A Mostly Sure-Footed Account of the Hand

Charles G. Gross and Asif A. Ghazanfar

In one of the first systematic attempts to describe the differences between primates and other mammals, Thomas Huxley argued that the former are distinguished by virtue of their adaptation to arboreal life (1). Central to this arboreal life is the grasping hand. Indeed, the primates are so fundamental to how we define ourselves that some, including Friedrich Engels (2), have claimed that hand use (particularly with tools) was the driving force that gave rise to our sophisticated cognitive abilities. Though this idea is an overstatement, our hands do represent a masterpiece of Darwinian evolution; its elegant design is on a par with the eyes and ears.

What is so special about primate hands? Few, if any, are more qualified to answer this question than Vernon Mountcastle. He and his colleagues have been the leading students of somatic sensibility (“somesthesis”) in primates for over half a century. In The Sensory Hand, he offers an overview of a lifetime of influential, and sometimes controversial, research. The massive treatise begins with a review of the evolution and structure of the hand. Mountcastle then ventures forth on a journey from manual behavior to tactile receptors all the way to the cerebral cortex. Through sixteen lengthy chapters, he reviews each level of the somatosensory pathway in rich detail. To give a sense of scale: there are chapters devoted to “Large-Fibered Peripheral Interface,” “Ascending Spinal Cord Systems of Intrinsic Origin,” “Postcentral Somatic Sensory Cortical Areas in Primates,” and the “Parietal Frontal Sensory–Motor Transition.”

Although the book is large and comprehensive, its intended audience is unclear. Is it meant to serve as a textbook, a critical review, or a theoretical statement? As a textbook, it provides a valuable summary of many aspects of somesthesis. The chapter on the various uses of somatosensory stimulation as a substitute for vision is a particularly welcome treat. However, unlike most modern textbooks, the illustrations are generally poor, usually appropriated, sometimes marginally legible and without adequate legends, and replete with unnecessary and unexplained detail. Some crucial figures—such as one showing the basic features of the hand (e.g., phalanges, metacarpals, and saddle joint)—are entirely absent. In another puzzling aspect of the production, the lengthy reference list includes a number of papers that we could not find mentioned in the text as well as a number of misspellings of author names. Lastly, there is essentially no mention of subjects of great interest to contemporary students (beginning or advanced), such as handedness, gestures, and tool manufacture. Surely handedness is directly relevant to the sensorimotor processing of tactile inputs, given that there is a direct link between lateralized hand use and sensorimotor skill in both humans and chimpanzees and, further, a putative link between these skills and the size of motor cortex. Such a discussion would have played nicely into an otherwise outstanding chapter on cortical plasticity.

As a critical review of exciting developments in the field today or as a theoretical statement, the book is even more deficient. One of the most important recent developments is the discovery by Giacomo Rizzolatti and his colleagues of “mirror neurons,” which respond both when a subject performs an action and when the subject observes the same action performed by another individual. These actions are often specific to particular types of grasping. Existing in humans and nonhuman primates, they are thought to be a neural link in understanding the social intentions of others and, perhaps, imitation and speech perception in humans. Although Mountcastle deals with the anatomy of the premotor area in which these neurons are found (“area F5”) and lists several papers by Rizzolatti’s group on mirror neurons in the references, he never mentions the phenomenon in the text.

In the past, Mountcastle has made strong claims for the existence of “command neurons” in parietal cortex that underlie reaching for visual targets. He hypothesized that these neurons receiveafferent signals descriptive of the position and movement of the body in space and contain a “command apparatus” for operation of the hands, limbs, and eyes within extrapersonal space. He argued that these neurons encode behavioral goals, not the details of their execution. Curiously, Mountcastle does not discuss these earlier claims or the controversy surrounding them, although several of his papers on this subject appear in the reference list. This is unfortunate, because recent work by Rizzolatti and his colleagues (3)—perhaps unavailable when the book went to press—support Mountcastle’s idea, at least in part. Their findings confirm that some parietal neurons have motor functions and encode behavioral goals. However, unlike Mountcastle’s claims, their and others’ results indicate that these parietal cells provide representations of potential actions rather than commands to move.

Another topic currently of major interest is multisensory integration, the phenomenon where neurons respond to more than a single sensory modality. For example, cells in the ventral intraparietal area and ventral premotor cortex respond to both somatosensory and visual stimulation. They have visual receptive fields “attached” to tactile receptive fields on the hand and thus move in space as the hand moves even when the eyes remain stationary. Even in primary somatosensory cortex, neurons can respond to visual stimuli and receive connections from the visual cortex, including the middle temporal (MT) area. Furthermore, tactile object recognition (haptics) by normal human subjects activates a large swath of extrastriate visual cortex. A discussion of these tactile-visual interactions would have led naturally to the last chapter on the haptic sense as a substitute for vision. As presented, readers may incorrectly infer that haptic-visual interactions are solely an adaptive by-product of blindness.

Despite our dismay at the absence or inadequate treatment of certain topics, we find the tome is an otherwise comprehensive compendium of a voluminous amount of data. For the most part, Mountcastle does a masterful job integrating the basics of what we know about how sensory information travels from the hand to the highest regions of the brain. Although there are a few excellent books on the evolution of the hands and how we use them, this is the only sophisticated book on the neural basis of how the hand works. Even with its excessive neuroanatomical detail, The Sensory Hand can serve as a reference for systems neuroscientists in fields outside of somesthesis. As Engels pointed out, “Man alone has succeeded in impressing his stamp on nature … and he has accomplished this primarily and essentially by means of the hand … step by step, with the development of the hand that went that of the brain.” (2). Mountcastle’s book shows us how we are beginning to understand this process.

References

The reviewers are in the Program in Neuroscience, Department of Psychology, Princeton University, Princeton, NJ 08540, USA. E-mail: cgross@princeton.edu; asifg@princeton.edu.