

Sensorimotor Learning in Virtual Environments

Spencer R. Wilson

February 5, 2021

1 Introduction & Aims

Movement is nothing but the quality of our being.

— Sunryu Suzuki, *Zen Mind, Beginner's Mind*

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

Over the last few decades, there has been considerable amount of work done to untangle the abilities of the motor system to flexibly control the body including through optimal control theory², reinforcement learning in continuous action space³, and detailed physiological studies⁴. However, as the quote above suggests, a holistic understanding of the computations underlying the generation of skilled movement remains 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.”⁵ The crux of this definition is the flexibility of such solutions. This flexibility, or robustness¹⁶, 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.

¹Kitano 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.

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 volitional². The hand is the pinnacle of dexterity and, as such, it is a fruitful testbed for studying the computations and circuitry that drive dexterous movement. A detailed physiological review of the hand and its relation to skilled movement is described in Section 2.

We are more interested in the leveraging the hand as a readout of flexible motor behavior than we are in the kinematics of hand movement itself. For this reason, we chose to develop an experimental setup that is capable of recording directly from muscle activations. We achieve this through surface electromyography 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 3.

how are value computations connected to action and policy selection how are feedback controllers adapted to motor errors, new environments, how are they learned as well as combined?

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 5.

2 Physiology of the Skilled Movement

Even a simple movement is a global body event.

— Bizzi & Ajemian, 2020

As we hope to make progress engineering naturalistic artificial movement, it will be beneficial to review what is known about the biological movement system. Beginning with the architecture of the motor system and its relation to dexterity will provide a scaffold on which we can hang our experimental and theoretical investigations detailed in Section 3 and Section 5. Specifically, we can use results from prior physiological investigations to ground our perspective on the computations relevant to skilled hand movements. We find that the dexterous solutions produced by the human motor system rely on an incredibly complex architecture, but one in which a spectrum of modularity and redundancy appear to be organizing principles.

2.1 Motor Units to Muscles

Muscles are composed of fibers which contract due to chemical gradients produced at the neuromuscular junction by action potentials emanating from alpha-motoneurons (AMN) in the ventral horn of the spinal cord. The quantum of motor output is the motor unit (MU), which is defined as a single motoneuron axon and the set of junctions its axon branches form with one or more muscle fibers. The innervation ratio of a particular muscle unit is the number of junctions it innervates. In muscles of the arm, the number of MUs and their innervation ratios each range from tens to hundreds per muscle and per motor unit, respectively, decreasing as muscles become more distal.

²It 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?

The MU thus provides the motor system with spatial redundancy at the muscle level: multiple muscle fibers contract due to a single AMN spike, and multiple AMNs may overlap in their innervations. The forces produced by motor units span several orders of magnitude, though most units produce very small forces. Here we find temporal redundancy: in order to produce movements, MUs combine to generate a range of forces⁷.

Since the innervation ratios of muscles in the forearm and hand are relatively small compared to more proximal muscles (which contain thousands of MUs), the logarithmic recruitment and redundancy of motor units enables the hand to produce movements with very fine spatiotemporal resolution. Paradoxically, however, the well-known signal-dependent noise in models of motor output has been found to be higher for hand muscles than for more proximal muscles, likely due to small numbers of motor units compare to larger muscles^{7,8}.

Muscle fibers are contained within muscle compartments, and each muscle may have one or more compartments. The fingers of the hand are extended by the extensor digitorum (ED) which contains four compartments, one for each of the tendons the muscle produces. Each tendon connects to the three metaphalangeal joints of each digit. The fingers are flexed by two muscles, the flexor digitorum superficialis (FDS) and the flexor digitorum profundus (FDP). Like the ED, these muscles produce four tendons, one to each finger from each of their four compartments. As such, one must coactivate these agonist and antagonist muscles in order to extend or flex a single finger in isolation⁷. Adduction and Abduction of the fingers is produced by the 19 intrinsic muscles of the hand, each of which has their origin and insertion points within the hand itself⁹. The intrinsic muscle tendons form a kind of network around each of the digits.

The human hand, thumb, and forearm system contains more than 30 muscles and at least 20 degrees of freedom are theoretically available for actuation. However, due to biomechanical coupling, the effective degrees of freedom is presumably less than 20. One study found that tendons of the fingers are arranged in such a way as to perform a kind of anatomical computation which expands the mechanical capabilities of the appendage by sharing force across its tendon network¹⁰. Such computations embedded in the musculoskeletal structure are additional complexity when theorizing about neural control of the hand.

