Hand function: peripheral and central constraints on performance

Marc H. Schieber¹ and Marco Santello²

¹Departments of Neurology and of Neurobiology and Anatomy and Brain Injury Rehabilitation Program at St. Mary’s Hospital, University of Rochester School of Medicine and Dentistry, Rochester, New York 14642; and ²Department of Kinesiology and The Harrington Department of Bioengineering, Arizona State University, Tempe, Arizona 85287

Schieber, Marc H., and Marco Santello. Hand function: peripheral and central constraints on performance. J Appl Physiol 96: 2293–2300, 2004; 10.1152/japplphysiol.01063.2003.—The hand is one of the most fascinating and sophisticated biological motor systems. The complex biomechanical and neural architecture of the hand poses challenging questions for understanding the control strategies that underlie the coordination of finger movements and forces required for a wide variety of behavioral tasks, ranging from multidigit grasping to the individuated movements of single digits. Hence, a number of experimental approaches, from studies of finger movement kinematics to the recording of electromyographic and cortical activities, have been used to extend our knowledge of neural control of the hand. Experimental evidence indicates that the simultaneous motion and force of the fingers are characterized by coordination patterns that reduce the number of independent degrees of freedom to be controlled. Peripheral and central constraints in the neuromuscular apparatus have been identified that may in part underlie these coordination patterns, simplifying the control of multi-digit grasping while placing certain limitations on individuation of finger movements. We review this evidence, with a particular emphasis on how these constraints extend through the neuromuscular system from the behavioral aspects of finger movements and forces to the control of the hand from the motor cortex.

finger; cortex; motor; muscle; tendon

THE HAND REPRESENTS AN EXCELLENT model in which to study one of the most intriguing issues in motor control: simultaneous control of a large number of mechanical degrees of freedom. The complex apparatus of the human hand is used both to grasp objects of all shapes and sizes through the linked action of multiple digits and to perform the skilled, individuated finger movements needed for a large variety of creative and practical endeavors, such as handwriting, painting, sculpting, and playing a musical instrument. A key feature of such tool use and manipulation is the ability to control fine movements and forces at individual fingers. This ability to individuate movements of particular fingers from the more fundamental multidigit closure of grasping has evolved to attain the variety of performance found in the human hand. In this evolutionary development toward increasing independence of the digits, the central control of the digits necessarily has progressed in parallel with changes in the peripheral neuromuscular apparatus. Nevertheless, even in the most sophisticated behaviors, the fingers do not move independently. Constraints in both the peripheral apparatus and its central control, although simplifying the control of multidigit grasping, also keep the fingers from acting completely independently. These constraints reflect two aspects of human hand use. First, most daily use of the hand is for grasping; second, even performances as sophisticated as playing the piano require only that one finger move more than the others. Although these constraints might appear to be vestiges of evolution, their continued presence ensures efficient control of the large number of degrees of freedom during the more frequent and fundamental uses of the hand. Control of the hand from the motor cortex can achieve a high-level performance during both multidigit grasping and single-digit movements even with these apparent limitations.

HAND BEHAVIOR

Hand use can be divided broadly into tasks requiring the use of multiple digits simultaneously in a grasp or the use of individuated movements in which one digit moves considerably more than other digits. The ability to make such varied use of the hand appears relatively late, both in evolution and in individual development. The appearance of multidigit grasping is followed by the appearance of individuated finger movements. Studies that have characterized the simultaneous motion or force production of the fingers indicate that, in grasping, the joints of multiple fingers are constrained to move or exert force in a relatively small number of coordination patterns (or “synergies”). Performance of more selective finger movements requires additional control to individuate the motion or force of particular digits.

