

Neural basis of haptic perception

Steven Hsiao and Jeffrey Yau

Introduction

A major challenge in neuroscience is to understand the neural basis of behavior. The problem is multifaceted. First one must understand which afferent type(s) and cortical pathways are involved in the aspect of perception that you want to understand. Then one must understand how information is represented and coded in the neural responses. The earliest attempts at addressing the neural pathways underlying perception relied on lesion studies in which animals were trained to perform specific behavioral tasks and then were retested following the ablations. If the animal could not perform the task then the area that was ablated was deemed essential for the behavior. More recently researchers use functional imaging techniques to address these questions. Understanding the neural codes underlying behavior has been elusive. The intellectual breakthrough came from studies that combined psychophysical studies in humans with neurophysiological studies in monkeys [1, 2]. In these pioneering studies, Mountcastle and his colleagues showed that there is a tight correspondence between human vibratory detection and the neural activity recorded in the peripheral afferents of non-human primates. These findings not only demonstrated that the neural mechanisms used by the two species are similar but more importantly provided a scientific approach for studying the neural mechanisms of behavior.

In Goodwin and Wheat's chapter they describe the physiological basis of the peripheral receptor systems that underlie cutaneous perception. However, that is only part of the story. In

addition to the four kinds of mechanoreceptors there are also other receptors that provide information about sensory inputs from the hand. These include receptors specialized for pain (two kinds), temperature (two kinds), itch (one kind) and, as noted by Goodwin, four kinds of afferents that are located in the muscles, tendons and joints that provide information about body position, movement and force. Together these afferents provide a rich multidimensional percept of the size, shape, texture, and temperature of objects that we hold and manipulate with our hands. In this chapter we describe the neural basis of size, shape, and texture perception. We first layout the basic architecture of the somatosensory system and briefly describe the regions of the brain that are involved in haptic perception. Next, we describe neural coding studies of texture and two- and three dimensional form and discuss how these aspects of haptic perception are represented in the somatosensory system. Finally we propose a working hypothesis of how we believe mechanoreceptive and proprioceptive information is integrated to form central representations of three-dimensional shape.

Anatomical basis of haptic perception

As described in the previous chapter, the neural basis for haptic perception begins with the activation of peripheral afferents in the skin, muscles, and joints that provides the initial representation of the external world. There are 13 different kinds of afferent fibers each with specialized receptor endings that allow them to encode information about different sensory inputs from the hand. Eight of the 13 provide information that is impor-

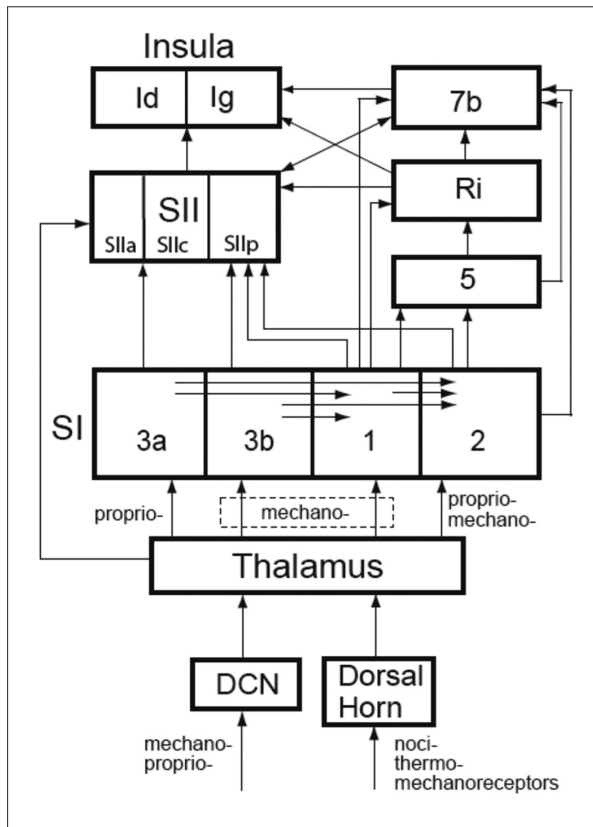


FIGURE 1. BLOCK DIAGRAM OF THE ANATOMICAL AREAS INVOLVED IN HAPTIC PERCEPTION

tant for haptic perception; four of these provide information about discriminative touch (slowly adapting type 1 – SA1, slowly adapting type 2 – SA2, rapidly adapting – RA, and Pacinian – PC) and four provide information about body position and movement (Muscle spindle types 1 and 2, golgi tendon organs, and joint receptors). During normal palpation, all afferent types (except perhaps the pain and itch receptors) are continuously active and provide a dynamic representation of the spatio-temporal profile of stimuli in contact with the skin along with a dynamic representation of the positions, movements, and forces of our limbs, digits and joints [3].

The large diameter A-beta axons initially carry sensory input from the mechanoreceptive and

proprioceptive afferents that innervate the hand to the cortex. The ascending pathway from the hand to cortex comprises three synaptic stages (Fig. 1) that appear to function as relay stations. The cell bodies of the primary afferents, which reside in the dorsal root ganglia send their projections to neurons in the dorsal column nuclei (DCN). Projections from these second-order neurons in the DCN cross the midline at the medulla in a fiber tract called the medial lemniscus and synapse onto type I cells in the ventral posterior lateral (VPL) nucleus of the thalamus. Neurons in VPL then send their projections to neurons in Layers III and IV of primary somatosensory cortex (SI), located in the post-central gyrus on the parietal lobe and to neurons in second somatosensory cortex (SII), located on the upper bank of the lateral sulcus.

VPL is organized as a patchwork of rod like structures that are functionally segregated into a central core region containing neurons that are thought to have cutaneous SA1 like properties. Surrounding the central core is another cutaneous region with neurons that have larger receptive fields that are both slowly and rapidly adapting. Surrounding this region is an outer shell region that contains neurons that respond mainly to deep or proprioceptive input. VPL is the first processing stage where modality information becomes segregated along separate parallel pathways. There have been few neurophysiological studies of the coding properties of neurons in the DCN or VPL; however evidence suggests that there is little convergence or divergence of sensory input at these stages. For example, recently it has been shown that there appears to be a tight correspondence between the firing of neurons in the DCN and their cutaneous and proprioceptive afferent inputs [2, 4, 23]. Those studies show that there is a high efficacy of firing whereby single impulses evoked in peripheral afferent fibers appear to directly generate spikes in target DCN neurons. This suggests that afferent information is faithfully reproduced in the responses of DCN neurons. While similar findings have yet to be demonstrated in thalamic neurons, other studies suggest that neurons in the thalamus have