals in these two cases, whereas a contiguous focus of attention should result in similar ERP signals. The experimental result showed that the former scenario was correct. Specifically, the P100 component in response to stimuli delivered to attended fingers was modulated by attention, but attention did not modulate the responses to stimuli presented to the unattended finger located between attended fingers (Eimer and Forster 2003b). Although ERPs afford a very crude spatial representation of intracranial neural activity, it is notable that the authors were still able to find a differential response between these two conditions. Studies that resolve neural activity at the single-cell level are needed to further understand the mechanisms underlying this spatial selection effect.

As noted earlier, the brain may use neural oscillatory mechanisms in the α-band to suppress sensory information that is irrelevant to the current goals of the task (the α-suppression effect). Selective attention can control the focus and magnitude of these α-oscillations according to the spatial location and perceptual load of the distracting stimulus (Foxe and Snyder 2011). This oscillatory suppression mechanism was initially reported in the visual modality (Banerjee et al. 2011; Foxe et al. 1998; Fu et al. 2001; Worden et al. 2000), but it is also observed in somatosensation (Haegens et al. 2011a, 2012, 2011b; Jones et al. 2010; van Ede et al. 2011, 2014) and audition (Banerjee et al. 2011; Fu et al. 2001; Gomez-Ramirez et al. 2011). In touch, this effect was originally reported in a MEG study of somatotopic attention (Jones et al. 2010). Participants were cued to direct attention to their left hand or foot and report whether a vibratory stimulus was presented to that location. The data showed increased α-band amplitude over areas responsive to stimulation of the hand in anticipation of a tactile stimulus delivered to the left foot, that is, α-amplitude increased over the representation of the unattended body location. The data further revealed that α-power over unattended areas was positively correlated with detection of tactile stimuli at the single-trial level. In separate studies, it was shown that the α-suppression effect increased systematically as a function of cue validity, with higher cue validity leading to greater α-power over unattended areas (Haegens et al. 2011a). Similar to the findings by Jones et al. (2010), Haegens and colleagues found a relationship between α-power and performance (Haegens et al. 2011a, 2011b, 2012). Taken together, these data indicate that the α-suppression effect is a supramodal neural mechanism controlled by attention to suppress distracting stimuli regardless of the sensory identity of the stimulus.

Much is known about how somatotopic (spatial) attention modulates behavior and neural processing of tactile stimuli (Burton et al. 1997, 1999; Burton and Sinclair 2000a, 2000b; Eimer and Forster 2003a; Forster and Eimer 2004; Gherri and Forster 2014; Gomez-Ramirez et al. 2014; Hsiao et al. 1993; Meftah el et al. 2002; Michie 1984; Michie et al. 1987; Sinclair et al. 1991; Steinmetz et al. 2000; van Velzen et al. 2002). However, the neural mechanisms that establish and maintain the control of attention in somatosensory cortexes are less well understood. Several human studies have characterized a series of ERP components that are associated with establishing and maintaining attention in space and body locations (Eimer et al. 2003b, 2004a; Eimer and Van Velzen 2002; Harter et al. 1989; Hopf and Mangun 2000; Kelly et al. 2009; Praamstra et al. 2005; Praamstra and Kourtis 2010; Seiss et al. 2009; Simpson et al. 2006; van Velzen and Eimer 2003). These studies have identified several early and late lateralized ERP components that emerge in anticipation of the target stimulus (i.e., during the cue-to-target interval). These components are observed in auditory, visual, and tactile attention tasks in normal healthy individuals (Eimer and Van Velzen 2002; Eimer et al. 2002) and in blind individuals performing spatial attention tasks in the tactile modality (Van Velzen et al. 2006). These data indicate that these anticipatory ERP components may reflect supramodal neural correlates of attention control.

The early directing attention negativity (EDAN) is one of the earliest ERP components ($\sim$250 ms postcue) that show cue-related attention effects (here, we refer to attention modulations of neural activity in response to the cue stimulus itself. These effects should not be confused with the attention effects mentioned earlier that reflect modulations in neural responses to attended and unattended target stimuli, which may occur as early as 55 ms after stimulus onset). The EDAN consists of a negative deflection over posterior electrodes that is contralateral to the direction of the cue stimulus and is believed to reflect decoding of the cue and initiation of an attention shift. However, some studies indicate that the EDAN may reflect processing of the physical attributes of a sensory cue stimulus (van Velzen and Eimer 2003). The EDAN is followed by the anterior directing attention negativity (ADAN), which is an enhanced negativity over the frontal scalp that is contralateral to the direction of attention. The ADAN is believed to index the control of spatial attention by neural populations in higher-order frontal cortexes. It emerges around 300 ms after the onset of the cue stimulus and lasts several hundred milliseconds.