Development of finger movements. Phylogenetically, although many amphibians and reptiles have forepaws with multiple digits, use of the hand for grasping appears only in mammals. Rats and cats adapt the orientation and shape of
their forepaws when holding food (28, 97) but cannot grasp objects firmly without the use of both forepaws; they also do not use movements of single digits. Monkeys are able to grasp objects firmly with a single hand and can also wrinkle small objects from a narrow hole using relatively independent movements of a single finger (48); however, monkeys neither show the variety of grasps (58) nor the sophisticated use of individuated finger movements observed in humans. A longer thumb relative to the length of the fingers and an ability to arch the palm of the hand are some of the most important anatomic differences underlying the more extensive range of grasp behavior found in humans (54).

Similarly, during human development, individuated movements of the fingers become superimposed on more fundamental grasping movements. Reflexive closure of the entire hand, which is present at birth, is followed by voluntary grasping at 2–3 mo of age. Thumb opposition and finger individuation start to appear at 10–12 mo, and further development of fine coordination between fingers, as well as between hand shaping and reaching, evolves throughout the first decade of life (27).

Multidigit coordination for grasping. Although primates have developed the ability to use individuated movements of single digits in special situations, most behavioral use of the hand, even in humans, entails simultaneous motion of multiple digits for one purpose: grasping. Although the final postures of the fingers as they are arrested at the surface of a solid object obviously conform to the shape of the object, the movements that close the fingers around an object in a coordinated fashion actually start long before contact. During reaching movements directed to objects with different shapes, the fingers move so as to gradually preshape the entire hand to approximate the object contours as the hand approaches (55, 73). Preshaping is affected little if at all by the removal of continuous vision of the hand and/or the object, indicating that stored information about the object is used to shape the hand in flight (69, 71, 75, 99). This simultaneous motion at all digits is characterized by consistent covariations in the simultaneous angular excursion at multiple finger joints (71); these covariation patterns are common to all subjects and are found across a large variety of object sizes and shapes. Similar kinematic coordination patterns have also been found when subjects were asked to mould their hand to the shape of the object without reaching (70, 72), although the extent to which hand shape resembled object shape was lower than when hand shaping occurred in a more natural fashion during the reach (73).

The coordination patterns used consistently during grasping have been examined with multivariate statistical techniques (71). Remarkably, only a small number of statistically identified kinematic coordination patterns [principal components or eigenpostures (55)] are required to reconstruct a large variety of natural hand postures. The hand coordination patterns found in grasping tasks seem to be organized along a gradient from lower to higher finger movement individuation. The lower order components are characterized by covariation in the motion at the metacarpophalangeal and proximal interphalangeal joints of all the fingers (70, 71, 89), which reflects the entire hand opening and closing as a unit. The higher order principal components represent coordination patterns needed to make fine adjustments of hand shape. Such observations of consistent coordination patterns across multiple finger joints, both within and across fingers, indicate that the number of independent degrees of freedom actively controlled during natural grasping is significantly lower than the available number of mechanical degrees of freedom. The kinematic coordination patterns revealed by multivariate statistical techniques, which reflect the net result of complex interactions between the simultaneous activation of many hand muscles and hand biomechanics, therefore may represent an important simplification of the computational processes needed to scale the entire hand shape to object geometry for grasping.

Once the hand is actually grasping an object, consistent coordination patterns also appear to characterize the control of grip forces, regardless of the number of digits used. During two-digit grasping, forces at the two digits normal and tangential to the object surface are finely coordinated throughout object lift and hold to maximize grasp stability (36). During grasping of vertically oriented objects with three digits, grasp stability is maintained by the constraint of the direction of forces toward the center of the object despite changes in object weight, roughness of contact surfaces, and finger combination (9, 23). In such a tripod grasp, the force exerted by the thumb is directed to a point approximately midway between the fingers despite changes in finger force directions induced by different configurations of the contact surfaces (2).

The temporal relationships between normal forces exerted by pairs of digits are also characterized by consistent coordination patterns; i.e., forces are synchronized across a variety of grasping task conditions (61–63, 74). However, these force synchronization patterns do not seem to be obligatory. Fingertip forces can be decoupled when required, as when one finger is released from an object during grasp (74). Furthermore, during multidigit force production without grasping, temporal relationships between pairs of fingertip forces are weaker than when forces must be coordinated to prevent object slip while holding an object (61).

