Sensorimotor Learning in Virtual Environments

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# 1 Introduction & Aims

*Movement is nothing but the quality of our being.*

— Sunryu Suzuki

Hans Moravec’s eponymous paradox states that it is easier to generate artificially intelligent performance on tasks we think of as intellectually challenging, such as chess, than to provide a machine with faculties we take for granted, such as movement. For example, Moravec’s Paradox encourages us to not look past the stunningly complex computations generated by the human motor apparatus. Following Moravec’s suggestion, this work focuses on the human motor system, the most advanced control apparatus in the known universe.

A recent review corroborates this perspective and provides a clear call to action:

The processes by which biological control solutions spanning large and continuous state spaces are constructed remain relatively unexplored. Future investigations may need to embed rich dynamical interactions between object dynamics and task goals in novel and complex movements.[1](#ref-McNamee2019)

The generation of skilled movement is an open problem. The aim of this thesis is to progress our understanding of skilled movement by studying the solutions produced by human subjects to motor tasks in dynamically rich, yet controlled, virtual environments. Our goal is to reverse-engineer the ability to acquire and perform novel motor skills. First we define what we mean by the terms *skill*, and *task*.

Humans produce a great variety of movements every day, often without conscious thought. For example, movements like bringing a cup of coffee to our lips for a sip are generally out of reach for state-of-the-art robotic systems. We claim that this “motor gap” between biological and artificial motor systems is due to a lack of *dexterity* in the latter. Soviet Neuroscientist Nikolai Bernstein defined dexterity as the ability to “find a motor solution in any situation and in any condition.”[2](#ref-Bernstein1967) The crux of this definition is the flexibility of such solutions. This flexibility, or robustness[[1]](#footnote-20)[3](#ref-kitanoBiologicalRobustness2004), is the ability to optimize internal parameters in response to external perturbations and adapt to new information to achieve the goals of an ongoing plan.

While a robot may be able to move a cup of coffee to a precise location in space, its solution is often found to be brittle in a new context, or unable to generalize to the movement of new objects. We define a skill as a behavior that involves dexterity in Bernstein’s sense. The use of a tool such as a screwdriver is an example of a motor skill. We define a task as the production of skilled movement in a particular context. Driving a screw in a particular posture using a particular screwdriver is an example of a task. These concepts will be further formalized in later chapters.

Human movement is ultimately the result of the activation and contraction of muscle fibers, and movements lie on a spectrum between reflexive and volitional. The supramuscular circuitry which determines the degree of volition we ascribe to movement, where volitional movement relies on supraspinal (though not necessarily conscious) processes. The human hand is a unique evolutionary invention that underlies our ability to perform various skills in a range of tasks– movements that are decidedly volitional[[2]](#footnote-21). The hand is the pinnacle of dexterity, and for this reason we make the computations and circuitry that that drive it’s movements our focus. The physiology of the hand and it’s relation to skilled movement is described in Section [2](#sec:physiology).

Rather than studying hand movement at the level of kinematics, we chose to develop an experimental setup that is capable of recording from muscle activations directly. We achieve this through surface electromyographic recordings taken from the forearms controlling subjects’ dominant hands. This allows us to track the sequential selection of muscle these contractions during skill acquisition and subsequent goal-oriented muscle activations. As we are interested in subjects’ abilities to acquire new skills, we design tasks that require subjects to use available, but uncommon, motor activations. We then track the selection and execution of these activation during virtual tasks. The details of how this is achieved are described in Section ??.

Using data from our experimental setup, we hope to gain an understanding of how the structure of muscle activation variability in evolves during skill acquisition and how the motor system constructs skilled movement through the composition of component muscle coactivations. We believe that to make progress on these two lines of enquiry we should work to reconcile the language of the experimental sensorimotor control and learning community with the language of the control theory and reinforcement learning community, as each of these communities shares a common goal of understanding the computation underlying the production of skilled movement. Here we develop several models in this direction, as described in Section ??.

# 2 Physiology of the Motor System

## 2.1 Corticomotoneuronal Connections

Recent work has shown that monosynaptic cortical projections controlling the digits, the corticomotoneuronal (CM) tract, act in coordination with synergistic muscle activations of the hand to achieve control that is balanced between modularity and flexibility. These findings suggest that this bipartite structure in human motor cortex driving dexterous control of the distal part of the upper limb is due to evolutionary pressure to quickly generalize between tasks.