We believe this structure exists in order to facilitate the acquisition of new skills and the generalization of existing skills to new contexts. While the anatomy of the hand and forearm presents constraints on movement, the system remains capable of producing a incredible variety of movement patterns^{11,123}. The structure of the neuromuscular system that underlies this variety offers many clues as to the relevant computations required for dexterous movement.

2.2 Coordinative Structures

We have some idea as to the intricate design of the puppet and the puppet strings, but we lack insight into the mind of the puppeteer.

— Bizzi & Ajemian, 2020

Nikolai Bernstein coined the phrase “the degrees-of-freedom problem” to describe the challenge the motor system faces in coordinating its many dimension to achieve a goal. Solving this problem requires dexterity.⁵ As we have seen, redundancy is present from joints and muscles to motor units and their upstream synaptic partners. However, rather than asking how the motor control system deals with this “problem” overwhelming complexity, we might instead question why this complexity is evolutionarily advantageous at all. What does the availability of this redundancy afford the motor system? How does this redundancy enable dexterous movement?

A considerable amount of discussion has focused on the existence of synergies as a simplifying structure which allows the motor system to “solve” the redundancy “problem”. The term motor synergy can be used descriptively to describe the spatiotemporal coactivation of muscles necessary for an ongoing task. Synergetic control implies control in the space of a low-dimensional set of

³In a classic study, Basmajian and colleagues showed that it is possible to activate single motor units in the thumb abductor.

synergy weights rather than independent control over the actuator dimensions themselves. The control dimensions are functionally coupled as a result of synergetic action, which both simplifies the control task and constrains behavior to the low-dimensional subspace defined by the synergy weights¹³. This is what Bizzi and colleagues refer to as “the puppet’s strings”. The term can also be used as a normative model of motor coordination which implies a constraint in the dimensionality of the descending supraspinal control signal, the simplifying movements of the puppeteer.

Many studies have contributed to the concept of synergies as a hard-wired organizing feature of the motor system^{14,4}. However, these works tend to extrapolate from non-primate preparations, particularly in the frog, and use tasks which are inherently low-dimensional to explain covariance structure in primate and human kinematic and electromyography data^{15,Gao2017?}. That said, it would be foolish to deny the existence of synergistic muscle coactivation even at the structural level. Careful studies of force control by the fingertips present a complex story of dimensionality of control in this regime.¹⁶ Constraints exist in the architecture of the hand as well as its control system, though we maintain that concept of synergies, especially in the context of dexterous movement, is often presented as an oversimplification rather than a mere simplification. We believe the story of the hand is more complex.

Studies have attempted to quantify the number of effective degrees of freedom of the hand with various methods. This has primarily been taken to be the number of linear features which contain a desired level of the original signal variance, where the signal is the joint angles of the hand engaged in various behaviors^{17,18}. These methods have resulted in roughly 8 linear features of hand kinematics to solve a variety of tasks, with subtleties found in inter-task and inter-subject variations.[^][It has been argued that the motor repertoire is hardly high-dimensional when compared to the dimensionality of the visual feature extraction system¹¹. A recent study found that low-variance linear, kinematic components displayed significantly higher correlation within condition (e.g. grasp of a specific object) than across condition. This suggests that these components carry task-dependent information rather than condition-independent, task-irrelevant noise¹¹. This suggests that the control of the hand is more nuanced than a set of fixed synergies.

What Bizzi and colleagues call “the problem of supraspinal pattern formation”—how synergies are activated through time— we argue, in the context of hand control, is not simplified by the existence of hard-wired or soft-wired synergies¹⁹. Rather, the CNS produces control signals in a range of contexts and in response to continually changing task demands. Rather than the CNS “simplifying movement” through synergetic action, it is more likely that hand synergies fall out of an optimization strategy which trades off effort and accuracy where effort may, in part, correspond to independent control of individual control dimensions. In this view, synergies, hard-wired or not, reflect the statistics of the environment in which movement is constructed²⁰. If we limit ourselves to synergetic control, then we have simply passed the problem to a lower-dimensional one of the same fundamental nature. Neural control of the hand likely contains a spectrum of modularity in order to maintain its role as a flexible instrument. Synergetic action is one end of this spectrum resulting from the computation and structure of the human movement machine.