Furthermore, the ADAN is modulated by distracter stimuli (Seiss et al. 2009) and occurs even when visual cue stimuli are replaced by auditory spatial cues (Van Velzen et al. 2006). The ADAN has also been shown to reverse polarity when the upper limbs are crossed, indicating that it operates in a propriocetive-centered reference frame because it follows the spatial location of the attended hand (Eardley and van Velzen 2011; Eimer et al. 2003a). However, in a separate study, it was found that this polarity reversal emerged during the later phase of the ADAN component (700–900 ms postcue), suggesting that neural activity during the latter part of ADAN (the so-called late ADAN or late somatosensory negativity) might represent a different mechanism of attention orienting compared with the early phase of the ERP component (Gherri and Forster 2012a). In particular, it was suggested that the early ADAN (300–500 ms) operates according to an external frame of reference that does not reverse polarity with crossed hands, whereas the late ADAN (or late somatosensory negativity) reflects selective activation of somatosensory neurons in anticipation of an upcoming tactile stimulus (Gherri and Forster 2012a).

The ADAN is followed by the late-directing attention positivity (LDAP), which is a contralateral positivity over the posterior scalp that is maintained until the presentation of the target stimulus. The LDAP is thought to reflect the activation of visual (or multisensory) areas in anticipation of stimuli at the attended locations. The LDAP is modulated by the distance between hands, with increased amplitude as the hands are placed farther apart (Eimer et al. 2004a). In contrast to the ADAN component, the LDAP does not reverse polarity when limbs are crossed, indicating that the LDAP operates in an external frame of reference (e.g., visual-spatial coordinate frame) (Eimer et al. 2003a, 2004a; Gherri and Forster 2012b).

Although it is predominantly believed that spatial attention is controlled by a frontoparietal network (Corbetta and Shulman 2002; Doesburg et al. 2008; Hopfinger et al. 2000; Kida and Kakigi 2013; Petersen and Posner 2012; Reynolds and Chelazzi 2004), recent work in nonhuman primates provides compelling evidence that spatial selection is also mediated by subcortical circuitry in the superior colliculus (SC). With the use of combined correlative (electrophysiological) and causal (pharmacological) methods, it was found that inactivation of the intermediate and deep layers of the SC via muscimol (a GABA agonist) led to profound impairments in selecting the visual stimulus informative of the behavioral response. What is more striking is that, while inactivation of the SC led to severe deficits in behavioral performance, neurons in neocortex that encode the stimulus features of the task (e.g., mediotemporal cortex for motion) still exhibited robust attention effects in their firing rates (Lovejoy et al. 2009; Zenon and Krauzlis 2012). This pattern of effects led to the hypothesis that spatial attention effects of SC on behavior are mediated by neural mechanisms that are independent of neocortical response modulations (Krauzlis et al. 2013, 2014). From a multisensory perspective, this model of spatial selection is attractive because the intermediate and deep layers of SC are composed of neurons with audio, tactile, and/or visual RF that are spatially aligned. Certainly, this spatially organized system is advantageous for facilitating spatial stimulus selection regardless of sensory identity of stimuli.

A fundamental question in the somatosensory field is whether tactile stimuli are selected in a somatotopic frame of reference (body location and/or proprioceptive coordinates), an external spatial frame (visual-spatial coordinates or extrapersonal space), or a combination of both. This question was initially addressed in a study that cued participants to two body locations in sequence and then asked participants to judge whether a puff of air was presented in the location indicated by the second cue (Lakatos and Shepard 1997). The first and second cues were presented at similar locations in 70% of trials, which increased the likelihood that attention was maintained on the first location. It was found that RTs to stimuli presented across hemifields (i.e., left to right body locations, or vice versa) were significantly slower than RTs to stimuli within the same hemifield. Moreover, and perhaps more importantly, RTs increased linearly with the Euclidean distance between body locations. These findings support the hypothesis that attention operates in a visual-spatial coordinate reference frame. Further supporting this view, studies show that tactile attention effects are modulated by the position of the eyes. Specifically, it was found that attention effects were reduced in eccentric compared with central fixation conditions (Gherri and Forster 2014).