Jean-Alban Rathelot and Peter L. Strick. Subdivisions of primary motor cortex based on cortico-motoneuronal cells. Proceedings of the National Academy of Sciences, 106(3):918– 923, 2009. Tomohiko Takei, Joachim Confais, Saeka Tomatsu, Tomomichi Oya, and Kazuhiko Seki. Neural basis for hand muscle synergies in the primate spinal cord. Proceedings of the National Academy of Sciences, 114(32):8643–8648, 2017. Yutaka Yoshida and Tadashi Isa. Neural and genetic basis of dexterous hand movements. Current Opinion in Neurobiology, 52:25–32, 2018.

* Subdivisions of primary motor cortex based on cortico-motoneuronal cells (Rathelot, Strick PNAS 2008) https://www.pnas.org/content/106/3/918

x Corticomotoneuronal cells are “functionally tuned” https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4829105/

Although CM synapses exert powerful excitatory effectson alpha-motoneurons, the same motoneurons also receivemany other inputs (Fuglevand, 2011), including thosefrom Ia afferents, spinal interneurons, propriospinalneurons, reticulospinal neurons and rubrospinal neurons(Mewes & Cheney, 1991; Flamentet al.1992; Porter& Lemon, 1993; Perlmutteret al.1998; Riddleet al.2009). Any individual alpha-motoneuron receives thousandsofsynapticcontacts.Thehandfulofsynapticcontactsfroma given CM cell therefore does not consistently drive thedischarge of any particularalpha-motoneuron. (Schieber 2011)

rathelot, strick?

* “Following a century of detailed anatomical tract-tracing, electrophysiological investigation and careful lesion studies, our knowledge of the executive pathways through which ‘commands’ for movement must pass is unrivalled, yet we are still some way from really understanding how a movement is generated, which structures and pathways are involved and how they interact during the period leading up to movement onset.”
* The intense, synchronised output generated by electrical stimulation of macaque motor cortex evokes responses in hand and digit muscles with onset latencies of only approximately 10ms. These latencies are much shorter than the 60–100 ms between the onset of changes in M1 activity and the onset of muscle activity during voluntarily generated movements (Cheney and Fetz, 1980; Porter and Lemon, 1993).
* The discovery that M1 neurons can become active during observation of the actions of others, but without any overt signs of movement in the observer (Vigneswaran et al., 2013) adds to a long list of evidence that motor cortex can be active in a number of different states, all of which are quite distinct from movement itself (Schieber, 2011). These include preparation for movement (Shenoy et al., 2013), mental rehearsal and imagination (Cisek and Kalaska, 2004; Dushanova and Donoghue, 2010; Macuga and Frey, 2012).
* PTNs exhibit additional features that are consistent with a role as ‘command’ neurons. These include the fact that they make many collaterals to important subcortical motor structures, such as the red nucleus and the pontine nuclei (Ugolini and Kuypers, 1986), thereby providing ‘efference copy’ of ‘commands’ to the cerebellum.
* A further feature of some primate PTNs is that they make direct cortico-motoneuronal (CM) connections to alpha motoneurons (Porter and Lemon, 1993; Rathelot and Strick, 2006; Zinger et al., 2013), allowing the motor cortex direct access to spinal motoneurons. Of course, the CM system does not act alone, but in parallel with many other local interneuronal mechanisms and other descending pathways (Baker, 2011; Lemon, 2008), seg- mental (Takei and Seki, 2010) and propriospinal systems (Kinoshita et al., 2012). It is interesting that CM synapses on motoneurons are not subject to presynaptic inhibition (Jackson et al., 2006), suggesting that other systems (e.g. peripheral affer- ent inputs from the moving limb) do not use this mechanism to modify CM inputs to motoneurons, which would mean that information delivered by CM projections is allowed unfettered influence over target motoneurons.
* CM cells show changes in activity long before movement onset, far longer than the esti- mated conduction delays: thus CM cells exert their influence long before movement starts, but at a level that is subthreshold for motoneuron activation and subsequent movement.
* **CM cells are active for a whole range of different limb move- ments, including reach-to-grasp, precision grip and during tool- use by macaques (McKiernan et al., 1998; Muir and Lemon, 1983; Quallo et al., 2012). CM connections are particularly well- developed in primates with a high level of dexterity and who use tools. Interestingly, CM cells are characterised by showing not only increases, but also decreases in activity before and during precision movements (Maier et al., 1993; Quallo et al., 2012). Indeed, one way that M1 appears to control the pattern of muscle activity during grasp is to ‘disfacilitate’ the excitatory drive to motoneurons.** (Lemon Kraskov 2019)
* The primate corticospinal tract shows many interesting features that distinguish it rather sharply from the rodent pathway. These include the size and dis- tribution of fibres within the tract, with a small but probably very significant population of fast-conducting axons (Firmin et al., 2014).