2.3 Fractionating Structures

At the other end of the spectrum, years of research has contributed to a more complex picture of hand function which embraces non-synergistic movement^{21–23}. The key insight of the work is that while “the organization of the spinal cord is based on relatively rigid muscular modes, 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.” Careful anatomical work has shown how monosynaptic corticospinal, or corticomotoneuronal (CM), connections provide such fractionation in primates which use tools requiring dexterity²⁴. M connections are specific to the primate corticospinal tract and specific to distal muscles of the hands and arm. It appears that the rodent CST contains CM connections until they recede around P10 at which point they recede^{25,26}.

⁴I should really have more studies here, or a really nice review.

Just as many muscle fibers may be innervated by a single AMN, up to thousands of neurons contact single AMNs through CM connections or a variety of spinal interneuron circuits. The hallmark of CM connections is their influence over multiple muscle compartments as well as multiple muscles, though typically agonist or antagonist sets²⁷. This may seem counter-intuitive as a means to produce individuated movement, but experimental evidence in primates has show that the convergence of many CM collateral fibers onto single AMNs driving the distal muscles in particular can produce a fine grading of activity over motor units driving the distal joints. CM cells also appear to play a role in the inhibition of antagonist muscles prior to contractions required for movement.²⁸ These findings confirm theories about the excitatory and inhibitory role of these connection dating back decades, and combine to suggest that variables encoded in cortical ensembles are more complex than kinematics or dynamics alone.²⁷.

The CM tract thus acts in coordination with synergistic muscle activations of the hand to achieve control that is balanced between modularity and flexibility. Findings suggest that there is a bipartite structure in human motor cortex driving dexterous control of the distal part of the upper limb which, it has been suggested, evolved under pressure to quickly generalize between tasks. This work argues that these two streams of hand control, namely “fractionated” and “synergistic” control, may interact to produce versatility, and balancing these subsystems may be a key part of the optimization function when learning new skills^{29–31}. This dualism is likely not rigidly dichotomous, but rather a spectrum of overriding fractionation (so-called “New M1”) atop a phylogenetically older system of synergistic action³². Griffin and colleagues found that CM cells are functionally tuned to a muscle’s mode of activity (agonist, antagonist, fixator) to “bypass spinal cord mechanisms and sculpt novel patterns of motor output that are essential for highly skilled movements”.³⁰

The degree to which fractionation of movement is learned is unknown. Skilled piano performers have been found to exhibit a higher degree of independent movement among the fingers compared to control participants. Control groups displayed a hierarchical, presumably lower dimensional, organization of finger movement patterns while pianists showed distinct but individuated movement patterns³³. These results are imply that with skilled practice humans can produce finer and more independent movements of the fingers, and construct bespoke coactivations to solve specific goals. Similarly, studies have found that coherence between the index finger and thumb is greater on the dominant hand. This might imply a developmental lateralization, but use-dependent plasticity due to greater precision grip behavior of the dominant hand is also a viable explanation⁷.

The concept of a balanced control may prove to be a fruitful direction for theoretical work on dexterous motor control, the goal being to construct a model which takes into account this spectrum of individuation into account. The experimental challenge is to identify tasks which ostensibly require the direct descending connections to fractionate learned synergies. There is work suggesting that CM connections synapse primarily on low threshold, low force 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 easily by including a force parameter in a hand control task. The hypothesis stemming from the previously described work is that CM connections override the “consolidated” patterns putatively generated via spinal interneuron circuitry.

2.4 Flexibility in Spinal Circuits

I added this section on Friday!

Looking at rapid visuomotor responses, this work found that these reflexive movement were modulated by the value of multiple goals, just as in cognitive tasks. This supports the idea that there exists flexibility at all “levels” of the hierarchy, all receiving similar feedbacks and all similarly modulated by context: > If low-level sensorimotor circuits can contribute to value-based decisions through continuous feedback control, rather than merely executing the outcome of discrete action decisions taken in higher-order brain areas, it would support for the hypothesis that value-based decision algorithms are distributed throughout multiple levels of sensorimotor and cognitive processing hierarchies (Hunt et al., 2014; Hunt and Hayden, 2017). This notion differs from the traditional view that decisions arise from a serial process with modular units for choice evaluation, value comparison and action selection. According to the alternative view, the basis for decisions is

mutual inhibition between neural representations of alternative options, and these computations occur simultaneously in multiple brain areas along both motor and abstract-value dimensions of tasks (Wang, 2012). Our current evidence that value-based decisions can be implemented through sensorimotor feedback control supports the alternative view, and the general notion that behavior emerges via a distributed consensus between circuits engaged nominally in decision and sensorimotor processes (Cisek, 2012).³⁴

