

## Human Hand Function: The Coupling of Sensory and Motor Systems

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From an evolutionary perspective the hands of primates are often considered the “absolute bedrock of mammalian primitiveness” with a skeletal structure that changed little over 65 million years. The hand evolved relatively early with capabilities that preceded the development of the cerebral structures required to make use of its potential. The importance of the evolution of cortical neuronal hardware that processes incoming sensory information from the hand and via corticospinal neurons directly controls movements of the fingers cannot be underestimated in analyzing the versatility of primate hands. One major evolutionary change that resulted in a remarkable increase in the functionality of the hand was the development of the opposable thumb. Opposition involves flexion, abduction and medial rotation of the thumb so that the top of the thumb can make contact with the tips of the fingers. This movement is essential for exploring and manipulating objects and in the absence of the thumb, for example following amputation, it is estimated that the hand loses 40% of its functional capacity. The extensive area of contact between the pulps of the thumb and index finger is a uniquely human characteristic that reflects the more distal position of the thumb and its longer length relative to that of the index finger. Another feature of the human hand that distinguishes it from other primate hands is the presence of rough horseshoe-shaped tuberosities on the distal phalanges to which the soft tissues of the palmar pads are attached. These pads facilitate the distribution of pressure during grasping and allow the fingertips to conform to uneven surfaces. Further evidence of the specialization of the hand comes from the relative mass of the musculature devoted to the thumb, which makes up about 39% of the weight of the intrinsic muscles within the hand.

Human dexterity has been studied experimentally from a number of perspectives ranging from detailed analyses of the sensorimotor control involved in object manipulation, to kinematic studies of skilled activities such as typing and piano playing. The manipulative skill of the human hand is most apparent in the tight coupling that occurs between the motor and sensory systems when the hand reaches and grasps an object. Within 70 ms of contact, the forces used to grasp an object are modified by feedback from mechanoreceptors in the skin. Numerous studies have recorded grip forces as the index finger and thumb grasp and lift an object and shown how these forces vary as a function of the geometry and weight of the object, the shape and texture of the contact surface, and the friction between the hand and the object. The crucial role played by cutaneous mechanoreceptors in the modulation of grip forces has been highlighted in microneurographic studies in which the activity of isolated tactile afferent fibers is recorded as people grasp and lift objects. These experiments show that tactile afferents encode the timing, magnitude, direction and spatial distribution of fingertip forces, and the friction between the skin and object. When these inputs are eliminated following local anesthesia, the hand is unable to compensate rapidly as an object slips between the digits, and grip forces are considerably larger than those used normally. In addition, the predictive control of grip force based on previous experience is impaired when the expected sensory feedback is not available.

Kinematic analyses of more complex manual tasks such as typing and piano playing have offered insight into the internal representation of motor activities and have shown that muscles controlling movements of the fingers are not controlled independently. Although keyboard tasks are often thought of as serial activities, analyses of the sequencing of finger movements indicate

that there is an anticipatory component to performance particularly when consecutive keystrokes are executed by different hands. Skilled typists commit themselves to typing a particular letter approximately three characters in advance of the current keystroke and can visually process up to eight characters in advance of the character being typed. For expert typists, the interval between successive keystrokes is typically 100-200 ms, but intervals as short as 60 ms are not infrequent. Piano playing and sending Morse code are performed at rates comparable to those reported for typing. Experienced Morse code operators can send code at a rate of 20-30 words per minute, and at faster tempos the inter-note intervals of pianists are often 80-100 ms, and for brief periods of time, such as when playing trills, they can produce 20-30 notes per second. The similarity in peak movement speeds recorded from skilled typists and pianists suggests that they are performing near the mechanical and neural limits of the human hand.

Skilled manual activities rely on sensory feedback from cutaneous, muscle and joint mechanoreceptors for successful execution. The ability to perceive finger movements and sense the position of the fingers is not limited to a single class of receptor, but is derived from a number of redundant sources. In muscle, spindle receptors respond to changes in muscle length, with spindle primary afferents being more sensitive to the velocity of muscle contraction and secondary afferents displaying much greater position sensitivity. The discharge rates of these receptors are not simply a function of changes in muscle length, but also reflect the activity of their own motor innervation, called the fusimotor system, which can regulate the sensitivity of muscle spindles. To decode signals from muscle spindle afferents the central nervous system must have access to information regarding the level of fusimotor activity to distinguish between afferent discharges that are proprioceptively significant from those that are the result of fusimotor activity. Mechanoreceptors (SA II) in hairy skin also discharge in response to finger movements which typically stretch the loosely connected skin on the dorsum of the hand; the majority of these receptors respond to movements of more than one joint and so the information that they provide the CNS is ambiguous with respect to movement direction and amplitude. However, the ensemble response from a population of SA II receptors can probably provide a population vector that differentiates individual finger movements.

In contrast to the tactile sensory system in which higher densities of mechanoreceptors are associated with superior tactile acuity, higher spindle densities do not appear to be associated with superior sensory acuity. For the muscles of the hand, the number of spindles has been estimated to vary from 12 to 356. There is no evidence indicating that the detection of movements or changes in limb position is superior as one goes from proximal to distal joints, and when expressed in terms of the absolute angular rotation of the joint, the ability to detect movements is better at more proximal joints such as the elbow ( $0.08^\circ$  at  $20^\circ/\text{s}$ ) than the distal joints of the hand ( $0.88^\circ$  at  $20^\circ/\text{s}$ ). The superior performance of more proximal joints is not surprising, as they move more slowly than distal joints and rotation of these joints results in a larger displacement of the end-point of the limb than the same angular rotation of a distal joint.

The forces generated by muscles are sensed by Golgi tendon organs normally found at the junction between muscle tendon and a small group of muscle fibers. These receptors are less numerous than spindle receptors and some muscles of the hand do not appear to have any tendon organ receptors. Results from a number of experiments suggest that the perception of force is derived from internal neural correlates of the descending motor command, and that peripheral feedback calibrates these signals to indicate whether the motor command is adequate for the task. Collectively, peripheral receptors together with central feedback systems provide the information required for the dexterous performance of the hand.