The vision of Hsiao on somatosensation

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Flanders M, Soechting JF. The vision of Hsiao on somatosensation. J Neurophysiol 113: 684–687, 2015. First published November 12, 2014; doi:10.1152/jn.00670.2014.—The goal of this review is to start to consolidate and distill the substantial body of research that comprises the published work of the late Professor Steven S. Hsiao. The studies of Hsiao began by demonstrating the receptive field properties of somatosensory neurons, progressed to describing cortical feature selectivity, and then eventually elevated the field to hopes of tapping into natural neural codes with artificial somatosensory feedback. With ongoing analogies to contemporaneous studies in visual neuroscience, the research results and writings of Hsiao have provided the fields of haptics and somatosensory neurophysiology with the conceptual tools needed to allow profound progress. Specifically, Hsiao suggested that slowly adapting tactile form perception could be restored with cortical microstimulation, rapidly adapting slip reflexes should be relegated to low-level, hard-wired prosthetic components, and Pacinian-corpuscle spatiotemporal population responses could potentially be decoded/encoded to provide information about interactions of hands and hand-held instruments with external objects. Future studies will be guided by these insightful reports from Hsiao.

somatosensory; haptics; touch; Pacinian corpuscle; neuroprosthetics

BEGINNINGS

Twenty-two years ago, we (Soechting and Flanders 1992) were neighbors with Steve Hsiao and his mentor in a volume of the Annual Review of Neuroscience (Johnson and Hsiao 1992). In their review, our contemporaries put forward the most lucid description of tactile receptor sensitivities that we have encountered to date, outlining the complementary nature of slowly adapting type one (SAI) afferents (from Merkel complexes), rapidly adapting type one (RAI) afferents (from Meissner corpuscles), and the rapidly adapting signals from Pacinian corpuscles (PC). They explained the preference of SAIs for isolated curves of skin indentation (LaMotte and Srinivasan 1987; Phillips and Johnson 1981) as a mechanical surround-suppression effect (implicitly analogous to the center-surround organization in the visual system) and went on to speculate that the SAI receptor density may be matched to the skin’s low-pass filtering to achieve the best possible spatial resolution. Whereas SAIs specialize in spatial resolution, encapsulated receptor structures make RAIs and PCs selective for higher frequency vibrations, and these latter two groups are complementary to each other in their superficial location/small receptive field size (RA) compared with deep location/large receptive field size (PC). With the example of tool use, Johnson and Hsiao (1992) concisely summarized that SAIs would give a maintained representation of the detailed form of the tool, while RAIs would, with high spatiotemporal fidelity, signal any slippage of the instrument within the hand. The authors envisioned that the population of PCs would transduce spatiotemporal patterns of transmitted vibrations to represent “transient mechanical events that occur at the working surfaces of the instrument” (p. 246). Regardless of whether these words were written by Hsiao or his mentor, this is the vision of somatosensation with which Steven S. Hsiao began his career.

Hsiao’s first publication was momentous (Phillips et al. 1988). In it, the authors used their new technique of characterizing the response of an individual neuron (peripheral or cortical) by generating a spatial event plot (SEP). Figure 1 expands on Fig. 1 from Phillips et al. (1988) to explain the approach. Immobilized monkeys were anesthetized for peripheral recordings but alert for cortical recordings as a mechanical surround-suppression effect (implicitly analogous to the center-surround organization in the visual system) and went on to speculate that the SAI receptor density may be matched to the skin’s low-pass filtering to achieve the best possible spatial resolution. Whereas SAIs specialize in spatial resolution, encapsulated receptor structures make RAIs and PCs selective for higher frequency vibrations, and these latter two groups are complementary to each other in their superficial location/small receptive field size (RA) compared with deep location/large receptive field size (PC). With the example of tool use, Johnson and Hsiao (1992) concisely summarized that SAIs would give a maintained representation of the detailed form of the tool, while RAIs would, with high spatiotemporal fidelity, signal any slippage of the instrument within the hand. The authors envisioned that the population of PCs would transduce spatiotemporal patterns of transmitted vibrations to represent “transient mechanical events that occur at the working surfaces of the instrument” (p. 246). Regardless of whether these words were written by Hsiao or his mentor, this is the vision of somatosensation with which Steven S. Hsiao began his career.

