

Chapter 2

Synergistic Control of Hand Muscles Through Common Neural Input

Marco Santello

Abstract Skilled grasping and manipulation rely on spatial and temporal coordination of multiple hand muscles. This chapter describes the phenomenon of common neural input to hand muscles as one of the mechanisms through which the Central Nervous system might coordinate the neural activation of groups of hand muscles acting on a single or multiple digits. The heterogeneous distribution of common input to intrinsic and extrinsic hand muscles is discussed in relation to its functional role for the coordination of hand muscles.

Keywords Synchrony · Coherence · Motor units · EMG

1 Introduction

The objective of this chapter is to provide an overview of how the Central Nervous System (CNS) controls hand muscles in tasks that require dexterous digit force control. The chapter focuses on studies that have characterized the neural control of hand muscles through the application of time and frequency domain analyses of electromyographical (EMG) signals. By determining and quantifying neural inputs that are common to concurrently active motor units of hand muscles, this work can provide significant insights into how the CNS coordinates the activity of multiple

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muscles during skilled grasping and manipulation. Therefore, the chapter discusses how experimental evidence from research on common neural input could be used to improve our understanding of muscle synergies and their implications for neural control of the hand.

The chapter starts by introducing the complex interactions between descending and ascending inputs to spinal motor nuclei of hand muscles (Sect. 2). A review of the most commonly used techniques to quantify common neural input follows, together with a brief review of the literature on their applications to characterize correlated inputs to motor unit pairs and populations (Sect. 3). The phenomenon of heterogeneous distribution of common neural input across intrinsic and extrinsic hand muscles is then discussed in relation to recent work on motor unit coherence (Sect. 4). Lastly, common neural input is discussed within the theoretical framework of synergies (Sect. 5), followed by a discussion of open questions and directions for future research (Sect. 6).

2 Neural Control of Hand Muscles

2.1 Inputs to Motor Units of Hand Muscles

The spatial and temporal convergence of several inputs onto alpha motor neurons dictates its final output to skeletal muscle fibers, hence motor neurons are referred to as the ‘final common path’ [1]. Descending inputs are mediated by highly divergent cortical inputs (corticospinal tract), as well as rubrospinal and reticulospinal tracts, whereas peripheral inputs are mediated by networks integrating signals from individual sensory modalities (muscle spindles, Golgi tendon organs, tactile afferents, joint receptors). Spinal interneurons contribute to the processing of descending and ascending inputs. The divergence of descending inputs to alpha motor neurons of hand muscles is the subject of ongoing investigation (for more details see Chap. 1). It should be emphasized that the divergence of inputs to several hand muscles does not seem to be a characteristic that is unique to descending inputs. Specifically, cutaneous reflex EMG responses elicited by stimulation of digital nerve branches of one digit occur not only at the muscles acting on the stimulated digit, but also at muscles innervating other digits (e.g., [2–4] unpublished observations). The following section discusses the approaches investigators have used to characterize and understand the functional significance of the organization of inputs onto the spinal motor nuclei of hand muscles.

2.2 Experimental Approaches

Inferences about neural control of hand muscles can be performed through a variety of experimental approaches, such as invasive and non-invasive recordings of cortical neuronal activity, transcranial magnetic stimulation, intraneural recording

or stimulation of peripheral nerves, and recording of electrical activity of hand muscles. This chapter focuses on inferences that have been made through the analysis of the EMG signals of hand muscles, and in particular on the quantification of temporal relationships between the activity of individual units (single motor unit recordings) and populations of motor units (interference EMG).

3 Common Neural Input: Methodological Considerations

3.1 Time and Frequency Domain Measures of Correlated Inputs

This section describes two techniques that have been widely used to quantify correlated inputs to motor units. One technique, *motor-unit synchrony*, quantifies synchronous activity of motor unit in the time domain, whereas the second technique, *motor-unit coherence*, quantifies correlations of motor unit activity in the frequency domain. Common neural input to motor units has also been defined by correlations between the firing rates of individual motor units, i.e., *common drive* [5–9]. For a discussion on methodological aspects of the common drive technique, the reader is referred to a simulation study by Lowery and Erim [10].

3.2 Motor-Unit Synchrony

The correlation for continuous functions $x(t)$ and $y(t)$ is computed by the cross-correlation function

$$R_{yx}(\tau) = (1/T) \int y(t)x(t - \tau)dt \quad (1)$$

where τ is the time interval and T is the period of integration. The special case of cross-correlation between spike trains uses computations based on peri-spike histograms [11, 12]. Motor-unit synchrony is defined as greater than chance tendency for concurrently active motor units to discharge at short time intervals from each other, e.g., [13] and has been used as an indirect measure of common synaptic input across motor neurons. More specifically, motor-unit synchrony has been attributed to excitatory or inhibitory postsynaptic potentials that arise from branched axons of common presynaptic neurons ([13–15]; Fig. 1). Motor unit synchrony can be subdivided into short- and long-term synchrony based on the width of the cross-correlogram peak, the latter type of synchrony being defined by time lags between motor unit discharges of larger than a few milliseconds [16]. Broader cross-correlogram peaks are thought to reflect synchrony due to separate presynaptic inputs onto the motor neurons (top, Fig. 1).