When we move, the brain specifies a set of feedback control gains that enable low-level motor areas not only to generate efficient and accurate movement, but also to rapidly and adaptively respond to evolving sensory information in a manner consistent with value-based decision-making.³⁴

Spinal stretch reflexes may also be modulated by posture, like in Graziano’s work: > We found that changing the arm’s orientation diametrically altered how spinal reflexes in the elbow muscles were evoked, and in such a way that were again efficiently scaled to the hand’s distance from the target. These findings demonstrate that spinal circuits can help efficiently control the hand during dynamic reaching actions, and show that efficient and flexible motor control is not exclusively dependent on processing that occurs within supraspinal regions of the nervous system.³⁵

This is supported by another paper: Our results reveal complex goal-dependent modulation of fast feedback responses in M1 that are present early enough to account for goal-dependent stretch responses in arm muscles³⁶

Feedback and internal dynamics play a role, and models reflect either (in this model they forgo sensory feedback, which we see as integral to modulating feedback control): > Sensory feedback takes at least 25 ms to influence cortical responses and >50 ms to reflect the current goal. Thus, during this ~200-ms interval, the neural dynamics are not yet affected by sensory feedback and should presumably be explained via internal dynamics. This is true even of optimal feedback control architectures, which employ a dynamically varying control policy and internal ‘efference-copy’ recurrence to generate time-varying output patterns before the arrival of feedback. Given the practical choice to use a model without sensory feedback, we verified with additional simulations that the solutions found by the model were robust to the addition of reasonable forms of feedback³⁷

2.5 Supraspinal Motor Maps

It is known from recent work that primary motor cortex (M1) is not an isolated movement-generating dynamical system, but rather a node in the network of a feedback-modulated, distributed movement machine. This is reflected in recent work in the rodent which suggests that task-relevant movement depends on these network connections.⁴ This finding is relevant for our purposes as it demonstrates a fundamental function for cortical input as opposed to a specific substructure of motor cortex as detailed above in the primate literature.

Thinking structural architecture of M1 as an input-driven system with outputs along a spectrum of modularity from synergistic to fractionated, we can then ask what kind of functional architecture might have evolved in the neuromuscular controller? Graziano and colleagues found that 500ms electrical stimulation to M1 reliably produced stereotyped movements in primates, shown in Fig. 1 **graziano ORGANIZATION BEHAVIORAL REPERTOIRE 2006?**. These movements appeared to produce goal-oriented actions pulled out of other contexts such as bringing food to the mouth, and seemed to be arranged on the cortical sheet topographically in terms of spatial endpoints rather than as a homunculus. Graziano refers to this as the cortical “action map”, that these stimulations tapped into the control mechanisms of the primate’s motor system³⁸. These results have recently been confirmed by optogenetics work in marmosets and macaques.^{39,40}

Recent work identifying movement syllables on a behaviorally relevant timescale has a similar flavor. Along with behavioral syllables, the motor map concept posits the idea that M1 might be looked at like a field of feedback control microcircuits, integrating and transforming inputs, both internal and external, to sculpt ongoing movement.⁴¹ This is in accordance with the idea that there is a structural hierarchy in M1 covering a spectrum of movement modularity. These ideas together form a picture of the motor system as a structural scaffold upon which behaviorally relevant feedback mappings

from cortex to the spinal cord are continuously activated and modulated based on information and estimates about the periphery. In this view, the encoded variables of interest depend on the goals, context, and perturbations of the intended movement. Graziano writes:

“The usefulness of a feedback-dependent mapping from cortex to muscles is that it can in principle allow neurons in motor cortex to control a diversity of movement variables, such as direction, speed, hand position, or posture that transcend a fixed pattern of muscle activation. If the network receives feedback information about a specific movement variable, then it can learn to control that variable.”

Muscle activity is, in a sense, a readout from a network transforming state-dependent inputs into movement goals. Rather than playing chords, the motor system is improvisational jazzmaster. The movement machine wields its complexity to construct a movement fit to purpose, to suit its context and the information it receives. Rather than choosing muscle patterns in reconfigurable blocks, it creatively constructs and sculpts movements. That is, the hierarchy of the motor system is not rigidly organized around a particular set of variables. Many loops exist connecting cortex with the spinal cord, the cerebellum, the basal ganglia, and the sensorimotor periphery. Each of these loops contributes information to flexibly activate the relevant action maps. Prevailing theory suggests that cerebellar loops provide predictive state information while basal ganglia loops provide state and/or action value information. Along these lines, recent work studying patients with cerebellar ataxia suggests that the cerebellum plays a role in the temporal recruitment of behavioral syllables, while motor cortex may be implicated in the spatial structure of synergetic action, though this study focused on 13 proximal muscles of the shoulder and arm rather than the distal muscles driving the hand⁴².