## 2.2 Synergies

A considerable amount of research has focused on the existence of synergies as a simplifying structure in the motor system. We believe that the concept of synergies is often attributed to the process of motor control as opposed to a strict structural constraint. In this work, we use a bespoke experimental setup to track spatiotemporal dynamics of synergistic muscle activations across learning in a virtual, high-dimensional, electromyographic-driven task involving muscle contractions of the hand and forearm. We find that over trials the motor system adapts its synergistic action to fulfill the predefined task requirements in an optimal manner.

There are many variations on the motor synergy concept61; here we mean functional couplings of different joints or muscles such that motor control operates at the level of multi-joint coordination patterns ratherthan through independent control of all joints. Producing actionsat this slightly higher level of abstraction can facilitate explorationand learning of new skills as well as simplify planning. (Wayne Nature Comms Hierarchical Motor Control)

There is a longstanding debate about the origins of muscle synergies that strongly mirrors the nature-nuture debate. Are synergies learned or are they hardwired? If they’re hardwired, what physiological subsystem contains this hardwiring? We don’t need to take a side because there is clear evidence that humans overcome synergies to adapt their motor outputs to solve novel tasks and overcome all types of changes in the motor loop (injury, fatigue, prism goggles, etc.) via well-studied (in laboratory tasks at least) adaptation mechanisms [Helmholtz, Wolpert, Todorov, newer work on synergy shifts such as.[**DeRugy2012?**](#ref-DeRugy2012) The more interesting questions ask on what timescales and by what mechanisms does learning occur, and can we reverse engineer paradigms and tasks that improve the learning rate.

*There are very few tasks dealing with the hand in particular. What type of task would test the hypothesis that CM connections act to fractionate synergies of the hand such that we can tune a parameter of the task to require more or less influence of these direct connections? We would like to ask a user to fractionate synergies of the hand to different levels.*

This requires first mapping the intrinsic available dynamics of the hand per user.

We then would like to present fixed mappings between hand output (either through direct muscle activity or through a controller such as a force pad).

There is work suggesting that CM connections synapse primarily on low threshold motor units that are recruited first. This would imply a difference in synergy fractionation at lower force as opposed to higher force. This can be tested by adding a force parameter within a task.

This hunch was bolstered specifically by the work of Takei et al. in their 2017 PNAS paper:

It is generally believed that the direct corticomotoneuronal (CM) pathway, which is a phylogenetically newer pathway in higher primates, plays a critical role in the fractionation of muscle ac- tivity during dexterous hand movements. However, the present study demonstrated that PreM-INs, which are phylogenetically older, have spatiotemporal properties that correlate with muscle synergies during voluntary hand movements. Therefore, it is likely that these two systems have specialized functions for the control of primate hand movements, namely “fractionated control” and “synergistic control,” respectively. The interaction of these two putative control systems might be the source of the exceptional versatility of primate hand move- ments. For example, a power grip (e.g., gripping a hammer) is characterized by the predominant coactivation of hand muscles. It is known that power grip requires less involvement of the CM system, and therefore might result more from the PreM-IN system. Conversely, fine control of individual finger movements (e.g., control of a fingertip force of a single digit) requires higher fractionation of individual muscles and probably depends more on the CM system. Indeed, muscle synergies are not active during fine individual finger movements in some cases. Precision grip requires the fractionation of hand muscles as well as their coactivation, and thus might depend on cooperation of both the CM and PreM-IN systems. These examples suggest that the optimal balance of the two control systems may vary according to task requirements. Optimization of balanced control may be an important factor also for the acquisition of new motor skills. For example, Berger et al. demonstrated that learning a new movement that is compatible with existing muscle synergies occurs much more quickly than learning a movement requiring new muscle synergies. This implies that establishing, modifying, or masking muscle synergies requires more training. This might explain our everyday experience that highly fractionated movements require extensive practice (e.g., using chopsticks requires more extensive training than using spoons). This conceptual framework of balanced control systems may help future studies to clarify how our nervous system controls and acquires versatile hand functions.[**Takei2017?**](#ref-Takei2017)

This notion of an “old” and “new” motor cortex is not conceptual, but has been shown using viral tracing techniques.[**Rathelot2009?**](#ref-Rathelot2009)

As I see it, the goal is to build a falsifiable model which takes into account the bipartite structure of M1 into account, and find tasks that ostensibly require the direct descending connections to fractionate learned synergies. In effect, the hypothesis to test is that CM connections override the “consolidated” patterns putatively generated via spinal circuitry.

Thus, this is a learning question, an experimental problem, and a modeling task rolled into one. We have a good hunch that is backed up by solid work. The question comes down to how much we can learn by recording as much muscle activity as we can and designing very clever tasks to test very clever models.