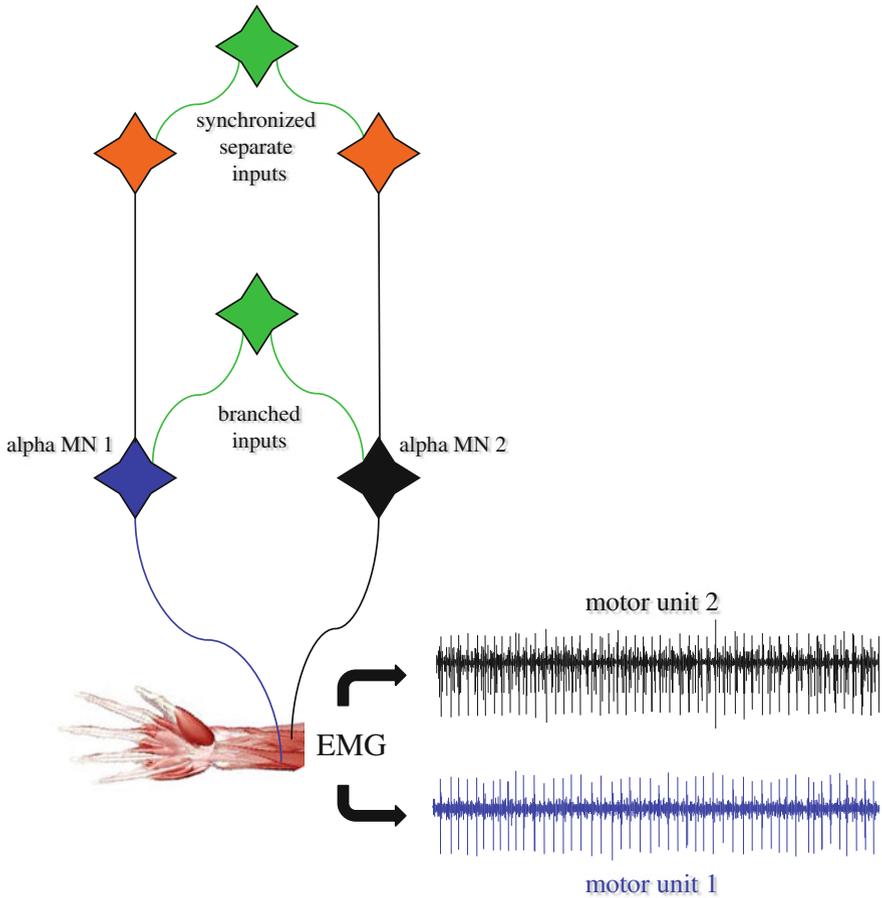


Fig. 1 Schematic description of common neural input through synchronized separate excitatory inputs and branched inputs to alpha motor neurons innervating two hand muscles

The strength of motor-unit synchrony is generally quantified by computing the ratio between the number of motor unit discharges within the central peak of the cross-correlogram histogram and that outside of the peak, e.g., time intervals between discharges of concurrently active motor units that are uniformly distributed and, therefore, not associated with synchronous discharges of the motor unit pair (Fig. 2a). The quantification of motor-unit synchrony focuses on well-defined temporal criteria. In contrast, frequency domain measures capture other features of relations that might exist in the discharges of two concurrently active motor units (see Sect. 3.3). Two examples of some of the most widely used techniques to quantify the strength of motor-unit synchrony are *common input strength* (CIS; [13]) and k [17]. The strength of motor-unit synchrony depends not only on

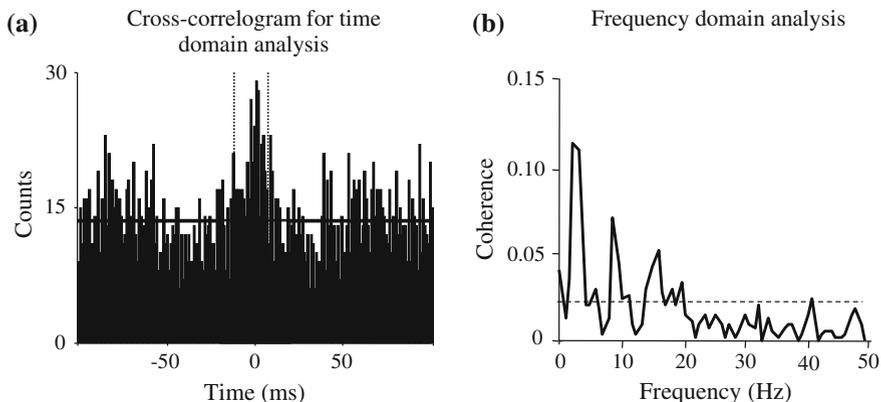


Fig. 2 **a** Cross-correlogram histogram obtained from cross-correlation of two motor unit spike trains. The *horizontal line* denotes mean counts outside of the cross-correlogram peak. **b** Coherence between spike trains of two motor units. The *horizontal line* denotes threshold for statistical significance

the number of shared inputs but also on complex interactions among several other factors such as background excitation and inhibition as well as the intrinsic properties of motor neurons [18–20].

3.3 Motor-Unit Coherence

Correlations in the discharge of a motor unit pair can occur at time intervals that might be longer than those defined by the quantification of short- or long-term motor-unit synchrony. These correlations are revealed by peaks and troughs occurring at consistent time intervals in the cross-correlogram and denote periodicities of correlated motor unit firing [21, 22]). Coherence can detect the existence of such periodicities by quantifying the linear relation between two motor unit spike trains in the frequency domain. Therefore, motor-unit coherence at a given frequency denotes correlated rhythmic activity between two motor units, which is thought to indicate the existence of a common periodic synaptic input ([23, 24]).

Coherence is computed as the modulus of cross-spectrum (f_{xy}) of two motor unit spike trains squared and normalized by the product of the autospectrum (f_{xx} , f_{yy}) of each spike train at each frequency (λ) in the frequency band of interest:

$$|R_{xy}(\lambda)|^2 = |f_{xy}(\lambda)|^2 / (f_{xx}(\lambda)f_{yy}(\lambda)) \quad (2)$$

After determining the frequency at which significant coherence occurs [25], the strength of coherence, bounded between 0 and 1, can be interpreted similarly to the strength of the coefficient of determination in linear statistics (Fig. 2b).

Most commonly, motor unit coherence studies focus on the peak value of coherence or the integral of coherence within specific frequency intervals (typically 0–55 Hz). Similar to motor-unit synchrony, motor-unit coherence reflects the efficacy with which a multitude of common inputs (see Sect. 2) of different strength and timing can elicit action potentials of the motor unit pair under investigation. Therefore, one may equate the strength of significant coherence and the frequency at which it occurs with the number of action potentials across two motor units that occur at similar times relative to the common input signal and the variability in the timing of discharges around the common input frequency. Coherence can also be computed from signals comprised of populations of motor units, e.g., interference EMG recorded through surface or intramuscular electrodes. In these circumstances, the strength of coherence will also depend on how many of the recorded motor units receive common neural input [26].

Besides assessing whether significant coherence may or may not occur between two motor units, often investigators are also interested in determining the frequency bands at which significant coherence occurs. This approach has been informative due to the fact that modulation of within- or across-muscle coherence to task conditions is often confined to specific frequency ranges (see Sect. 4.4 for more details). Furthermore, there is evidence to suggest that the sources of coherence differ across frequency bands. For example, healthy subjects exhibit significant coherence in both 1–12 and 16–32 Hz frequency bands. In contrast, coherence is markedly reduced in patients affected by cortical strokes, but only in the 16–32 Hz frequency band [22]. These authors suggested that the 1–12 Hz frequency may therefore reflect subcortical common inputs to hand muscles, as opposed to the 16–32 drive for which intact cortical inputs appear to be necessary.