Additional features of the organization of force coordination patterns have been revealed through analysis of the structure of the variability of individual finger forces when subjects hold an object vertically. When all digits are engaged in object lift and hold, subjects tend to use a few, repeatable force-sharing patterns (i.e., distributions of total force across the different digits) despite the large number of patterns that would satisfy the conditions of force and moment equilibrium (74). The force-sharing patterns employed during grasping appear to optimize control of certain higher level task parameters, such as grip force or hand torque, by constraint of the theoretically available variability in the forces exerted simultaneously by different fingers (52, 86, 100). Analysis of the structure of the variability of individual finger forces relative to the net rotational moment, for example, suggests that much of the apparent variation in individual finger forces is controlled actively across multiple digits to minimize the rotational moment of the hand about its longitudinal axis and stabilize the object held in the vertical (roll) dimension (47). Actions involving multiple digits could be controlled more efficiently by mechanisms that employ such hierarchical control strategies to take advantage of simultaneous action at several digits rather than by mechanisms that control each digit independently (51).

Individuated finger movements. In multidigit grasping, the coordination patterns that simplify the simultaneous control of numerous redundant degrees of freedom in the joints and/or muscles are supplemented by some degree of individuation.
Some degree of finger individuation during grasping enables the hand to form to a specific object shape and permits some fingers to be lifted off the object while maintaining a stable grasp. During other types of hand use, such as tying a knot or fine manipulation of a small object, finger movements are individuated considerably more, although multiple fingers still tend to move together. Even during sophisticated tasks such as typing and piano playing, which typically are conceptualized as sequential movements of single fingers, kinematic studies have revealed that all the fingers of the hand are in motion simultaneously at the time of individual keystrokes (18, 22, 24, 89). Elegant performance is achieved nevertheless because these tasks require not that only one finger move but instead that one finger move enough to strike the intended key while the other fingers move little enough not to strike any unintended keys. Similarly in finger spelling, although some digits move together, information can be transmitted clearly by the configurations of certain critical digits (35).

As in grasping, multivariate statistical analyses have shown consistent coordination patterns in the simultaneous motion of multiple digits during piano playing (16), typing (20, 25, 26, 68, 69), and finger spelling (34, 35). As in hand shaping for grasping (see above), adjacent digits tend to be more highly correlated than nonadjacent digits. Interestingly, in typing, the correlation in the movement of pairs of fingers does not seem to be obligatory, as the correlation between fingers is weaker when one of the fingers is used to press the key than when neither finger of the pair is acting on a key (22). This implies that neural control allows adjacent fingers to move together when they are not acting on keys but actively dissociates them when one must act without the other.

Even when subjects are not asked to perform a natural or trained behavior but instead are asked explicitly to move a single digit or to exert force voluntarily with a single digit, motion or force occurs at other digits as well (64, 102). In both monkeys and humans, the thumb and the index finger have the greatest degree of independence in such tasks, whereas the middle and ring fingers have the lowest (29, 77). Humans, however, show a higher degree of movement individuation than that observed in monkeys.

When human subjects are asked to exert maximal voluntary force with one digit, the forces produced unintentionally by fingers not explicitly involved in the voluntary task (termed “force enslaving”) can reach amplitudes up to 50% of the force produced by the instructed digit (101, 102). In an experimental protocol designed to dissociate, as far as possible, the action of superficial extrinsic flexors, deep extrinsic flexors, and intrinsic hand muscles, force enslaving was similar regardless of the muscle groups involved (102), suggesting that force enslaving cannot be ascribed solely to biomechanical constraints (such as mechanical coupling between the muscles acting on different digits, which is stronger for the extrinsic muscles). Instead, it must have some origin in the neural control of the hand. Interpretation of the similarity in the magnitude of force enslaving across extrinsic and intrinsic conditions is complicated, however, by the possibility that both sets of muscles were coactivated in all experimental conditions. Indeed, electromyograph (EMG) studies of hand muscles during force-production tasks have shown that significant cocontraction of extrinsic and intrinsic hand muscles does occur during single fingertip force production (57, 94).

