Why the Hand?

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Surely all neuromuscular systems are complex, and complex enough that our understanding of them (e.g., as described in this book) is universally regarded as challenging. Nevertheless the neuro-musculo-skeletal complexity of the human hand has an aura of being somehow different to that of limbs, and somehow vital to our identity as a species. In fact, the naming of our palenteological lineage emphasizes two biomechanical and one cognitive milestone: *homo erectus, homo abilis,* and *homo sapience*, where *abilis* suggests the manual ability for tool making as a critical evolutionary stage. A reasonable question is, therefore, whether and how the neuromuscular control of the human hand is different from other neuromuscular systems in our body, or other species even. This short Introduction attempts to provide a perspective from which to understand the breadth and depth of today's lines of inquiry on the neuromuscular control of the hand. As such, it is incomplete and does not do justice to the many investigators currently working in this field, of which the four chapters of this section are only a small sample. Thus my sincerest apologies to those I do not mention in this short overview. As a form of imperfect excuse, I suggest that a reason why it is impossible to do justice to all investigators and lines of inquiry is because the sensorimotor versatility of the hand spans an uncommonly large number of dimensions. Few other neuromuscular systems in our bodies can claim to being important to our biomechanical, manipulative, perceptual, cognitive, psychological, social, linguistic, and artistic everyday activities.

The role of the hand in the evolution of the physical and cognitive features of our species is a subject of longstanding interest and intense debate (Brand and Hollister 1999; MacKenzie and Iberall 1994; Napier 1956; Tubiana 1981; Winslow 1732; Zancolli 1979 and references therein). Aristotle gives us a synopsis of this debate as far back as c. 350 B.C.E. by saying "...Now it is the opinion of Anaxagoras that the possession of these hands is the cause of

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D. Sternad (ed.), *Progress in Motor Control*,
DOI 10.1007/978-0-387-77064-2_29,

man being of all animals the most intelligent. But it is more rational to suppose that his endowment with hands is the consequence rather than the cause of his superior intelligence." (Aristotle 1911) The debate continues to this day, as exemplified by the work of Mary Marzke (e.g., Marzke 1971; Marzke and Shrewsbury 2006; Wolfe et al. 2006) and Frank Wilson's 1998 book "The Hand: How Its Use Shapes the Brain, Language, and Human Culture" (Wilson 1998). The modern terminology of brain-body co-evolution, while soothing and apparently conclusive, in fact reveals little. There is still much work to be done to identify the features (anatomical and neural) responsible for, and instrumental to, the specific functional features of versatile hand function. For example, it is unclear which anatomical or neural features are unique to the human hand. Of these, which are shared by other species? Are we dexterous because of, or in spite of, these anatomical features of our hands? Or, are we dexterous because of, or in spite of, the information processing capabilities of our nervous system? Answering these questions will enable us to understand the fundamental mechanisms that link developmental, aging or disease processes to manipulation function, dysfunction and its clinical restoration. Moreover, it will also allow us to decide on the most effective biomimetic approaches to build machines that replicate the functionality of the human hand (Murray et al. 1994; Paul et al. 2006; Valero-Cuevas 2005; Valero-Cuevas et al. 2007).

The following four chapters are representative of some approaches centered on neuromuscular science taken to understand hand function. In some of his work Dr. Marc Schieber represents a group of scientists seeking to establish the structure and function of the brain as it relates to hand function in humans and non-human primates (e.g., Kelly and Strick 2003; Lemon and Griffiths 2005; Marder and Strick 2006; Scott 2003; Strick 2002 and references therein). Working within and across species, this group of scientists seek to find the networks of brain structures necessary for hand function, and to develop and test theories of how to restore hand function following neurological diseases and injures (e.g., stroke, cerebral palsy, Parkinson's disease, multiple sclerosis, traumatic brain injury, or even simple aging). An important aspect that Dr. Schieber's work touches upon is the ongoing debate on "synergies." Synergies are thought to be used by the nervous system to simplify the control of numerous muscles by actuating them in task-relevant subgroups (i.e., it is better to control fewer degrees of freedom) (e.g., Bizzi et al. 2002; d'Avella and Bizzi 2005; Soechting and Lacquaniti 1989; Tresch et al. 2006; Weiss and Flanders 2004 and references therein). While many investigators seek to detect and describe such simplifying functional muscle groupings (and how to interpret them reveal the underlying control strategy the brain uses to coordinate muscles), Dr. Schieber points out the importance of the ability of the brain to break and dissolve such patterns of neural synchrony to enable flexible and individuated control of hand muscles (i.e., it is better control more degrees of freedom). He presents these ideas in the context of evidence that neurological diseases often result in the pathological inability to break out of such synergies.

Moving towards the motor system, in some of his work Dr. Marco Santello is representative of a group of scientists who are devoted to understanding the role of the spinal cord (and interactions of the spinal cord with the cortex) in enabling effective control of the limbs (e.g., Mussa-Ivaldi and Bizzi 2000; Ting et al. 1998; Tresch et al. 1999, and references therein). Given the rich connectivity of the spinal cord, and the fact that the α-motoneurons driving the activity of limb muscles reside in the spinal cord, it stands to reason that spinal circuitry is critical to proper hand function. Therefore, hand function in the developing, mature, aging, trained and injured nervous system must also be understood in the context of cortico-spinal and spinal circuits.

Moving towards the periphery, other scientists rely mostly on kinematic and kinetic measurements to infer the organization and nature of hand control - as opposed to relying mostly on direct measurements from the nervous system like EMG or extra cellular recordings (e.g., Cole and Abbs 1988; Cole et al. 1998; Gordon et al. 1991; Hajian and Howe 1997; Hogan 1985; Johansson et al. 1992; Soechting and Flanders 1992; Yokogawa and Hara 2002, and references therein). In some of their work Drs. Latash and Zatsiorsky use measures of finger forces within and across fingers to infer the anatomical and neural connectivity within and among finger muscles. They are members of a community who use kinematic and kinetic data to form and test theories of motor control, specifically in the context of the role of muscle redundancy, abundance and variability. These studies fit within the larger group of investigators asking whether and how the nervous system may "optimize" muscle function in some way (for a review see Todorov and Jordan 2002).

Lastly, my own chapter presents an aspect of my work that is representative of a community that takes a mechanical and mathematical modeling approach to the study of motor control. This approach insists on defining the anatomical and mechanical system that the nervous system controls (e.g., An et al. 1979; Brand and Hollister 1999; Buchholz and Armstrong 1992; Chao and An 1978; Chao et al. 1989; Dennerlein et al. 1998; Hajian and Howe 1997, and references therein). This enables asking questions such as whether and how the nervous system can exploit the inherent mechanical capabilities of the system. This approach also provides a mathematical framework to ask whether and how the musculature of the body is "redundant" (for a commentary on this topic, see Loeb 2000). This framework is critical to forming and testing theories of motor control because it can be easy to misinterpret features of motor control as a choice the nervous system makes, when in reality the mechanical makeup of the musculoskeletal system may require counter-intuitive control strategies (see for example the need to use "extensor" muscles to produce pinch force Valero-Cuevas et al. 1998). This chapter also highlights how some anatomical features of the hand such as the extensor mechanism and the multiarticular nature of all finger muscles lead to important features in the control of the hand.

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