3.4 Relation Between Motor-Unit Synchrony and Coherence

As indicated above, motor-unit synchrony and coherence capture different aspects of common neural input. Linear regression analysis has often been used to assess the extent of overlap in the information provided by motor-unit synchrony and coherence (e.g., [27]). The existence of significant linear correlations between these two measures of common neural input are interpreted as reflective of common periodic input to the motor neurons through branched presynaptic pathways [22, 28]. Overall, the literature suggests that linear correlations between across-muscle motor-unit synchrony and coherence are very weak and vary broadly across muscle pairs. This suggests that common neural inputs to hand muscles are delivered through different combinations of indirect and direct branched presynaptic pathways, as well as, independent pathways (weak motor-unit synchrony and coherence; [27]). The finding that motor units can exhibit significant motor-unit coherence and no motor-unit synchrony (e.g., [29, 30]) emphasizes the need to use both measures, when possible, to further delineate the nature of divergent inputs to motor units. For further discussion on the relation between

time- and frequency-domain measures of common neural input to motor units, the reader is referred to Semmler et al. [31, 32] and computational modeling by Enoka and colleagues [19, 20, 33] and Lowery et al. [34]. Additional methodological issues, such as assessing EMG–EMG coherence through recording EMG activity of motor unit pairs versus motor unit populations, or the effect of EMG signal rectification on coherence estimation, are discussed in [26].

4 Common Neural Input to Hand Muscles: Experimental Evidence

4.1 Functional Considerations

The extent to which hand muscles in humans receive common input has been extensively studied by recording EMG from single motor units. These studies can be broadly classified based on whether they target correlated neural activity of motor units belonging to the same or different muscles, i.e., *within-* or *across-muscle* common neural input. Early studies of within-muscle motor unit synchrony of hand muscles were performed to quantify the strength of divergent inputs to motor units innervating a single hand muscle (often the first dorsal interosseus, FDI; [35]) or for comparing the strength of motor unit synchrony among hand muscles [36] as well as other upper or lower limb muscles [6, 37]. Studies of correlated neural activity across motor units belonging to different hand muscles often aimed at comparing the strength of synchrony of motor units belonging to the same versus different muscles. An important observation is that motor-unit synchrony across hand muscles tends to be weaker than within-muscle synchrony ([37–40]; but see Sect. 4.2). Similar considerations and experimental questions motivated studies of coherence between motor units within and across hand muscles (see Sect. 4.3).

More recently, however, the objective of quantifying correlated neural activity across hand muscles has been pursued to better understand constraints that might contribute to the coordination of digit movement or forces. Specifically, tasks involving individuated digit motion or forces, as well as reaching to grasp object with different shapes, have described the tendency for joint excursions and forces across digits to be correlated (this is discussed in more detail in Sect. 6). Therefore, correlated neural input across motor units of hand muscles has been studied as a potential mechanism that might contribute to constrain neural drive to hand muscles, hence contributing to the synergistic coupling of digit actions.

An important distinction, however, should be made between the contexts in which common neural input affects the hand behavior. Specifically, tasks that require independent action of one digit (e.g., index finger) would be potentially penalized by the existence of common neural input to muscles acting on the ‘instructed’ digit *as well as* the digits that are required to remain stationary

(e.g., thumb, middle, ring, and little finger). Thus, it has been suggested that common neural input across finger muscles is one of the factors responsible for the limited extent to which fingers can move or generate forces independently [41, 42], therefore causing ‘unwanted’ coupling among the digits [43, 44]. Besides peripheral constraints such as passive linkages among muscles and tendons, central limitations contribute to limit the degree to which fingers can be controlled independently. However, superficial finger flexors appear to be under more independent volitional control than deep flexors [45] (for recent studies on the issue of independent finger control, the reader is referred to [46] and [47]; the interaction between central and peripheral factors in hand control is discussed in more detail in Chap. 1).

It has also been suggested that such neural constraints, limiting the independent action of the fingers, might be considered as a desirable feature in contexts where coupling of digit actions is required by the task, e.g., to prevent object slip while holding an object against gravity [48]. Specifically, a tendency for correlated inputs to motor units acting on different hand muscles or compartments of a multi-tendoned muscle, e.g. flexor digitorum profundus (FDP), would enhance the temporal coupling of digit forces [49, 50]. These considerations motivated studies of common neural input across hand muscles to address the following main questions: *What is the strength of correlated neural inputs across motor units of hand muscles? Does the strength of common neural input vary across hand muscles? Is the strength of correlated neural input task-dependent?*

4.2 Strength and Distribution of Across-Muscle Motor-Unit Synchrony

Motor unit studies of force production and object hold tasks have reported moderate to strong common neural input across thumb and extrinsic finger muscles and compartments, as well as across compartments of finger flexors and extensors [30, 40, 42, 48, 51]. Interestingly, the strength of common neural input is not uniformly distributed across hand muscles or muscle compartments. For example, Winges et al. [52] found moderate to strong synchrony across motor units innervating FDP compartments as well as between FDP compartments and flexor pollicis longus (FPL). However, synchrony across FPL and the FDP index finger compartment was significantly stronger than for FPL and any other FDP compartment. Similarly, significant differences have been found when comparing motor unit synchrony measured on extrinsic versus intrinsic muscle pairs. Specifically, intrinsic muscle pairs (FDI and palmar interossei, FPI) are characterized by weaker across-muscle motor unit synchrony than extrinsic muscles [48, 53]. This is a striking finding when considering that within-muscle synchrony to FDI and FPI is significantly stronger than across them [30, 48]. Therefore, there appears to be an important difference between within- and across-muscle common neural input,

which has led to the speculation that these two forms of correlated inputs and their distribution among hand muscles may reflect differences in the muscles' functional roles (this is further discussed in [Sect. 4](#)). Another important observation is that motor units of adjacent finger flexor compartments tend to receive stronger common neural input to motor unit pairs than non-adjacent compartments [36, 42], thus lending support to the above notion that common input may contribute to the limited ability of moving adjacent fingers independently (see also a recent study on motor units of extensor digitorum profundus by van Duinen et al. [46]). The distribution of common neural input across motor units of thumb and finger flexor muscles during object hold does not follow the same gradient, however, this difference is likely due to methodological and task differences (see [48] for details).