* Neural basis for hand muscle synergies in the primate spinal cord https://www.ncbi.nlm.nih.gov/pubmed/28739958

Two mutually non-exclusive scenarios can be envisioned as to how corticospinal (and reticulospinal –see Baker, 2011, this issue) pathways might be organized to coordinate the activities of multiple muscles needed to perform finger movements (Schieber, 1990). In one,separate pathways operate on each of the requisite motor nuclei. In the other, selection of the muscles into functional groups is determined in part by the pattern of divergence of individual descending pathways across different motor nuclei in the spinal cord. This latter type of organization,while less flexible, might underlie the assemblage of muscles into synergistic groups that serve as the building blocks of the behavioural repertoire of an animal. In contrast to the extrinsic muscles of the dominant hand described above, virtually no short-term synchrony was observed across intrinsic muscles participating in the precision grip (McIsaac & Fuglevand, 2008). This result suggests that the descending pathways that control the activities of intrinsic muscles provide more concentrated input to individual motor nuclei than those pathways destined for motor nuclei innervating extrinsic hand muscles. The contrasting organizations of the descending pathways targeting extrinsic and intrinsic muscles seem in harmony with postulated functions of these two groups of muscles(Longet al.1970). Intrinsic muscles configure the digits to the unique dimensions of an object to be handled. HighlyFigure 5. Mean (SD) common input strength (CIS – index representing magnitude of short-term synchrony; Nordstrometal.1992) for pairs of motor units residing in the same compartment or adjacent compartments of three human multi-tendoned hand muscles, extensor digitorum (ED), flexor digitorum superficialis (FDS) and flexor digitorum profundus(FDP)Mean (SD) CIS values: ED same=0.70 (0.30), ED adjacent=0.41(0.18), FDS same=0.45 (0.30), FDS adjacent=0.27 (0.17), FDPsame=0.47 (0.19), FDP adjacent=0.36 (0.21). Values inside ofbars indicate number of motor unit pairs. Data compiled from:†Keen & Fuglevand (2004b); McIsaac & Fuglevand (2007); McIsaac& Fuglevand (unpublished data); Winges & Santello (2004).independent pathways, therefore, enable the fractionated actions of the digits needed for such a function. Extrinsic muscles provide the primary gripping forces during object manipulation. Because gripping necessitates the production of precisely counterbalanced forces between the thumb and one or more fingers, extrinsic muscles have their activities linked by divergent descending inputs. (Fuglevand 2011)

### 2.2.1 Precision Grip

Results imply that descending pathways diverge extensively to operate on the two motor nuclei supplying thumb and index finger muscles as a unit and thereby compel them to operate in unison. Interestingly, such across-muscle synchrony was seen only in the dominant but not in the non-dominant hand (Fig. 4). Whether such lateralized differences are laid down early in development or represent plastic changes associated with chronic usage are questions currently under investigation. (Fuglevand 2011)

Statistics of Natural Movements Are Reflected in Motor Errors (Wolpert) https://www.ncbi.nlm.nih.gov/pubmed/19605616

Structural Learning, Wolpert+Braun+Mehring https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2692080/

### 2.2.2 Skilled Piano Performance

In piano performance, for keystrokes with each of the four fingers during playing various tone sequences, the hand kinematics was characterized by three distinct patterns of finger joint coordination (Furuya et al., 2011a). The motion of the striking finger was consistent across these patterns, whereas the motion of the non-striking fingers differed across them. This was interpreted as evidence for the independence of movements across fingers. In addition, the amount of movement covariation between the striking and non-striking fingers was similar, independent of which finger was used for a keystroke. The finding was in contrast to non-musicians who displayed a hierarchy of independence of finger movements, the middle and ring fingers being less individuated than the index and little fingers (Häger-Ross and Schieber, 2000; Zatsiorsky et al., 2000). The equal independence of movements across fingers can be therefore achieved by extensive piano training. This idea is supported by superior independence of finger movement control for pianists as compared to non-musicians (Slobounov et al., 2002; Aoki et al., 2005), which possibly occurs due to changes at biomechanical and neural levels (Chiang et al., 2004; Smahel and Klimová, 2004). (Shinichi Furuya\* and Eckart Altenmüller 2013)