Several ERP and behavioral studies indicate that proprioception (e.g., body posture) also plays a fundamental role in tactile spatial selection (Eimer et al. 2001; Gherri and Forster 2012b; Kennett et al. 2001; Roder et al. 2008; Schicke and Roder 2006; Yamamoto and Kitazawa 2001). In particular, crossing the upper limbs (i.e., placing the left and right hands on the right and left sides of the body, respectively) can lead to increased RTs and decreased discrimination (Spence et al. 2000b; Yamamoto and Kitazawa 2001). This tactile remapping effect also occurs for crossing of lower body parts (e.g., feet) (Schicke and Roder 2006). Furthermore, reduced performance due to crossed limbs is accompanied by a reduction (or even absence) of early attention effects on target stimuli measured with ERPs (Eimer et al. 2001). Moreover, recent behavioral studies indicate that this tactile remapping takes place around 180–360 ms after stimulus presentation (Azanon et al. 2010; Azanon and Soto-Faraco 2008), indicating that this somatotopic reconfiguration occurs in higher-order somatosensory cortical areas or is mediated by cortico-cortico feedback to early somatosensory areas. In support of the latter hypothesis, a recent neurophysiological study in nonhuman primates revealed a subpopulation in SI whose responses to tactile stimuli were modulated by proprioception after the initial response to cutaneous stimuli (after 100 ms) (Kim et al. 2015). Taken together, these data indicate that stimulus selection in the tactile modality is not solely based on a somatotopic reference frame but rather on the interplay between proprioceptive, visual-spatial, and anatomically defined coordinates.

Feature selection in the somatosensory system. When holding an object with our hands, we effortlessly sense a multitude of tactile features, such as its local curvature, texture, edges, or motion (e.g., when the object is slipping). Often it is necessary to focus on just one (or a set) of these features because recognition of a particular object may rely on identifying a specific feature of the stimulus (e.g., its texture or size). This is shown in Fig. 2A, which shows three objects with similar shape, size, and local curvature. Without assistance from the visual system (e.g., in dark environments), the most effective approach for differentiating between these particular objects is to base discrimination on their texture. This requires selective

deployment of attention to textural features while ignoring irrelevant or redundant tactile information (e.g., local curvature). The neural mechanisms mediating this ability were recently investigated in a study (Gomez-Ramirez et al. 2014) in which nonhuman primates were trained to perform tactile orientation and frequency discrimination tasks as well as a visual luminance discrimination task. Neural activity was recorded from SII neurons that were selective for orientation and/or vibrating (i.e., frequency) tactile features. The data revealed increased firing rates when attention was directed toward a neuron's preferred feature (e.g., enhanced activity in orientation selective neurons when performing the orientation

A Discrimination of objects based on texture

B Spike-synchrony between feature selective neurons

● Attend Frequency   ● Attend Orientation
● Attend Visual
Frequency Selective

Orientation Selective

C Spike-synchrony & Behavior

● Attend towards preferred feature
● Attend towards non-preferred feature
● Attend towards vision

task). More strikingly, the frequency of spike-synchrony events between two neurons that were selective for the same tactile feature was also increased when attention was deployed to their preferred stimulus feature (Fig. 2B). Importantly, spike-synchrony attention effects correlated with performance. Specifically, higher accuracy was associated with increased spike synchrony in feature-selective neurons, but only when attention was directed to the preferred feature of the neurons (Fig. 2C). The opposite effect was found when animals performed the visual task, that is, greater spike synchrony between feature-selective somatosensory cells was correlated with decreased performance in the visual task. These findings highlight the effectiveness of attention to enhance the neural circuits that process relevant stimuli but also to disengage the circuits encoding distracting inputs.

The effects of feature-based attention have been shown to spread across neural populations with different spatial or somatotopic RFs (Martinez-Trujillo and Treue 2004; Schweisfurth et al. 2014; Serences and Boynton 2007) and even across similar features of other sensory systems (e.g., visual and tactile motion) (Konkle et al. 2009). In particular, Schweisfurth and colleagues (2014) had participants perform a tactile task in which they discriminated between bar stimuli with different orientations delivered to their index and middle right fingers. Participants were significantly faster in detecting oriented bars that matched the orientation of the cued stimulus, regardless of whether the stimulus was presented to the cued location or not (i.e., left or right finger). These data indicate that attention biases activity of large numbers of neurons in the population that encodes the relevant features of a task, even neurons whose RF are not colocalized with the spatial spotlight of attention.