4.3 Strength and Distribution of Across-Muscle Motor-Unit Coherence

Johnston et al. [27] reported significant across-muscle coherence across a thumb flexor muscle, FPL, and FDP compartments, as well as across FDP compartments during a five-digit object hold task. Interestingly and consistent with the above results on motor-unit synchrony, coherence across FPL and the index finger compartment of FDP was significantly stronger than across FPL and other FDP compartments. From a functional perspective, it is noteworthy that coherence between thumb and index finger forces in the low-frequency range (2–10 Hz) was significantly stronger than across thumb and other fingers [54]. Examination of across-muscle coherence to hand muscles has recently been extended to a larger number of muscles comprising intrinsic and extrinsic muscles of thumb, index, and middle fingers [55, 56]. This work has also revealed the existence of significant across-muscle coherence occurring primarily at low frequencies (<15 Hz), even though coherence strength varied significantly across muscle groups (the heterogeneous distribution of coherence across hand muscles is further discussed in [Sect. 4](#)).

4.4 Task-Dependency of Common Neural Input

Motor unit studies of within- and across-muscle synchrony have also addressed the question of whether and the extent to which correlated neural input is task-dependent. To date, a definite answer to this question is not available; therefore a general consensus has yet to be reached on whether the above described distribution of common input to motor neurons of hand muscles can be changed acutely or chronically. Lack of a clear answer is mostly due to differences in how

task-dependency has been studied or defined, as well as contrasting results from studies of motor-unit synchrony versus coherence. It is also important to note that clear evidence for task-dependency would imply a functional role for common neural input in relation to a behavioral goal, e.g., coordinating multi-digit movements to grasp an object (this is further discussed in [Sect. 5](#)). However, the literature discussed below suggests that common neural input appears to be sensitive to some task parameters but not others.

Task-dependency has been described for motor-unit synchrony within and across hand muscles as a function of finger movement direction [57]. The strength of within-muscle motor-unit synchrony is also sensitive to the type of muscle contraction, e.g., motor unit synchronization is greater during lengthening than shortening contractions [28]. Task-dependency of motor-unit synchrony has also been studied in the context of grasping, in particular on the effects of grip type (power vs. precision). Wings et al. [30] hypothesized that synchrony between hand muscle motor units will be dependent on grip type. This expectation was based on evidence from a study of hand muscle interference EMG [58] indicating a higher synchronization for power than precision grips. The interpretation of this finding was that the control of power grip might be simplified by having common neural drive to all digits, whereas precision grips might require a higher degree of independence among digits. Wings et al. [30] asked subjects to hold the same grip device using either thumb and index or thumb and middle finger while measuring EMG from single motor units of FPL, FDP2 and FDP3. The experimental question was whether the weaker synchrony exhibited by thumb-middle finger flexors relative to that of thumb-index finger muscles when holding the object with five digits [48] would still be found when using two-digits. Such result would support the notion of muscle-pair specificity of common neural input despite the re-organization of force relations required to hold an object with two instead of five digits. If, however, thumb-middle finger flexors had exhibited a significantly stronger synchrony when holding the device with two versus five digits, the authors would have concluded that across-muscle motor-unit synchrony can be modulated based on grip type. It was found that across-muscle motor unit synchrony of thumb and index finger flexors was stronger than that from thumb and middle finger flexors regardless of the number of digits (five vs. two) and the digit pair (thumb-index finger or thumb-middle finger) used to hold the device. The stronger common motor-unit synchrony across motor nuclei of thumb and index finger muscles could reflect neuromuscular adaptations to their greater degree of involvement in many types of dexterous manipulation relative to other digit pairs. Specifically, thumb and index finger are engaged in nearly all hand-object interactions, whereas other thumb-fingers pairs are not. Wings et al. [30] therefore concluded that common neural input is distributed in a muscle-pair and/or specific fashion, a proposition that received further support through studies of EMG–EMG coherence (this is further discussed in [Sect. 4](#)).

It should also be noted that motor unit synchrony is not correlated with digit force output during five-digit object hold. Specifically, Wings et al. [48] reported that motor unit synchrony was strong (CIS: 0.48) across FDP muscle compartments

(e.g., FDP3-5) innervating digit pairs (middle-ring fingers) that exerted significantly less normal forces than most digit pairs. However, the long flexors of the thumb and index finger were characterized by synchrony of similar strength (CIS: 0.49) and were also the digits that exerted the largest grip force. The lack of correlation between the strength of common neural input and forces exerted by most muscle pairs receiving such input indicates that motor unit synchrony is not directly associated with grip force. Later studies have extended this observation by showing that a significant increase in maximal index finger abduction force elicited by strength training (4–8 weeks) does not affect synchrony of motor units innervating an intrinsic muscle (FDI; [59]).

With regard to evidence from studies of coherence, two main frequency ranges, $\sim 1\text{--}12$ Hz and $\sim 16\text{--}32$ Hz, have been defined based on the extent to which the strength of coherence can be modulated to task requirements. Coherence in the low frequency band ($\sim 1\text{--}12$ Hz) is stronger during position holding and lengthening muscle contractions when compared to shortening contractions [28]. It has been suggested that coherence in the higher frequency range reflects a “binding” mechanism [60] enabling efficient activation of task-related groups of neurons [61, 62]. In contrast to coherence occurring at higher frequencies, the low frequency range does not appear to be affected by the degree of object compliance during grasping [63], although a later study showed that displacement accounted for the coherence modulation [64]. Furthermore, Kakuda et al. [65] observed an increase in the magnitude of 6–12 Hz coherence between motor units from the Extensor Carpi Radialis during slow wrist movements versus position holding.

Evidence for task-dependent modulation of common neural input in the low frequency range has also been provided by studies of grasping. Winges et al. [30] found that coherence was significantly stronger during two- than five-digit object hold although, importantly, this observation was not associated with a re-distribution of common neural input across different muscle pairs for variations in task requirements (two vs. five-digit grip). Specifically, coherence across FPL and FDP2 was still stronger than across FPL and FDP3. The authors interpreted these findings as indicative of an invariant muscle-pair specific *distribution* of common neural input that, nevertheless, still allows for modulation of common neural input *strength*. It should also be noted that grip type affected across-muscle coherence but not motor-unit synchrony [30], further stressing the potential independence of these two mechanisms underlying correlated neural input and suggesting that motor-unit coherence might be more sensitive to modulation of neural drive as a function of task characteristics. This might be mostly due to the ability of coherence to detect correlations in motor-unit activity at longer time lags than those required for detection of short-term synchrony, e.g., outside of the central peak region of the cross-correlogram (Fig. 2a; see Sect. 3).