In piano performance, not all digits necessarily move for the production of a tone. Depending on contexts and task demands, some digits either move anticipatorily to facilitate production of upcoming acoustic events or even do not have to move. The former anticipatory modification of the movements is called coarticulation and serves as a mechanism that ensures smooth succession of sequential movements such as speech (Ostry et al., 1996) and finger spelling (Jerde et al., 2003). This coarticulation was also evident in piano playing, particularly when the hand posture changes dynamically (Engel et al., 1997). For example, the fingers and wrist initiated preparatory motions 500 ms prior to the thumb-under maneuver, which facilitated the subsequent horizontal translation of the hand. Finger muscular activity also provided evidence supportive for co-articulation in piano playing (Winges et al., 2013). The balance of burst amplitudes across multiple muscles depended on the characteristics of the preceding and subsequent keypresses, forming neuromuscular co-articulation throughout the time course of sequential finger movements. (Shinichi Furuya\* and Eckart Altenmüller 2013)

### 2.2.3 Muscular and Postural Synergies of the Human Hand (Weiss & Flanders 2004)

Single motor units receive a variety of motor commands, and the net result may be that neighboring units in the same muscle are preferentially recruited to produce forces in different directions 3D space or to hold the hand in different static postures. The corollary to this is that a given force or posture involves a collection of units that spans many muscles.

The motor system is distributed in order to solve the redundancy problem as well as to learn new control schemes.

### 2.2.4 Analysis of the synergies underlying complex hand manipulation (Todorov & Ghahramani 2005)

Remarkably, the dimensionality in the individuated joint task was 8.7, or only 2 higher. The latter task is designed to reveal the maximal number of degrees of freedom humans have access to. Why this number is not 20 is unclear; the most likely reason is biomechanical coupling, although limitations in neural control may also play a role. Furthermore, the number 8.7 intuitively seems too low suggesting that such counting methods may underestimate the true dimensionality.

### 2.2.5 The statistics of natural hand movements (Ingram & Wolpert 2008)

### 2.2.6 Neural Basis of Muscle Synergies, Bizzi Cheung 2013

Note that there are a great number of tasks, and the case for synergies in the motor system cannot be answered simply. Here we are concerned with motions of the hand because we know that this is the endpoint of CM connections. There are many fewer tasks dealing with this system in particular. Most tasks deal with arm reaching, though the most highly cited synergy paper deals with a 1DOF kick.[**DAvella2003?**](#ref-DAvella2003)

### 2.2.7 Porter & Lemon

It is clear that humans have the capacity to learn single motor unit (SMU) activation of the digits. Given what we know about voluntary movement and human digit control it is likely that this activation is under motor cortical control. This ability is somewhat surprising for two reasons:

1. Individual corticomotoneurons contact multiple motor pools, and rarely (if ever) individual motor neurons.
2. There is no physiological reason for the nervous system to have the ability to control individual muscles. The CNS (motor cortex in particular) is more likely to generate “complex” movements requiring simultaneous control of multiple synergistic muscle groups.

Given the fact that most CM cells appear to facilitate activity in several muscles, inhibition would appear to be essential for the recruitment of an individual muscle without any concurrent activity in its functional or anatomical synergists. But how is this inhibition recruited and maintained during and after learning?

I see two opportunities with this project. The first is practical: if we can generate definitive experimental evidence and a working theory for what is involved in voluntary control of single MUs in the forearm, we can build a ground-truth dataset for spike waveforms of various muscles under various conditions. The second is experimental: we can manipulate pertinent types of sensory feedback with the goal of answering interesting questions about the interplay between proprioception, agonist-antagonist interaction, and Renshaw cell functionality while building an understanding of how dynamics can be shifted for voluntary action to reverse engineer a learning process from the cellular level.

I’ve written below a little more background and detail on what I am thinking about, and would welcome your feedback and critique.

insights from studying the corticospinal tract

The brain seems a thoroughfare for nerve-action passing on its way to the motor animal. It has been remarked that Life’s aim is an act, not a thought. Today the dictum must be modified to admit that, often, to refrain from an act is no less an act than to commit one, because inhibition is co-equally with excitation a nervous activity. (Sherrington, Rede Lecture, 1933)

Since we’re working with a voluntary movement ostensibly of the digits, we know that we’re going to be dealing with the corticospinal tract. I discovered a book called The Corticospinal Tract and Voluntary Movement by Porter and Lemon (1995) – it’s awesome. I highly recommend it, especially Chapter 4. The book focuses mainly on the hand, and Roger Lemon seems to be a living legend.

The key insights from P&L:

The spinal cord’s neuronal organization is based on relatively rigid muscular synergies, and a mechanism to fractionate this is of particular importance for the muscles of the hands and digits which may need to be employed in a variety of flexible associations during voluntary movements.

[Obviously] the structure of corticospinal connectivity places a constraint on the number of possible output arrangements that can be employed by the cortex…

We can conclude that the fundamental organizing principle of the cortico-motoneuronal output is one of influence over activity in multiple muscles.