Control of force at a single fingertip. The problem of multiple, potentially redundant degrees of freedom appears again in the muscular control of force at a single fingertip. Because many intrinsic and extrinsic hand muscles insert on each digit (e.g., 7 muscles acting on the index finger), the contribution of each muscle to the net force exerted at a given fingertip could vary substantially, both from trial-to-trial and when scaling fingertip forces to different magnitudes. This raises the question of whether individual hand muscles are activated independently or together as functional units, which has been tested experimentally by correlating the level of EMG activation of pairs of muscles when scaling fingertip force. During force production in precision grip, although the muscles were not found to be activated completely independently of each other, correlations in both the temporal and spatial domains described initially were weak and highly variable, both within and across subjects (53). In other words, the EMG amplitude of a given hand muscle was not constrained to covary consistently with the EMG amplitude of other hand muscles, suggesting that subjects may not rely on repeatable patterns of hand muscle activation.

Subsequent studies of EMG activity during precision grip, however, reported contrasting results. Maximal index fingertip forces were measured in four directions (i.e., flexion, extension, abduction, and adduction), isolating specific force components associated with EMG patterns in the amplitude domain. This revealed subject-independent EMG amplitude patterns in the intrinsic and extrinsic hand muscles for all force directions, patterns that were repeatable across trials (94). Similar results were obtained in a submaximal force-production task (92). Interestingly, the relative activity among contributing muscles did not change when fingertip force magnitude was modulated across the submaximal voluntary force range. Hence, the apparent redundancy of many equally valid solutions (i.e., muscle activity patterns) for the production of fingertip forces becomes reduced to a single, specific ratio of muscle contractions constraining multiple muscles to act together as a unit when precise control of force direction is required. The unique ratio of activity in multiple muscles used to exert varying levels of precisely directed fingertip force might appear to contradict other evidence that highly individuated movements reflect a greater variety of coordination patterns. Even when precisely directing fingertip forces, however, any change in finger joint angle will require a corresponding change in the ratio of muscle activity.

To summarize, most of the time, the human hand is used for grasping objects. In grasping, a number of coordination patterns have been identified that might simplify the control of the large number of mechanical degrees of freedom and muscles of the hand. These coordination patterns emerge as kinematic and kinetic relationships among the simultaneous motion and/or force of multiple fingers, ensuring that the fundamental task of grasping can be performed simply, frequently, and reliably. As the hand is used for increasingly fine manipulation and as more and more fine finger movements are considered, the need for independent control of individual degrees of freedom increases. Each degree of freedom becomes necessary for some particular manipulative finger movement. Higher order principal components are needed to describe the increasingly individuated motion of the fingers, and a limited set of coordination patterns constraining the behavior of multiple degrees of freedom becomes less helpful as a control strategy. The same
underlying constraints that are important for simplifying the control of fundamental multidigit grasping may then limit the independence of the fingers in fine, manipulative performance, whether the constraints arise biomechanically in the peripheral apparatus or through neural control.