Probably one of the most convincing arguments for plasticity of motor-unit coherence has been provided by Semmler and colleagues [32]. This study reported that within-muscle coherence in the 16–32 Hz frequency range from motor units of the FDI was stronger in strength-trained than skill-trained and untrained subjects. The authors interpreted this finding by considering the potential functional

consequences of coherence in relation to habitual muscle usage. Specifically, weaker across-muscle coherence might correlate with generating a more independent control of motor units relative to tasks that would benefit from a more global activation of motor units for the production of large forces (the relation between common neural input and muscle synergies is further discussed in [Sect. 5](#)).

To examine whether digit force affects the strength of across-muscle coherence, Poston et al. [56] studied brief submaximal isometric force production tasks using a three-digit grip (thumb, index, and middle fingers) while interference EMG activity was simultaneously recorded from six intrinsic and six extrinsic hand muscles. The total target forces (the sum of all digit normal forces) were 5, 20, 40, 60, and 80 % of the maximal voluntary force. To quantify changes in coherence, the integral of coherence was computed on pooled coherence from all muscle pairs ($n = 66$). Interestingly, force modulation over the voluntary range did not affect the strength of coherence [56]. This result suggests the existence of a force-independent distribution of excitatory drive to the hand muscles that were studied and is consistent with the results of the analysis of EMG amplitude from the same muscles. Specifically, the distribution of EMG amplitudes of each muscle remained consistent across target forces. Therefore, despite force-induced changes in motor unit recruitment and discharge rate to implement force modulation—and quantifiable as a modulation of EMG amplitude, no significant changes occurred in how neural drive was distributed to hand muscles. The finding of a invariant distribution of EMG amplitude *and* across-muscle coherence should not be considered obligatory, as a dissociation between these two variables has also been found, i.e., fatiguing contractions cause an increase in both EMG amplitude and EMG–EMG coherence [55]. To conclude our discussion of studies on the effect of force on common neural input, it has been found short term strength training does not elicit a modulation of across- or within-muscle coherence, respectively. These findings, together with the above observation that coherence is affected by long-term *skill* training, further support the notion of correlated neural input as a functional mechanism for coordinating the activity of motor units within a muscle and, possibly, across muscles.

The extent to which correlated neural input to hand muscles might be sensitive to sensory input from tactile receptors has been addressed by several studies. The question is particularly important when assigning a functional role to across-muscle motor-unit synchrony or coherence. For example, tonic input from the fingertip mechanoreceptors elicited by static grasping or holding of an object might potentially modulate the efficacy with which a diverging descending neural drive can temporally couple the activity of target motor neurons. Similarly, such a modulatory effect driven by tactile mechanoreceptors might also be elicited by different tactile stimuli, e.g., frictional properties of the contacts. It should be noted, however, that these questions assume a functional role of common neural input whereby its modulation might fulfill a given behavioral goal that might rely on tactile sensing, e.g., preventing an object from slipping when sensing a low friction object surface. Our preliminary work (unpublished) addressed these questions by having subjects hold against gravity objects with different frictional

properties (sandpaper and rayon). We found that, although holding the object while contacting a more slippery surface elicited larger digit normal forces, across-muscle coherence was not significantly affected by contacting surfaces with different textures. These results further point to a dissociation between the modulation of total digit force magnitude and coherence (see also [Sect. 5](#)). Most importantly, however, they suggest that changes in tactile afferent activity associated with sensing the object's different frictional properties do not significantly modulate the strength of common neural input to hand muscles. These findings are consistent with other reports showing that the strength of across-muscle motor unit synchrony is not affected by tactile input during a simulated two-digit grip [66]. However, there appears to be other instances in which differences in tactile afferent activity can modulate common neural input. Following digital nerve anaesthesia, Fisher et al. [67] observed a reduction in the high frequency coherence across hand muscles during the static phase following a dynamic phase of a force production task. These authors suggested that tactile afferents might play a role in modulating across-muscle coherence when neural drive has to be changed during transitions from dynamic to static muscle contractions. Therefore, it would appear that tactile input might play a role in certain, but not all tasks.

To further investigate the issue of task-dependency of common neural input, we have compared the task of holding an object against gravity (unpublished data) with generating the grip forces of comparable magnitude on an object that was clamped to the table [56]. Our preliminary analyses indicate that object hold is associated with significantly weaker across-muscle coherence than generating forces on a fixed object. These two tasks are characterized by several differences. For example, the weighting of sensory modalities involved in monitoring ongoing task performance is mainly visually-driven for the force production task (visual display of the target force on a computer monitor), whereas tactile input is likely to dominate object hold against gravity to prevent the object from slipping. Another difference between the two tasks is that little or no load forces are generated or required during the force production task, whereas during object hold subjects modulate digit force vectors such that load forces match the gravitational force acting on the object. A more important factor, however, might be the mechanical requirement of generating net zero normal forces and moments associated with object hold, but not explicitly required by the force production task, e.g., exertion of non-zero torques on the object do not interfere with producing the target force as the object is clamped to the table. Therefore, holding an object might require a greater degree of independence in the neural drive to hand muscles to enable continuous force compensations across digits, such that changes in force at one digit are compensated by force modulation at other digits, thus minimizing net torques. This proposition, however, requires further testing across a wider variety of task conditions and is the subject of ongoing investigations.

5 Heterogeneous Distribution of Common Input to Hand Muscles

5.1 *Motor-Unit Synchrony and Coherence: Studies of Single Motor Units*

Bremner and colleagues [36, 37] first reported that motor-unit synchrony is heterogeneously distributed across motor units of hand muscles revealed through isometric contractions of the index and/or middle finger. Specifically, the occurrence and strength of motor-unit synchrony was higher for hand muscles with similar mechanical actions on different digits than muscles with different actions inserting on the same digit. Studies of object hold using a multi-digit grip have extended these observations by revealing significantly stronger motor unit synchrony and coherence across motor units of thumb and index finger flexors (FPL-FDP2) than thumb and all other FDP compartments [27, 52]. These findings demonstrated that the strength of across-muscle synchrony, traditionally considered to be weak [36, 37], can be significant. These authors speculated that the strong across-muscle synchrony exhibited by FPL-FDP2 might reflect the relatively more important role of thumb and index finger among all thumb-finger combinations for grasping and fine manipulation. Therefore, the stronger synchrony of thumb-index flexors relative to all other thumb-finger muscles suggested a distribution of common neural input that might be muscle-pair specific. Subsequent work [30, 48] further revealed the existence of heterogeneous distribution of common neural input to motor units innervating intrinsic (1DI-1PI) and intrinsic-extrinsic muscle pairs (FPL-1PI, FPL-1DI), the former muscle pair being characterized by weak synchrony. This was an unexpected result as, traditionally, synchrony across intrinsic muscles has been reported to be stronger than across extrinsic muscles [36, 37]. We also recorded motor unit synchrony within each intrinsic muscle and found that within-intrinsic muscle synchrony (1DI-1DI, 1PI-1PI) was three times stronger than across intrinsic muscle synchrony (1DI-1PI). These results are consistent with results reported by McIsaac and Fuglevand [53] about weak synchrony across motor units of two intrinsic muscles, adductor pollicis and FDI. The same group also reported that synchrony of motor units belonging to a given compartment of flexor digitorum superficialis (FDS) was significantly stronger than across adjacent FDS compartments, such difference being even larger when comparing within-compartment synchrony versus across non-adjacent compartments [68].