[Fetz 1980] found that 67 percent of their corticomotoneuronal cells contacted more than 2 of the 5–6 different muscles sampled, and that the mean number of muscles facilitated per cortico-motoneuronal cell was 2.4. […] The majority of CM neurones (59 per cent) produced pure facilitation of either an agonist or antagonist, and cofacilitation of both was extremely rare. The second most common pattern (30 percent of CM cells) was facilitation of agonists and postspike suppression of antagonists.

Findings suggest that CM cell axons branch to innervate many (if not all) motor units within the motor nucleus of its target muscle.

The widespread synaptic impacts made within the motor nucleus of a single muscle would allow a single CM cell to exert a facilitatory influence over many different motoneurones, and therefore to contribute to motoneuronal activity over a range of EMG and force levels. A similar distributed system of synaptic connections has also been observed for muscle spindle afferents (Mendell and Hennemann 1971).

There are a large number of possible sources of common input to spinal motoneurones, including segmental afferent inputs from muscle spindles and other peripheral receptors. However, several lines of evidence suggest that, at least for hand muscle motoneurones, much of the short-term synchrony has a corticospinal origin.

Both refined histological and electro-anatomical observations on single corticomotoneuronal fibres in the monkey indicate significant divergence of the intraspinal collaterals of these fibres to impact on a large number of motoneurones. It is possible that, for some muscles acting about the distal joints of the limb, most or all of the motoneurones are engaged by synapses from each cortico-motoneuronal fibre which includes that muscle within its muscle field. The synaptic boutons that generate the cortico-motoneuronal synapses are small in size and only one or a few boutons are contributed to the motoneuron’s dendritic surface by each cortico-motoneuronal collateral. The contribution to the synaptic excitation of a motoneurone that is made by any one cortico- motoneuronal fibre is small. However, because of the high degree of convergence of intraspinal collaterals from a large colony of cortico-motoneuronal neurones on to each motoneurone of a distally acting muscle, this synaptic influence could allow fine grading of the depolarization of the motoneurone, contribute to the selective activation of motor units during voluntary movement and be critically effective in the fractionation of muscle usage during different motor tasks.

other literature (work on the extensor digitorum communis)

Things we still don’t fully know (that are probably beyond the scope of this project):

1. How extensive is the CM projection?
2. How many CM cells project to a given motoneuron or to a given muscle?
3. how large are the postsynaptic CM effects in a given motoneuron? [Lemon 2008]

Renshaw cells might play a role in isolating single MUs:

It is concluded that Renshaw cells de-correlate discharge patterns of different motoneurones of the same pool by injecting uncorrelated signals into them. This decorrelation is an important prerequisite for distortion suppression of signal transmission in a multi-channel system, like that of stretch reflex, and for its linearization. [Adam 1978]

Another report that people don’t know how they’re learning to isolate SMUs:

Although subjects used auditory synchrony feedback, they were generally unable to evaluate their success in modulating the amount of MU synchrony; nor could they describe any conscious strategy used during the successful sessions. They concentrated on the

occurrence of the synchrony pulses, rather than on the amount of EDC contraction or the concurrent force output. [Schmeid, 1993]

Implications that CM cells are responsible for fast changes in MU dynamics:

The present changes in short-term synchronization were detected in the course of the conditioning session and must reflect rapid alterations in the relative contributions of common inputs. One direct mechanism would involve a change in the proportion of descending monosynaptic input, such as the corticomotoneuronal cells that strongly affect EDC motoneurons (Phillips and Porter 1977; Fetz and Cheney 1980). [Schmeid, 1993]

Statement of unknowns about how dynamics are shifted at the MU level in terms of spinal circuitry:

Indirect control of MU synchronization might also be mediated by supraspinal modulation of the Renshaw decorrelating action (Gelfand et al. 1963; Adam et al. 1978), or by enhanced activity of spindle afferents via selective activation of gamma-motoneurons (Rudomin 1989). These possibilities suggest further experiments to resolve the neural mechanisms by which humans could rapidly alter short-term synchrony of MUs and, by implication, control the proportion of last-order common inputs to motoneurons. [Schmeid, 1993]

# 3 Motor System Physiology

Muscles are collections of fibers that contract when chemical gradients are produced at the neuromuscular junction by action potentials emanating from neurons in the ventral horn of the spinal cord.

Electromyography is the detection of changes in chemical potential using electrodes. In my setup, we use a total 64 monopolar surface electrodes and monopolar needle electrodes to record chemical potentials from muscles in the forearm and hand.