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shifted 0.2 mm along its long axis (i.e., perpendicular to the direction of the scanning movement) so that the neuron’s receptive field (dashed circle) now scanned across the letter on a different row. The SEP in Fig. 1B is constructed so that, within each row, recorded action potentials can be positioned according to the location of the receptive field relative to a raised letter stimulus at the time when they occurred. In this study, there were 64 sweeps across the letter by the receptive field of a somatosensory neuron, resulting in 64 rows of action potentials in the SEP.

Figure 1 of Phillips et al. (1988) exhibited the action potentials of a cortical area 3b SA neuron that always fired when the leading edge of the letter “K” was in its receptive field, and fired with high fidelity whenever a raised portion occupied its receptive field. Figure 2 of Phillips et al. (1988) then revealed that a similarly high spatial resolution was observed in recordings from SAI afferents. We exhibit this phenomenon in Fig. 2 (row 2), which is reprinted from a subsequent study where raised dot patterns (350 µm) were slowly scanned (20 mm/s) and applied with a servo-controlled normal force of 30 g (Connor et al. 1990). As first shown by Phillips et al. (1988), Fig. 2 (row 3) demonstrates that RA afferents also had sufficiently small receptive fields to provide an isomorphic representation of the stimulus pattern. In contrast, PC afferents (Fig. 2, row 4) failed to do so because of their large receptive fields and preferred vibration rates (100–300 Hz) above the speed of the scanned stimuli.

Hsiao and colleagues (Phillips et al. 1988) explained that these SEPs truly represented the response of a single neuron to a stimulus moved across the skin, but also, especially in the case of dense and uniform SAI and RA afferent populations, they could be interpreted as representing the population response, or the “neural image” of the stimulus. They went on to discuss the sensitivities of various somatosensory cortical neurons as a progression from an isomorphic to an abstracted touch representation.

Fig. 2. Example SEPs gathered while grids of 0.5-mm-diameter raised dots were scanned across the distal finger pad of an anesthetized macaque monkey. Row 1 shows the dot spacing (1.3–6.2 mm) of the stimuli. Rows 2 and 3 show that slowly adapting (SA) type 1 and rapidly adapting (RA) peripheral afferents can provide nearly isomorphic neural images of the pattern; row 4 suggests that Pacinian corpuscle (PC) afferents cannot. [Reproduced with permission from Connor et al. 1990, Fig. 4.]
As a sign of the times, this 1988 paper was entitled “Spatial pattern representation and transformation...” similar to our own titles involving sensorimotor transformations (e.g., Soechting and Flanders 1989a, 1989b), where we conceptualized neural processing as occurring in successive stages with information being serially transformed from one stage to the next. The framework laid by Phillips et al. (1988) also broke transformations into sequential stages. They hypothesized that cortical area 3b RA neurons and area 1 neurons may exhibit intermediate representations, much like the hidden units in Zipser and Anderson’s (1988) model of transformation in parietal visual cortex.

FEATURES OF SENSORY RESPONSES

In the 1990’s and beyond, Hsiao and colleagues continued to develop sophisticated methods for precise stimulation (e.g., Lane et al. 2010) and analysis of receptive fields, while their conceptual framework evolved toward feature selectivity and perceptual constancy. The early work on SAI and RA afferents was extended and elaborated by showing the precise features of the stimuli encoded by the afferents, and by deducing that roughness can be encoded by the spatial variations in the firing rate of a population of SAI afferents (Blake et al. 1997; Connor et al. 1990, see Fig. 2). More recently, Hsiao’s former coworker, Bensmaia, further extended this interpretation by showing that the finer features of texture stimuli are represented by spike timing in RA and PC afferents and has emphasized the central convergence of these different types of peripheral afferent inputs (Saal and Bensmaia 2014; Weber et al. 2013).

Just as visual cortical neurons are tuned to the orientations of bars, neurons in primary (S1) and secondary (S2) somatosensory cortex are tuned to the orientation of edges impressed on the hand, a feature extracted from the response of populations of SAI afferents (Hsiao et al. 2002). S2 neurons have receptive fields extending over multiple digits, with markedly similar tuning properties for each finger (Fitzgerald et al. 2004, 2006), facilitating the haptic discrimination of the shapes of large objects. Hsiao and colleagues noted the similarities in orientation selectivity in primary visual and somatosensory cortical areas and suggested that these similarities arose from analogous neural mechanisms in these areas (Bensmaia et al. 2008).