CONSTRAINTS ARISING IN THE PERIPHERAL APPARATUS

To what extent does the simultaneous motion of multiple fingers result from biomechanical constraints in the periphery? The fingers are coupled to a measurable degree by a number of biomechanical factors. Some degree of mechanical coupling between adjacent digits is produced by the soft tissues in the web spaces between the fingers (95). Additional coupling is produced by interconnections between the tendons of certain muscles. In humans, the juncturae tendinum between the different finger tendons of extensor digitorum communis (EDC) are well known (96), although a recent study that used intramuscular electrical stimulation indicates that, under typical conditions, the juncturae of EDC may transmit relatively little tension from one tendon to another (39). The tendons of flexor digitorum profundus (FDP) to the four different fingers are also interconnected in the palm, both by thin sheets of inelastic connective tissue and by the origins of the lumbrical muscles (19). In macaque monkeys, these interconnections between the tendons of multitendoned muscles are more pronounced than in humans (85). In the macaque FDP, tendon interconnections have been shown to cause tension exerted at one point on the proximal aponeurosis of the insertion tendon to be distributed to the distal insertions on multiple digits (82). Such species differences in the biomechanical coupling between tendons to adjacent fingers contribute to greater ability of humans to individuate their finger movements and forces.

The multitendoned extrinsic finger muscles (flexor digitorum superficialis, FDP, and EDC) present another potential form of biomechanical coupling. If single motor units have muscle fibers that insert on tendons to adjacent digits, then these motor units will act on both digits simultaneously when they contract. In macaque monkeys, another multitendoned muscle, extensor digiti quinti et quinti, has a significant fraction of single motor units that act on both the ring and little finger tendons (81). In humans, the homologous muscle, extensor digitii quinti, has no tendon to the ring finger and acts exclusively on the little finger, eliminating any coupling that might be produced by motor units acting on both tendons. However, in other human multitendoned muscles, including FDP and EDC, the contraction of many single motor units is statistically associated with a rise in force on more than one finger (39, 41). The extent to which the multidigit effects of these motor units result from physical distribution of tension to adjacent or interconnected tendons vs. synchronized contraction of two motor units each acting on a single digit is presently the subject of active investigation.

CONSTRAINTS PRODUCED BY INNERVATION OF SPINAL MOTONEURON POOLS

Short-term synchronization that may functionally couple motor units acting on different digits can be found between many but not all pairs of motor units in the same muscle or in different muscles (6, 31). The two motor units of a synchronized pair discharge more action potentials within a few milliseconds of one another than can be accounted for by chance alone, implying that the two motor units receive a common neural input that excites the two simultaneously. For two motor units in the same muscle, synchronization can be attributed to axons that ramify within the spinal motoneuron pool, synapsing on multiple motoneurons serving the same muscle. Synchronization between muscles acting on different fingers or between motor units in regions of multitendoned muscles serving different fingers, however, indicates that single premotor input neurons make connections to motoneuron pools or subpools that act on different fingers. These diverging premotor input neurons may produce part of the “spillover” that causes adjacent fingers to move when a normal subject voluntarily moves a given finger. Indeed, EMG studies have shown that, during flexion of a given finger, EMG activity appears not only in the region of FDP acting on that finger but also in regions acting on adjacent fingers (40, 66). Theoretically, the premotoneurons responsible for short-term synchronization of motor units could be any last-order inputs to the motoneuron pools, such as IA afferents, spinal interneurons, or corticomotoneuronal axons. In humans, lesions of the corticospinal system eliminate the majority of short-term synchronization between motor units, implying that most of the synchronizing input comes from the cortex itself (14, 20).

Ongoing investigations of between-compartment motor-unit synchronization suggest possible differences in the organization of common inputs to the multitendoned finger flexors vs. extensors, which might in part reflect differences in their functional roles in manipulative actions. Between-compartment synchronization of motor units in EDC is weaker than within-compartment synchronization, indicating that common inputs are stronger to motoneurons acting on the same digit than those common inputs that diverge to motoneurons acting on different digits (38). In FDP, however, during a force-production task, the strength of synchrony between motor units belonging to the same compartment is similar to that found between adjacent compartments but greater than the strength of synchrony between motor units in nonadjacent compartments (e.g., index-little or index-ring) (65). These observations suggest that last-order inputs may constrain FDP, more so than EDC, to act to some degree simultaneously on adjacent fingers.