## 3.1 Motor Units

The motor unit, namely a motoneurone and the many muscle fibres singularly innervated by branches of the motoneurone’s axon, is the quantal element underlying the transduction of neural commands driving the exquisite motor behaviours produced by the hand. (Fuglevand 2011)

Experimental work characterizing motor unit properties in humans and other mammals has been consistent with regard to two findings(see Fuglevandet al.1993). First, twitch or tetanic forces of motor units that constitute a muscle vary over an extremely wide range, usually 100-fold or greater. And second, the frequency distribution of motor units according to force capacity is markedly skewed toward motor units that produce small forces, with few units that generate large forces. (Fuglevand 2011)

One consequence of this organization is that fine resolution of force is an in-built control feature, such that when performing delicate motor tasks involving weak muscle contractions, subtle adjustments in force can be accomplished by drawing upon a large population of weak motor units. (*this is logarthmic in the number of units recruited*) (Fuglevand 2011)

**Motor unit number itself seems to play a critical role in determining precision of muscle force. When human subjects attempt to produce a constant force during isometric contractions, the force inadvertently fluctuates about the specified target level. Such force variability increases in roughly in proportion to the target force(Enoka et al.2003). Unexpectedly, this noise in force control is greater for hand muscles compared to more proximal muscles (Hamilton et al.2004). Furthermore,based on available estimates of motor unit numbers and computer simulation, a key factor underlying greater noisiness in hand muscles was relatively low numbers of motor units (Jones et al.2002; Hamilton et al.2004). In addition, augmented force variability in hand muscles maybe related to greater variability and common modulation in motor unit discharge rate compared to more proximal muscles (Negro et al.2009). Therefore, the widely held view that hand muscles are optimally designed for fine control may require reconsideration.** (Fuglevand 2011)

While there are anatomical (Feinsteinet al.1955) and electrophysiological (McComaset al.1971; Bromberg,2007) means to estimate motor unit numbers in humans,both methods are susceptible to several sources of error.Perhaps the most reliable information at present available about relative numbers of motor units supplying different muscles comes from retrograde labelling of motoneurones in non-human primates. In such studies, intrinsic hand muscles have been shown to be innervated by approximately 50–200 motoneurones, while more proximal muscles like biceps and triceps brachii are each supplied by more than 1000 motoneurones (Jenny & Inukai, 1983). (Fuglevand 2011)

## 3.2 Kinematics

The human hand has approximately 20 degrees of freedom in its 19 joints, but the number of dominant modes of activity is much lower due to mechanical coupling.

27 bones and 36 muscles (???)

There are 31 muscles of different and often complex architecture involved in hand movement with 19 residing in the hand (the intrinsic hand muscles). The hand has 19 articulations, 18 tendons crossing the wrist, and at least 25 degrees of freedom. (Duinen & Gandevia 2011)

## 3.3 Forearm

the deep flexor attaches to the distal phalanx the superficial flexor attaches to the middle phalanx

The main finger extensor, extensor digitorum (ED), when active generates torque about the elbow, wrist, metacarpalphalanegeal, proximal interphalangeal and distal interphalangeal joints simultaneously (Anet al.1981). Moreover, ED, likeits flexor counterparts, flexor digitorum superficialis and flexor digitorum profundus, gives rise to four distal tendons that insert into each of the fingers.Therefore, attempts to move a single finger in isolation require that other muscles be co-activated to counteract the unwanted actions produced by the agonist (Schieber, 1995; Valero-Cuevas, 2000). (Fuglevand 2011)

Three major forearm muscles consist of multiple muscle bellies with tendons to each finger so that the muscles have four ‘compartments’ (Duinen & Gandevia 2011)

Force and displacement interactions can occur within muscles, an issue of particular concern given that ﬂexor digitorum profundus (FDP), ﬂexor digitorum superficialis (FDS) and extensor digitorum (ED) are muscles with tendons to each of the fingers. These interactions may occur, for example, because a motor unit’s territory is such that force is ‘injected’ into more than one distal tendon. This sort of ‘lateral’ force transmission exerted by individual muscle fibres and motor units can be significant in some animal preparations (e.g. Street, 1983; see also Young et al. 2000). The topic of lateral force transmission is controversial but it appears that such an effect can even result in inter-muscle force transfer (e.g. for review Patel & Lieber, 1997; Huijing, 1999, 2009). This process has been most studied in the lower limb for gastrocnemius and soleus in animals (for details see Maas & Sandercock, 2008) but some evidence exists for it in humans (e.g. Bojsen-Moller et al. 2010). However, the unresolved issues are the magnitude of these effects and the conditions under which they are functionally significant. (Duinen & Gandevia 2011)