Neural Code Mediating Selection of Somatosensory Stimuli

So far we have established that attention influences the firing rates of neurons and the correlated spiking activity between neurons. A major debate in the literature is whether stimulus selection is encoded in the firing rate of a population or the synchronized (or correlated) activity between neurons. Advantages and disadvantages to both types of coding schemes have been discussed (Mazurek and Shadlen 2002; Niebur et al.
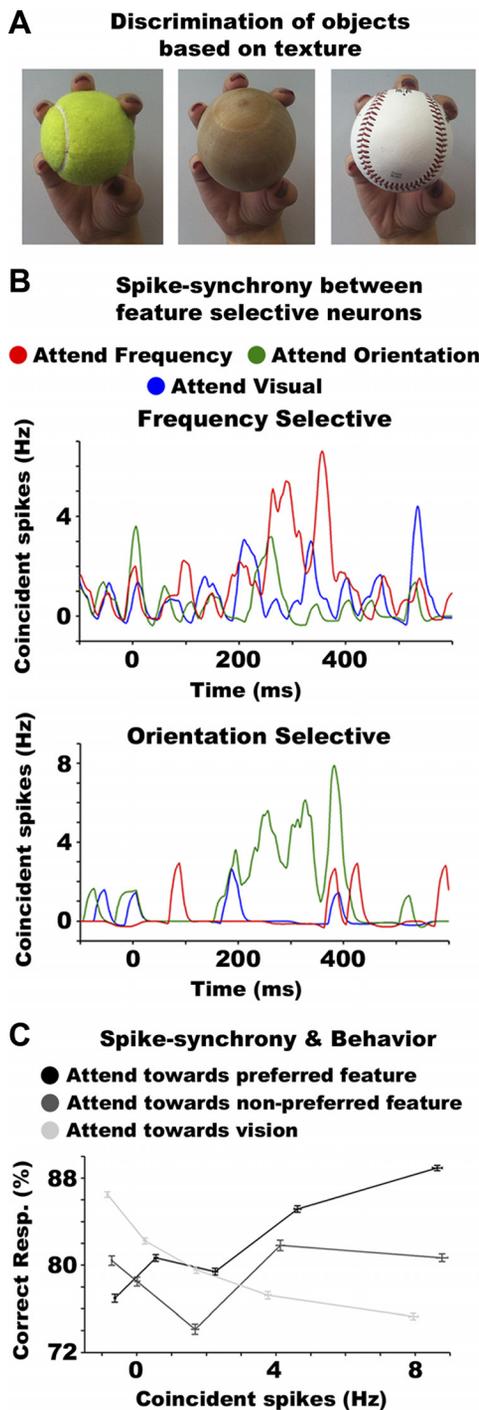
Fig. 2. Feature selection mechanisms in the somatosensory system. A: example of a situation in which tactile feature-based attention is required to recognize and discriminate between objects. All three objects have similar size, shape, and local curvature. To distinguish between them in the absence of visual inputs, one needs to focus on their surface texture. B: instantaneous spike synchrony between two neural pairs selective for frequency (*top*) and orientation (*bottom*) tactile features. Frequency of coincident spikes of both neurons is shown when attention is directed toward the orientation (green lines) and frequency (red) of tactile stimuli and toward visual stimuli (blue). Synchrony due to chance for each attention condition was subtracted using the method by Amarasingham et al. (2012), resulting in below-zero synchrony at certain time points. This also applies to C. A synchronous spike was defined as spikes between two neurons occurring within ± 2 ms. C: percentage of correct responses as a function of spike synchrony between feature-selective neural pairs, for the "attention toward the preferred feature" (solid black trace), "attention away from the preferred feature" (dark gray trace), and "attention toward vision" (light gray trace). The data reveal systematic, but opposite, relationships between spike-synchrony attention effects and behavior for attending toward the preferred feature of cells and attending toward vision. B and C were adapted with permission from Gomez-Ramirez et al. (2014).

1993, 2002; Shadlen and Movshon 1999; Zohary et al. 1994), and some are addressed below.

A firing rate code for stimulus selection functions by raising the gain of a neural ensemble encoding the relevant stimulus. In contrast, in a synchrony code, the correlation between neurons encoding the relevant stimuli is enhanced. One of the main criticisms of the firing rate code is that it may interfere with other neural codes that rely on gain increases to represent information about sensory stimuli. This is shown in the following example: if attention and stimulus intensity both increase the firing rate of neurons, how do downstream neural populations dissociate between a strong unattended and a weak attended tactile stimulus since both would result in a spike train of intermediate firing rate? This ambiguity places significant limitations to the ability of neural populations to convey the behavioral relevance of their signal to other neural ensembles. This suggests that stimulus selection may rely on a different neural coding scheme.