The above results support the notion that the distribution of across-muscle motor unit synchrony may reflect the functional role of specific digit pairs. Pairs of extrinsic flexors of the digits, capable of generating large forces and essential for coordination of grip forces receive stronger common neural input than pairs of intrinsic muscles that are important synergists for controlling force direction but not strong force producers. Similarly, stronger common neural input within than

across finger flexor compartments might reflect the functional requirement of decoupling the action of individual fingers. Nevertheless, additional or alternative factors underlying the heterogeneity with which common neural input is distributed to hand muscle should be considered (see below).

5.2 Motor-Unit Synchrony and Coherence: Studies of Interference EMG

Coherence analysis has further confirmed and extended previous observations of synchrony between motor-unit pairs regarding the existence of a heterogeneous distribution of common neural input to muscle and muscle compartment pairs [27, 30, 48, 55, 56]. For example, the muscles innervating the thumb and index finger (FPL and FDP2) and thumb and little finger (FPL and FDP4) were characterized by the strongest coherence among all muscle pairs during a five-digit object hold [27]. Furthermore, during a static three-digit force production task, Poston et al. [56] recorded intramuscular EMG from 12 concurrently active hand muscles innervating the thumb, index, and middle fingers. The coordination of hand muscles was quantified in two ways, one based on EMG amplitude of each muscle (this is further discussed in Sect. 5) and one as across-muscle coherence from all muscle combinations ($n = 66$). A main finding of this study was that coherence was muscle-group dependent, the strongest and weakest coherence being found across extrinsic and intrinsic muscle pairs, respectively. Interestingly, this pattern was preserved across a wide range of digit forces (5–80 % of maximal voluntary force). Such force-independent distribution of common neural input suggests that increases in descending drive to the motor neuron pool, which result in an increase in motor unit recruitment and rate coding, do not significantly change how correlated inputs are distributed to multiple motor nuclei of hand muscles. These data, consistent with the above described results from motor-unit synchrony [48], point to a muscle-pair specific distribution of common neural input. Poston et al. [56] speculated that the stronger coherence exhibited by extrinsic versus intrinsic muscle groups could be associated with differences in their functional properties, e.g., how much force they can produce, and/or their innervations. As described above, extrinsic and intrinsic muscles can also be distinguished based on their functional role for grasping and manipulation. However, it should be noted that the muscle-pair specificity of common neural input should not be interpreted as a discrete and invariant categorization of how neural drive is distributed to hand muscles for a number of reasons. First, from a behavioral perspective both sets of muscles interact and contribute to modulate fingertip force vectors. Second, inputs to spinal motor neurons can undergo plastic changes. This plasticity might, in turn, alter how motor neurons respond to common neural input and, therefore, in how it is distributed across hand muscles. Last but not least, the observations of muscle-specific distribution of common

neural input have been obtained through a fairly restricted set of experimental conditions. Therefore, the extent to which they generalize to other tasks involving coordinated actions among the digits require further experimental work.

The finding of stronger coherence across extrinsic than intrinsic muscles is particularly interesting because it provides further insight into the principles underlying how correlated neural input is distributed across hand muscles. As noted above for coherence measured from motor unit pairs (Sect. 5.2), weaker coherence across intrinsic than extrinsic muscles might be related to their different role in manipulation and force production capabilities. Ongoing work aims at determining the key factors responsible for the heterogeneous distribution of common neural input among hand muscles. Of particular interest are the questions of (a) whether the heterogeneity of common neural input is relatively fixed and (b) whether there are factors—other than the above-mentioned functional differences among hand muscles—that might account for the wide range of common neural input strengths.

The question of whether the distribution of correlated neural input is fixed or, conversely, sensitive to task demands or training is reminiscent of the question discussed in Sect. 3 (*E, F*), e.g., whether the *strength* of common neural input is task-dependent. However, it has been reported that modulation of common neural input strength can occur within an invariant distribution among hand muscles [27]. Therefore, the question arises as to whether and the extent to which the force-independent distribution of common neural input generalizes to other tasks. In a follow-up study of muscle fatigue, Danna-dos Santos and colleagues [55] observed a similar, but not identical distribution among the same 66 muscle pairs studied by Poston et al. [56]. Specifically, the comparison of across-muscle coherence between the first and last quarter of a fatiguing contraction (three-digit force production) revealed that fatigue caused an increase in coherence but not in how coherence was distributed among hand muscles. Therefore, significant changes in the mechanisms responsible for motor unit recruitment and rate coding underlying voluntary force modulation [56] or maintaining a constant force while fatigue develops [55] do not seem to affect the distribution of neural drive to hand muscle motor nuclei. Another important consideration is that the distribution of common neural input remains invariant regardless of whether coherence magnitude is modulated [55] or not [56].

A difference between the results of these two studies, however, was that in the study by Danna-dos Santos et al. [55], no statistically significant difference was found in coherence from extrinsic and intrinsic muscle pairs. These authors speculated that methodological and task differences may underlie the different result. Specifically, Danna-dos Santos and colleagues [55] measured coherence over a significantly longer time period than Poston et al. [56]. Another major difference between the two studies is the examination of fatiguing versus non-fatiguing contractions, respectively. Therefore, it is possible that the distribution pattern of correlated neural input is sensitive to the duration of a voluntary contraction and/or to peripheral and central impairments associated with fatigue, e.g., increased descending drive from supraspinal sources and recruitment of larger

motor units, transmitter depletion at IA afferent terminals, and increased presynaptic inhibition of IA afferents mediated by activation of group III and IV afferents by muscle metabolite accumulation (for review, see [69]). One may conclude that the distribution of correlated neural input to hand muscles is not fixed or insensitive to the characteristics of a task. Further investigations are warranted to determine the relation between coherence magnitude and distribution in relation to task demands. However, the evidence from these interference EMG studies as well as single motor unit studies seem to indicate that (a) correlated neural input to hand muscles is heterogeneously distributed and that (b) this distribution appears to reflect anatomical and/or functional differences among hand muscle groups.