This trend in FDP was not as clear, however, when fingertip forces were required to prevent object slip during multidigit grasping (98). Indeed, because short-term synchronization reflects the pattern of active last-order inputs to motoneuron pools, synchronization might be expected to vary depending on the task being performed. When finger forces were exerted in different directions, short-term synchronization differed for motor unit pairs within the same intrinsic hand muscle as well as for pairs having one motor unit in each of two different intrinsic muscles (5). Similarly, higher degrees of synchronization have been observed during power grip than during precision grip, suggesting that power grip involving the entire hand might benefit from a common action at all fingers facilitated by motor unit synchronization, whereas precision grip would require a higher degree of independence in the movement of individual fingers and therefore less synchronization (30).

STABILIZING CONTRACTIONS

Because of both the biomechanical coupling between digits produced by the peripheral apparatus and the neural coupling
arising from divergent last-order inputs to motoneuron pools, muscle activity intended to move one digit will tend to move adjacent digits as well. To move one digit more individually, additional muscles may be activated to check the coupled motion of the adjacent digits. Such stabilizing contractions have been observed in the EMG activity of finger muscles in both monkeys and humans. When a monkey flexes its little finger, for example, extensor digiti secundi et tertii contracts to minimize simultaneous flexion of the index and middle fingers (78). In humans, the portion of FDP that acts chiefly on the middle finger contracts as the subject extends either the index or the ring finger, apparently to minimize coupled extension of the middle finger (66). The combination of contractions that move the intended finger(s) and that stabilize other fingers to minimize unintended motion in other digits requires descending neural control more complex than alternating activation of agonists and antagonists.

CONTROL OF THE HAND FROM THE MOTOR CORTEX

The primary motor cortex (M1) and its descending projection to the spinal cord in the corticospinal tract (CST) are crucial for the normal control of hand and finger movements. In humans, lesions of these neural structures result in the syndrome of hemiparesis, in which voluntary effort produces sluggish, weakened movements. In addition, hemiparetic movements are less individuated. Attempts to move or exert force with a single finger result in simultaneous action of all the fingers, and attempts to grasp an object with the hand may result in simultaneous motion at the elbow and shoulder (8, 46, 50, 91). In monkeys, CST lesions produce a more transient weakness, although a persistent inability to perform fine, relatively independent finger movements also occurs (49). Similar deficits are observed temporarily during reversible inactivation of the monkey M1 hand representation (7, 44, 84). These observations suggest that noncorticospinal descending pathways are capable of generating more rudimentary, less individuated movements, whereas the output of M1 normally acts, largely via the CST, both to facilitate contraction of those muscles actively generating the intended movement and to suppress unintended motion of other body parts. In this respect, M1 somehow reduces constraints, acting to fractionate the more limited set of coordination patterns that can be produced by other parts of the nervous system (76).

The organization of M1, with both divergence and convergence of its corticospinal output, provides a neural substrate for the control of such complex movements. Many M1 neurons have outputs that diverge to innervate the spinal motoneuron pools of several forearm and intrinsic hand muscles (10, 21, 87, 88). Spike-triggered averaging of EMG activity shows that M1 neurons may have either facilitatory or suppressive effects on the motoneuron pools of different muscles. (Because M1 output neurons all are excitatory, suppressive effects on motoneurons are exerted via inhibitory interneurons.) Some M1 neurons that project to wrist and finger muscles also produce effects in elbow and/or shoulder muscles (56). Single M1 neurons thus may influence the activity of multiple muscles used simultaneously in a particular task. Indeed, small groups of M1 neurons with outputs to similar sets of muscles are found close to one another (12, 13) and may show increased synchronization with one another (33). Via their monosynaptic connections to spinal motoneurons, such M1 neurons may produce much of the short-term synchronization between motor units described above.