I added this on Friday: Fig. 1 depicts the hierarchical nature of the motor system that enables its dexterity. The motor system is tuned to produce varying levels of modularity, and this is shown in Rasthelo’s work at a structural level: CM cells evolved to provide modifications to coarse, synergistic action. This is reflected in Graziano’s work where, loosely, more dexterous behaviors are produced when stimulation is applied to the caudal regions of motor cortex. These dexterous behaviors are driven by a hierarchical stack of cellular machinery, each level of which is modulated by estimated state, goals, uncertainty, and value.

The movement machine reasons in the space of feedback control systems and their ensuing trajectories. The phenomenal thing about the motor system is that it is able to tune itself rapidly with both high-dimensional sensory inputs and sparse reward signals^{43,44}. This has some precedence in the literature and will be discussed further in Section 5. This section has attempted to illustrate the complexity of the motor control system specifically with regard to dexterous control of the hand, with an eye toward experimental and theoretical avenues for exploration. The goal is to build and test a theoretical scheme for aspects of the compositional nature of the neural hand controller.

3 Experimental Methods

4 Data Analysis

5 Theory

6 Next Steps

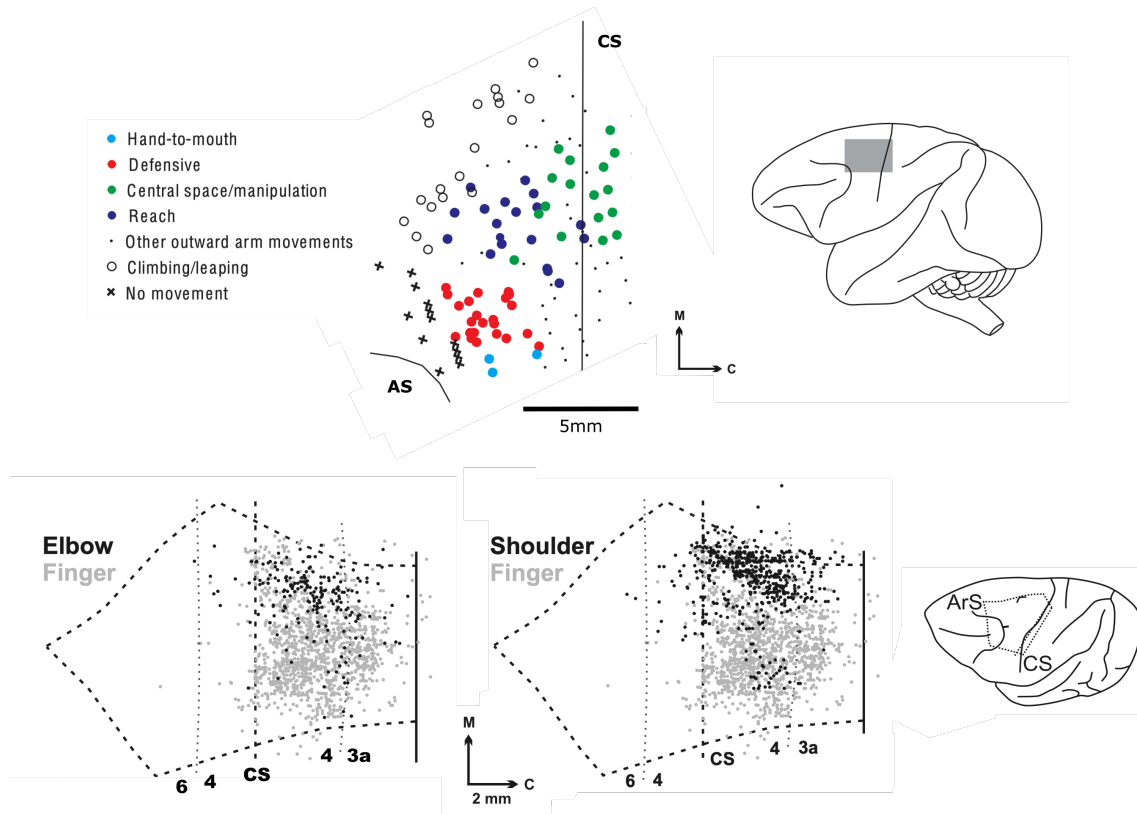


Figure 1: Similarities between electrical stimulation on behavioral timescales and rabies tracing identification of CM cells. CM cells are largely confined to the caudal half of M1, while this region tends to evoke complex manipulatory movements when electrically stimulated. (Top Left) Corticomotoneuronal (CM) cells traced using rabies from muscles of the elbow and finger. (Top Right) CM cells traced using rabies from muscles of the shoulder and finger. (Bottom) Complex movements evoked by 500ms electrical stimulation pulse trains. *Adapted from Graziano 2005 and Rathelot 2009*