With regard to the question of whether factors other than functional differences among hand muscles might contribute to the heterogeneous distribution of common neural input, another factor that should be considered is the nerve supply to given muscle pairs. Specifically, it has been suggested that hand muscles that share the same nerve innervation might be characterized by stronger common neural input than muscle that are innervated by different nerves [37]. For example, the results of Wings et al. [48] could be interpreted as due to the fact that each pair of muscles (extrinsic, FPL-FDP2; intrinsic, 1DI-1PI) shares the same innervation (median and ulnar nerve, respectively), whereas the muscle pair characterized by the weakest coherence (1DI-FDP2) are innervated by two different nerves. Lastly, an additional factor that might account for the heterogeneous distribution of common neural input to different hand muscle pairs is the digit they insert on. Therefore, a digit-specific distribution of common neural input might also be expected. Preliminary (unpublished) results from our laboratory further indicate that muscles inserting into digits involved in a three-digit grasping receive common neural input of different strength. This result was obtained by comparing a three-digit object hold with force production performed by individual digits, the thumb, index, and middle fingers muscles being characterized by the strongest across-muscle coherence.

6 Common Neural Input and Hand Muscle Synergies

6.1 *Functional Role of Motor-Unit Synchrony: Theoretical Considerations*

As indicated in Sect. 4, probably the most important question about common neural input is: “*What are the functional consequences of common neural input on motor control?*” This is a difficult question to answer experimentally because divergence is a defining characteristic of descending neural inputs to hand muscles in primates (see Chap. 1). One would need, for example, to ‘turn off’ the mechanisms responsible for constraining the correlations in motor unit firings to measure the consequences in how digit forces are coordinated during grasping or manipulation.

Alternatively, one may wish to modulate the strength with which the neural drive to muscle pairs is correlated, and measure what aspect, if any, of grasp behaviors is affected. These approaches, however, are not feasible as they would require selective *and* tonic activation, deactivation, or modulation of specific cortical and/or spinal networks. Nevertheless, insights have been provided by studies of task-dependency of common neural input as well as by computational models. Specifically, the studies reviewed above (Sect. 4.4) suggest that the strength of common neural input in time and frequency domains does not correlate with the magnitude of digit forces, but does correlate negatively with the requirement of fine motor control of hand muscles, e.g., the extent of digit movement fractionation. This observation points to a potential role of common neural input for the temporal coordination of neural drive to hand muscles.

Santello and Fuglevand [70] addressed the question of whether common neural input might be important for regulating the temporal relations among grip forces using a motor unit simulation. The focus on the temporal coordination of grip forces was motivated by previous work on five-digit grasping [49, 71, 72]. Specifically, this work revealed that each pair of digit normal forces during object hold exhibits in-phase relations. Importantly, this behavior was highly reproducible in a wide variety of task conditions, e.g., regardless of whether subjects could anticipate the object's mass distribution on a trial-to-trial basis or used the dominant versus non-dominant hand. These early observations raised the question of whether this 'default' pattern of digit force synchrony was a mere byproduct of biomechanical constraints (e.g., multi-tendoned finger flexors) or whether neural factors, e.g., common neural input, should also be considered. To address this question, Rearick et al. [50] compared multi-digit grasping of an object that remained stationary on the table versus holding it against gravity. By matching the total normal digit force required by the 'force production' task with that elicited by the object 'hold' task, these authors could dissociate the (common) force output requirement from the mechanical constraints that were unique to each task, e.g., time-to-time fluctuations in force at one digit must be compensated by force modulation at one or more digits to prevent object slip in the 'hold', but not in the 'force production' task. Therefore, the authors hypothesized that in-phase digit force relations are the byproduct of digit force production *per se* and thus, force synchronization should be found in both tasks. Conversely, a task-dependent modulation of digit force synchronization would indicate that different neural mechanisms are selectively involved in the two tasks, the expectation being that holding an object against gravity—challenging grasp stability to a greater extent than force production—would be associated with more consistent force synchronization among digit pairs. The results supported the latter prediction, between-digit force synchronization being consistently high when holding the object, but much weaker and less consistent in the 'force production' task. This finding, therefore, points to neural mechanisms that, by interacting with biomechanical constraints, can independently modulate the temporal relationships between digit forces while maintaining the same force output.

Santello and Fuglevand [70] identified and tested motor unit synchrony as a mechanism that could potentially account for the experimental results of Rearick et al. [50]. These authors used a motor unit model developed by Andrew Fuglevand and colleagues [73, 74]. In the model, the authors imposed varying levels of across-muscle synchrony to two simulated motor unit populations that activated two ‘virtual’ muscles and quantified the correlations among simulated forces (a) to establish whether across-muscle motor unit synchrony could reproduce the above experimental findings on the coupling of grip forces and (b) to determine values of across-muscle synchrony that are behaviorally important. Both of these questions were highly significant as the functional consequences of across-muscle motor unit synchrony for motor control had not been investigated or quantified. Santello and Fuglevand [70] reported that moderate across-muscle synchrony, normally found in motor-unit synchrony studies (e.g., CIS: 0.3), could lead to force coupling that was quantitatively similar to that found during multi-digit grasping (see above). This result is consistent with the notion of across-muscle motor unit synchrony as a mechanism that can modulate the temporal coordination of digit forces.

The results of the motor unit simulation study appears to contradict the above-mentioned unpublished results from a study of EMG–EMG coherence where the same tasks (force production vs. object hold) were compared using a three-digit grip (Sect. 4.4). Specifically, across-muscle coherence was stronger in the force production than in the object hold task, the interpretation being that a higher degree of independent control of digit forces might be necessary. However, a direct comparison between the simulated and experimental results might be premature because it is limited by three main factors: [1] the simulation study examined motor-unit synchrony, defined as near-coincident firing of motor units, whereas the identification of coherence is not restricted to synchronous events (see Sect. 2); [2] motor-unit synchrony and coherence can operate independently, e.g., the task-dependent modulation of coherence might have not involved a modulation of motor-unit synchrony; and [3], to date no simulation study has quantified the affect of across-muscle coherence modulation on digit force coordination, and therefore the speculation that weaker coherence is associated with the requirement of higher digit force individuation during object hold remains to be validated.