These corticomotoneuronal connections that diverge from single M1 neurons to innervate multiple motoneuron pools thus may appear to constrain the independence of activity in different muscles. How then could M1 act to provide increased individuation of finger movements? Divergent corticomotoneuronal output connections would reduce independence if only a limited number of output patterns to various sets of muscles were present. Such might be the case in lower mammals, such as rats and cats. As nonhuman primates and humans evolved, however, different M1 neurons may have dropped their output connections to different muscles, resulting in an extremely large variety of different muscle combinations controlled by various M1 neurons. Such a wide variety of available output combinations would permit extensive individuation of finger movements and forces when needed.

Besides having divergent outputs, M1 neurons that provide input to any given muscle are distributed over a relatively large cortical territory (typically a few millimeters in diameter in nonhuman primates) (45), and the territory providing input to one muscle overlaps extensively with the territory providing input to other muscles (1, 16). Because outputs to a given muscle converge from an extensive M1 territory, because outputs from single M1 neurons diverge to multiple muscles, and because peripheral constraints require stabilization of other digits during individuated movement of a single digit, active neurons are found throughout the M1 hand representation when any single finger is moved, and similar territories are activated for movements of different fingers. In monkeys, single M1 neurons discharge in relation to multiple finger and wrist movements (83). Often, a given neuron discharges in relation to movements of nonadjacent digits. The distribution of neurons active during movements of particular digits gives little if any evidence of somatotopic segregation of neurons controlling different digits. Horizontal intracortical axon collaterals that interconnect the entire M1 hand representation (32), therefore, may coordinate the necessary pattern of outputs to multiple muscles simultaneously. Similarly in humans, functional magnetic resonance imaging shows that a similar cortical territory is activated no matter which digit is moved (68). In humans, however, subtraction of the widespread activation common to all finger movements leaves a remainder of specific activation for each digit; this remainder shows some degree of somatotopic segregation for movements of different digits (3, 43).

A somewhat greater somatotopic gradient of digit representation in human M1 than in macaque M1 is suggested as well by the effects of lesions. In macaque M1, partial inactivation of the hand representation impaired some finger movements and not others, but adjacent fingers were not affected more readily than nonadjacent fingers, and the finger movements that were affected were not systematically related to the mediolateral location of the inactivation (84). In humans, however, small strokes can impair the thumb and index finger more than the little and ring fingers or vice versa (79). Moreover, the thumb and index finger are impaired more severely by more lateral lesions, and the little and ring fingers are more impaired by more medial lesions (42). These lesion studies, as well as the studies of neural activity described above, thus suggest that a somatotopic gradient of digit representation, with the thumb...
represented more heavily laterally and the little finger represented more heavily medially, is present in the human M1 but is not so evident in the macaque M1 hand representation. This species difference in M1 parallels the other species differences described above: humans can produce more highly individuated finger movements than macaque monkeys and have less biomechanical coupling between the digits. Together, these observations suggest that evolution of more highly individuated finger movements, resulting in part from evolution of more mechanically independent digits (reducing the need to stabilize other digits during individuated movement of a given digit), has proceeded in parallel with evolution of somatotopic gradients of digit representation in the human M1.

Divergence of output from single M1 neurons to multiple muscles, convergence of output from large cortical territories onto individual muscles, horizontal interconnections, and widespread activation in the M1 hand representation during movement of a single finger all constrain the degree to which the control of finger movements can be explained by selective activation of somatotopically organized regions of cortex. Although not somatotopically organized to represent different fingers, M1 neuronal populations do transmit firing rate information specifying which finger movement is made. Population analyses that used population vector or logistic regression approaches have shown that the discharge of M1 neurons transmits information that specifies which finger movement will be performed (4, 25). Without being arranged somatotopically, how could a population of M1 neurons generate the various patterns of concurrent activity in multiple muscles needed to produce specific finger movements?