Theoretical and computational studies indicate that spike synchrony can be a powerful mechanism for stimulus selection and perception. In particular, they show that spikes arriving in synchrony in downstream neural ensembles can aggregate and evoke large postsynaptic potentials compared with asynchronous spikes. Synchronized spiking from a neural cohort (e.g., a feature-selective neural population) will thus be weighted with "higher priority" at the downstream target location (Niebur et al. 2002).

Spike synchrony is a different correlation mechanism than spike-count correlation (R_{sc}), also called noise correlations (Bair et al. 2001; Cohen and Maunsell 2009, 2011; Ecker et al. 2010; Mitchell et al. 2009; Zohary et al. 1994). Although both quantify correlated spiking activity between neurons, they do so across different temporal windows and seem to be driven by different sources. In particular, spike synchrony refers to the near-simultaneous discharge of spikes between cells, on a scale of a few milliseconds or less. Furthermore, spike synchrony is thought to arise from a source (or sources) that increase(s) a population's signal-to-noise ratio by promoting the temporal alignment of spikes or raising the membrane potential levels across cells to evoke common spikes across the population. In neural correlation models of attention, this serves to enhance spike synchrony across neurons encoding relevant inputs of the task (Gomez-Ramirez et al. 2014; Steinmetz et al. 2000). In contrast, R_{sc} refers to the trial-by-trial response variability shared between multiple cells to a repeated stimulus. Unlike spike synchrony, R_{sc} does not depend on the strict alignment of interneuronal spiking. Rather, R_{sc} is defined as the covariability between neuronal spiking across large time windows (>100 ms to s). R_{sc} is believed to be deleterious to perception because it makes the readout of a population more difficult by adding common noise and/or redundant information. Thus, as expected, R_{sc} between neurons with a spatial or somatotopic RF over the attended area has been shown to be reduced (Cohen and Maunsell 2009; Gomez-Ramirez et al. 2014; Mitchell et al. 2009; Ruff and Cohen 2014). The opposite is the case for spike synchrony. The relationship between these two correlation mechanisms is not fully understood, but studies show a linear correlation between spike synchrony and R_{sc} based on the stimulus selectivity of neurons (Bair et al. 2001; Gomez-Ramirez et al. 2014).

Conclusions

We reviewed the neural mechanisms of attention in the somatosensory system based on psychophysical and neurophysiological data from humans and nonhuman primates. An overwhelming number of studies show that attention to a particular part of the body enhances the likelihood that stimuli delivered to that location are detected more accurately and faster compared with stimuli presented to other locations. Similar to the visual and auditory modalities, the presence of distracters impairs discrimination of target stimuli at attended locations. This performance deficit decreases as the distance between distracters and targets increases.

Attention effects on somatosensory cells emerge during the early phases of stimulus processing, commencing as early as 55 ms after stimulus onset. The magnitude and prevalence of these effects increase across the somatosensory hierarchy, having greater impact on neuronal responses in SII compared with SI. Spatial selection of tactile stimuli is a neural process that likely precedes feature-based attention mechanisms.

Spatial selection of somatosensory stimuli is based on the interplay between proprioceptive, visual-spatial, and anatomically defined coordinates. Feature-based selection is mediated by modulations of neural populations encoding the relevant features of a task. Stimulus selection (both spatial and feature) appears to be driven by neural mechanisms that leverage the correlated activity within neural populations. In particular, somatotopic selection is mediated, at least in part, by reducing spike count correlations across neurons with similar RFs, whereas feature-based attention in the somatosensory system increases spike synchrony between neurons selective for the attended feature.

These spatial- and feature-based attention mechanisms are controlled by a cross-cortical neural network that is located over frontal and parietal cortices. However, recent studies provide strong evidence that SC neurons (Krauzlis et al. 2013, 2014; Lovejoy et al. 2009; Zenon and Krauzlis 2012) may also play a significant role in this process. Future studies are needed to understand how these higher-order and subcortical areas modulate neural activity in sensory cortices.

AUTHOR CONTRIBUTIONS

M.G.-R. and E.N. conception and design of research; M.G.-R. and E.N. performed experiments; M.G.-R. and E.N. analyzed data; M.G.-R. and E.N. interpreted results of experiments; M.G.-R. and K.H. prepared figures; M.G.-R. and E.N. drafted manuscript; M.G.-R., K.H., and E.N. edited and

revised manuscript; M.G.-R., K.H., and E.N. approved final version of manuscript.

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