6.2 Hand Muscle Synergies

The concept of common neural input as a mechanism that might play a functional, task-dependent role for the neural control of the hand is related to the broader concept of *muscle synergies*. Briefly, muscle synergies are defined as combinations of groups of muscles. The criteria underlying how certain combinations are selected by the CNS, the extent to which they are fixed or flexibly adapted to task conditions, and whether they serve a functional purpose for the control of movement are questions that are still debated and are subjects of ongoing

investigations (for a more comprehensive discussion of muscle synergies and related issues, the reader is referred to a recent review by [75]; see also a recent study on forelimb muscle synergies in non-human primates associated with reach-to-grasp and manipulation by [76]). Note that the concept of ‘muscle synergies’ described here is different from the definition of ‘synergies’ used by clinicians in relation to neurological disorders, e.g., leg flexion synergy also known as ‘Babinski sign’.

Within the framework of the above-reviewed studies of common neural input, constraints on the temporal relations in the activity of motor unit populations within and across hand muscles, and/or how common input is distributed across hand muscles, can be viewed as building blocks for muscle synergies. Specifically, it has been suggested that the correlated firing of motor units, as measured by coherence, might be a mechanism by which the central nervous system reduces the number of independent degrees of freedom to be controlled (e.g., motor units, forces) [32, 61, 77]. Although the coordination of motor units within a given muscle can be considered an example of ‘muscle synergy’, often this term is used in relation to the spatio-temporal coordination of multiple muscles. When examining neural control of the hand, this problem is equivalent to fingertip forces are modulated within a digit or, for grasping and manipulation tasks, across digits.

A more viable approach to study common neural input as a mechanisms contributing to muscle synergies is interference EMG, e.g., the recording of electrical activity of multiple motor units from concurrently active muscles. Studies of interference EMG of hand muscles have described a tendency for covariation in EMG amplitude of multiple hand muscles acting on one digit [78, 79] or multiple digits [55, 56]. Such covariation results from neural constraints through which the orderly recruitment of motor units and increase in motor unit discharge rate, indirectly quantified as EMG amplitude, is coordinated across multiple muscles in a fairly stereotypical fashion, e.g., as a scaling of the EMG vector length but not orientation, across the range of voluntary forces. As discussed above, the observation that both EMG–EMG coherence and the distribution of EMG amplitude across muscles does not change as a function of grip force might suggest a functional link between these two phenomena.

To further test the phenomenon of covariation of EMG amplitude across multiple muscles, a recent study of interference EMG examined the relation between EMG of intrinsic and extrinsic hand muscles during a two-digit grip as a function of wrist joint angle [80]. This study was designed to determine whether EMG activity of intrinsic muscles, whose length does not change with wrist angle, might be modulated in response to an expected EMG modulation of extrinsic hand muscles. Two alternative scenarios were envisioned: (a) both sets of muscles are modulated as a function of wrist angle, or (b) EMG amplitude modulation occurs only in those muscles in which changes in muscle length with wrist angle requires a concurrent modulation of neural drive to maintain the desired force output. Johnston et al. [80] reported that EMG amplitude was modulated in both intrinsic and extrinsic muscles, thus suggesting the existence of a muscle synergy as defined

above. Common neural input across these two sets of muscles might contribute to their concurrent modulation in order to generate the desired force output.

Last but not least, and as mentioned in [Sect. 2](#), divergence of inputs to motor units is not limited to descending inputs as indicated by one-to-many divergence of tactile stimuli to EMG reflex responses in muscles. One such recent observation shows that electrotactile stimuli to branches of the digital nerve elicit cutaneous reflexes across multiple hand muscles (unpublished observations). Most importantly, however, cutaneous reflexes occur in several hand muscles innervating different digits *regardless* of which digit is stimulated. This observation points to the existence of spinal circuitry that transmits sensory information from one stimulated digit to muscles that act on stimulated *and* non-stimulated digit(s). This concept is similar to that introduced above of a force- or fatigue-independent distribution of common neural input to hand muscles, both underscoring the usefulness of analyzing patterns through which correlated inputs might be revealed by quantifying motor-unit synchrony and/or coherence. The concept of hand muscle synergies can also inspire the design and control algorithms of robotic hands. Specifically, for anthropomorphic robotic hands, controls signals that are shared by task-specific groups of joint actuators—the artificial counterpart of biological common neural input—could potentially simplify the spatial and temporal coordination of digit forces for grasping and manipulation.

7 Conclusion

The analyses of common neural input, quantified through motor-unit synchrony and coherence, has provided significant insights into how the Central Nervous System controls hand muscles, including the task-dependency of common neural input and a functional gradient in its distribution.

Plasticity has been described for within-muscle motor-unit synchrony and coherence both at the acute and chronic level. Interestingly, however, short-term force training has no effect on the strength of common neural input, whereas long-term skill training does. These observations have been interpreted as indicative of a functional role of common neural input whereby constraints on motor unit recruitment can be modulated according to task requirements, e.g. movement direction and lengthening versus shortening contraction. However, task-dependency (grip type, frictional properties of the contacts) has been found for across-muscle coherence but not motor-unit synchrony measured during multi-digit tasks (force production or object hold). These and similar observations suggest separate mechanisms as well as differential sensitivity of motor-unit synchrony and coherence in detecting common neural inputs. Several important questions, however, remain, the most important one being what is the functional role of common neural input. This question has been addressed mostly using motor unit simulations indicating a potential role for motor-unit synchrony for the temporal coordination of digit forces, but further simulation work is needed to

further characterize the functional consequences of common neural input. Although it is difficult to directly measure the effect of common neural input modulation on grasp or manipulative behaviors, experimental work is also needed to improve our understanding of the link between plasticity and function. If, as suggested by some authors, common neural input is associated with the requirement of coordinating the action of multiple muscles, further studies are needed to define the range of task conditions within which common neural input should or should not be modulated.

Even though the functional role of common neural input remains to be understood, analyses of the pattern of distribution of motor-unit synchrony have revealed important features of how neural drive is shared among hand muscle motor nuclei. Specifically, common neural input appears to be distributed in a muscle-specific fashion. The features of these patterns suggest the existence of a ‘functional gradient’ along which common neural input tends to be stronger across extrinsic than intrinsic hand muscles. Importantly, voluntary force modulation or fatiguing contractions do not affect the distribution of common neural inputs, therefore suggesting a fairly invariant neural network that might reflect functional differences across muscle groups. However, invariance of muscle-specific distribution of common neural input during short-term experimental manipulations does not rule out the possibility of plasticity in response to more prolonged practice or skill learning. A related question is whether the strength and distribution of common neural input is sensitive to sensory inputs. Although it appears that tactile feedback is not essential for across-muscle motor-unit synchrony or coherence, further work is needed to establish the role of sensory modalities that might be relevant to the performance of grasp or manipulation tasks.

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