One possibility would be that groups of similar neurons controlling particular movements or subsets of movements are present, but the members of each group are spatially distributed throughout the M1 hand representation. Cluster analysis has been used to search populations of M1 neurons for such groups of functionally similar neurons (60). In three monkeys, however, cluster analysis revealed only two consistent groups of M1 neurons. A relatively large group consisted of neurons that increased discharge during most if not all finger and wrist movements; another small group decreased discharge during most movements. These two groups were found in all three monkeys, were robust against changing the method of quantifying neuronal activity or changing the clustering algorithm, and were not reproduced when the data were randomly reshuffled. In contrast, small groups of neurons that discharged during particular subsets of finger and wrist movements varied from monkey to monkey, changed when the means of quantifying neuronal activity or the clustering algorithm was changed, and appeared in randomly reshuffled data. This analysis indicated that, even for a set of 12 distinct individuated finger and wrist movements, the number of different activity patterns found among M1 neurons may be large relative to the number of movements observed. M1 neurons appear to be functionally quite diverse.

These observations in turn suggest that the connections from M1 to motoneuron pools function as a network. M1 neurons then could be quite diverse, without categorical groups of similar neurons. M1 neurons could be diverse both in terms of the particular motoneuron pools to which they connect and in terms of their activity patterns across a set of movements. Activity of a selected subset of M1 output neurons could facilitate activation of the correct motoneuron pools for a given movement. Such a widely distributed network of diverse elements would provide a flexible substrate for practice-driven plastic reorganization, advantageous both for the motor skill learning needed to play a musical instrument and for functional recovery after nervous system injury (11, 59, 67, 80).

Future work may delineate how a network of functionally diverse M1 neurons can control generation of specific hand and finger movements. A network of intermingled and overlapping representations may be able to control the biomechanically coupled peripheral apparatus of the hand more efficiently than a network of discrete, spatially segregated nodes. Because the fingers are biomechanically coupled at the periphery, independent neural controllers for each digit would need to communicate extensively to accomplish the required control of all the fingers simultaneously. This communication may be more efficient when the controllers are intermingled and overlapping than when they are separate. Segregation of the controllers then would become more efficient as the peripheral elements become more biomechanically independent, as seen for the M1 representations of the face vs. hand. Evolution of increasingly independent digits thus may be paralleled by evolution of increasing separate M1 representations.

CONCLUSIONS AND FUTURE DIRECTIONS

The complexity of the hand’s neural and biomechanical architecture underlies its ability to grasp, manipulate, and perform complex tasks, such as typing, by using a very large number of hand configurations. The study of tasks requiring individuated finger movement or forces has revealed that finger independence has limitations. Both biomechanical and neural factors constrain the extent to which individual fingers can be controlled independently of the others. Mechanical coupling between neuromuscular compartments serving different fingers, short-term synchrony between motor units acting on different fingers, and the broader central coactivation of hand muscles all appear to limit independent action of the fingers. Even more limited degrees of movement and force individuation become evident in tasks such as whole hand grasping, which requires the coordination of multiple fingers. In these circumstances, the relationships among the large number of degrees of freedom of the hand become constrained to a limited number of coordination patterns. Lack of complete finger individuation and partial biomechanical coupling are paralleled by the lack of a discrete somatotopy in the cortical hand area. The divergence of M1 neuron output to multiple hand muscles as well as the convergence of output from large cortical territories to individual muscles highlight the complexity of the input-output relationship between the motor cortex and the control of the hand. Finger movements are controlled by a highly distributed network rather than by functionally and spatially discrete groups of neurons controlling each finger.

Further research will be needed to better understand both the peripheral apparatus that operates the hand and the central neural systems that control it. Understanding control of the hand may find application in hand surgery (93), in rehabilitation for functional recovery after hand reattachment or transplantation surgery (17, 26, 37), as well as after stroke or other central lesions (46, 50). Design and implementation of neural prostheses (15, 90) that might drive functional electrical stim-
ulation to restore hand function after spinal cord injury would also be facilitated by more detailed knowledge of the hand’s normal biological control. And finally, the advantages provided by the biological system may provide insights for engineering more dexterous robotic hands.

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Central and Peripheral Factors in Hand Function