In the visual system, it is well known that the representation of motion is transformed from a representation of the components of a pattern (e.g., the stripes of a plaid) to one of the motion of the entire pattern (the plaid) as one ascends the hierarchy of visual cortical areas (Movshon et al. 1985). Furthermore, this “dorsal stream” transformation evolves gradually over time (Masson and Stone 2002). Hsiao and colleagues discovered an analogous phenomenon in the tactile perception of motion (Pei et al. 2008) and subsequently demonstrated a similar hierarchy in the somatosensory cortical areas (Pei et al. 2011). Neurons in S1 area 3b responded to local (component) motion (analogous to neurons in V1 area 17). However, in S1 area 1, some neurons encoded the pattern motion while others were tuned to component motion or exhibited intermediate characteristics (analogous to the medial temporal visual area).

Ascending the hierarchy of “ventral stream” areas, cortical neurons are tuned to progressively more complex features of contours and objects (cf., Brincat and Connor 2004). In a collaboration of the Hsiao and Connor laboratories, Yau et al. (2009) explicitly tested the idea that there are analogous coding schemes in visual and somatosensory areas. They recorded activity from intermediate visual area (V4) for visual stimuli, and somatosensory area (S2) for tactile stimuli. In each case, monkeys were presented with contours whose directions of curvature were systematically varied. Indeed, they found neurons in both areas that responded briskly to such stimuli and found very similar patterns of tuning in both areas. Thus the concept of hierarchies of feature representation holds well for both vision and somatosensation.

GOALS FOR THE FUTURE

In a recent paper on neuroprosthetics, Hsiao et al. (2011) gave their forecast and recommendations on the prospect of providing artificial somatosensory feedback. Building on decades of his work on feature selectivity, Hsiao predicted that it will eventually be possible, using electrical or optical stimulation in cortex, to find the “natural neural codes” (p. 76) to provide SA-type perception of form. Regarding the restoration of RA-type input, Hsiao et al. (2011) recommended hard-wiring slip reflexes into the mechanical hand itself. The authors reasoned that the user need not be consciously aware of slippage, as long as it is automatically corrected. They compared this to the case of Dr. Strangelove, where the movie character’s funny right hand had a mind of its own. The authors also saw promise in the prospect of tapping into the PC channel, if we can “mimic the temporal pattern of what a PC afferent would have experienced under the same circumstances” (p. 73). The idea is to use the spatiotemporal patterns that naturally arise when a person uses a tool to interact with external objects. In this case, the authors mentioned examples of a blind person using a cane and, more dramatically, Luke Skywalker using his prosthetic hand to wield his lightsaber weapon!

Another current topic that will extend beyond the work of Hsiao is research on spinal circuits, where we are beginning to gain an appreciation for the processing of tactile feedback in the dorsal horn. At the end of their detailed review of peripheral and spinal “touch” representations, Abraira and Ginty (2013) thanked their close colleague Steven Hsiao for his helpful comments on the manuscript. Remarkably, these authors analogized the spinal dorsal horn to the retina, for its complexity and importance in early sensory processing. Indeed, individual peripheral afferent neurons may serve as the first stage of directional feature selectivity (Pruszynski and Johansson 2014). Furthermore, this dorsal-horn spinal circuit may be essential for comparing cortical motor commands with somatosensory feedback during tool use and tactile exploration (Flanders 2011; Weiss and Flanders 2011).

Whereas the pioneering approach of the SEP (Johnson and Hsiao 1992; Phillips et al. 1988) was necessarily done with the hand immobilized, a challenge for future experimentation is to put tools in the hands and let them move freely along surfaces. This future research will be guided by the vision of Hsiao.

GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: M.F. and J.F.S. interpreted results of experiments; M.F. prepared figures; M.F. and J.F.S. drafted manuscript; M.F. and J.F.S. edited and revised manuscript; M.F. and J.F.S. approved final version of manuscript.

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