If hand muscles do not always behave as simple in-line motors, then the spread of their mechanical effects must depend on the links of force–length curve, viscoelastic properties, and the changes induced by muscle contractions. Such detailed biomechanical information is largely lacking. (Duinen & Gandevia 2011)

Spillover has been shown in experiments studying the ‘recruitment thresholds’ (defined below) of motor units ac ting on other digits during single digit contractions (Kilbreath & Gandevia, 1994; Butler et al. 2005; van Duinen et al. 2009). In these experiments, motor units were recorded from one (test) compartment of the respective muscles, while subjects were asked to contract the compartment of the other digits up to 50% of their maximal force. When the subjects contracted these other digits (one by one), motor units of the test compartment were often recruited. The amount of force produced by the other digits at the time of recruitment of the motor unit of the test compartment is termed the recruitment threshold. The general finding for all three muscles was that, the closer the contracting compartment to the test finger, the more motor units were recruited. (Duinen & Gandevia 2011)

One has to ask whether this spillover is functional. Is the frequent recruitment of motor units ac ting on the little finger when we extend the thumb part of a fixed pattern of muscle activation, perhaps to balance forces around the wrist? (Duinen & Gandevia 2011)

Until recently, most studies looked at either flexion or extension, but when we compare the amount of enslavement in flexion and extension, the enslaved forces in extension are higher than in flexion, when recorded in the same apparatus. We hypothesise that the level of enslavement might depend on the amount of individual daily usage (for data on usage see Ingram et al. 2008). (Duinen & Gandevia 2011)

When multiple digits had to contract, the subjects were not able to reach their maximal force, thus showing a force ‘deﬁcit’. These deﬁcits may be comparable to those when trying to produce force with two hands or arms, a phenomenon known as the bilateral deﬁcit (Gandevia, 2001).

## 3.4 Hand

The intrinsic hand muscles can also be activated almost maximally (e.g. Merton, 1954; Herbert & Gandevia, 1996), but they are special in that they can be ‘controlled’ at very low levels, even below the recruitment threshold for the earliest recruited units (Gandevia & Rothwell, 1987). (Duinen & Gandevia 2011)

## 3.5 Thumb

The human thumb confers great scope for dexterity and its long length relative to the index gives it the highest ‘opposability index’ among primates (Napier, 1972), while its rotated first metacarpal and unique carpometacarpal joint enhance its range of movement for grasping and manipulation (Wood-Jones, 1949). Furthermore, the thumb is moved by a muscle in the forearm, ﬂexor pollicis longus (FPL), which provides the only way to ﬂex its distal joint and is rudimentary in apes. (Hiske van Duinen and Simon C. Gandevia 2011)

The presence of FPL in humans is associated with a high capacity to s ense thumb voluntary forces at remarkably low levels compared even to intrinsic hand muscles (muscles with their origin and insertion in the hand; Kilbreath & Gandevia, 1993) and to detect length changes at its distal joint (Refshauge et al. 1998). (Hiske van Duinen and Simon C. Gandevia 2011)

## 3.6 Muscle Spindles

Arm movements are sensed via distributed and individually ambiguous activity patterns of muscle spindles,which depend on relative joint configurations rather than the absolute hand position. Interpreting this high dimensional input (around 50 muscles for a human arm) of distributed information at the relevant behavioral level poses a challenging decoding problem for the central nervous system. Proprioceptive information from the receptors undergoes several processing steps before reaching somatosensory cortex (3,8) - from the spindles that synapse in Clarke’s nucleus, to cuneate nucleus, thalamus (3,9), and finally to somatosensory cortex (S1). In cortex, a number of tuning properties have been observed, such as responsiveness to varied combinations of joints and muscle lengths (10,11), sensitivity to different loads and angles (12), and broad and unimodal tuning for movement direction during arm movements (11,13).The proprioceptive information in S1 is then hypothesized to serve as the basis of a wide variety of tasks, via its connections to motor cortex and higher somatosensory processing regions. (Sandbrink & Mathis, 2020)

## Bibliography

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3. Kitano, H. Biological robustness. *Nature Reviews Genetics* **5**, 826–837 (2004).

1. Kitano defines robustness as “the maintenance of specific functionalities of the system against perturbations, and it often requires the system to change its mode of operation in a flexible way.” He claims that robustness requires control, alternative mechanisms, modularity and decoupling between high and low level variability. [↑](#footnote-ref-20)
2. It could be argued that the hand is in fact a crucial aspect of humanness. It is thought that the human cerebellar and neocortices evolved reciprocally to expand and support the computational burden of increasingly complex motor tasks such as tool-making and language production. REF? [↑](#footnote-ref-21)