Bibliography

1. McNamee, D. & Wolpert, D. M. Internal Models in Biological Control. *Annual Review of Control, Robotics, and Autonomous Systems* **2**, 339–364 (2019).
2. Todorov, E. Optimality principles in sensorimotor control. *Nature Neuroscience* **7**, 907–915 (2004).
3. Kober, J., Bagnell, J. A. & Peters, J. Reinforcement learning in robotics: A survey. *The International Journal of Robotics Research* **32**, 1238–1274 (2013).
4. Sauerbrei, B. A. *et al.* Cortical pattern generation during dexterous movement is input-driven. *Nature* (2019) doi:10.1038/s41586-019-1869-9.
5. Bernstein, N. *The coordination and regulation of movements*. (Pergamon, 1967).
6. Kitano, H. Biological robustness. *Nature Reviews Genetics* **5**, 826–837 (2004).
7. Fuglevand, A. J. Mechanical properties and neural control of human hand motor units: Control of human hand motor units. *The Journal of Physiology* **589**, 5595–5602 (2011).
8. Harris, C. M. & Wolpert, D. M. Signal-dependent noise determines motor planning. *Nature* **394**, 780–784 (1998).
9. van Duinen, H. & Gandevia, S. C. Constraints for control of the human hand: Control of the hand. *The Journal of Physiology* **589**, 5583–5593 (2011).
10. Valero-Cuevas, F. J. *et al.* The tendon network of the fingers performs anatomical computation at a macroscopic scale. *IEEE Transactions on Biomedical Engineering* **54**, 1161–1166 (2007).
11. Yan, Y., Goodman, J. M., Moore, D. D., Solla, S. A. & Bensmaia, S. J. Unexpected complexity of everyday manual behaviors. *Nature Communications* **11**, 3564 (2020).
12. Basmajian, J. V. Control and Training of Individual Motor Units. *Science* **141**, 440–441 (1963).
13. Merel, J., Botvinick, M. & Wayne, G. Hierarchical motor control in mammals and machines. *Nature Communications* **10**, 5489 (2019).
14. D’Avella, A., Saltiel, P. & Bizzi, E. Combinations of muscle synergies in the construction of a natural motor behavior. *Nature Neuroscience* **6**, 300–308 (2003).
15. Giszter, S. F. Motor primitives: new data and future questions. *Current Opinion in Neurobiology* **33**, 156–165 (2015).
16. Rácz, K. & Valero-Cuevas, F. J. Spatio-temporal analysis reveals active control of both task-relevant and task-irrelevant variables. *Frontiers in Computational Neuroscience* **7**, (2013).
17. Ingram, J. N. & Wolpert, D. M. The statistics of natural hand movements. *Brain* **188**, 223–236 (2009).
18. Todorov, E. & Ghahramani, Z. Analysis of the synergies underlying complex hand manipulation. in *The 26th Annual International Conference of the IEEE Engineering in Medicine and Biology Society* vol. 4 4637–4640 (IEEE, 2005).

19. Bizzi, E. & Ajemian, R. From motor planning to execution: A sensorimotor loop perspective. *Journal of Neurophysiology* **124**, 1815–1823 (2020).
20. Bruton, M. & O'Dwyer, N. Synergies in coordination: A comprehensive overview of neural, computational, and behavioral approaches. *Journal of Neurophysiology* **120**, 2761–2774 (2018).
21. Lemon, R. N. Cortical control of the primate hand. *Experimental Physiology* **78**, 263–301 (1993).
22. Lemon, R. N. Mechanisms of cortical control of hand function. *Neuroscientist* **3**, 389–398 (1997).
23. Lemon, R. N. Descending Pathways in Motor Control. *Annual Review of Neuroscience* **31**, 195–218 (2008).
24. Lemon, R. & Kraskov, A. Starting and stopping movement by the primate brain. *Brain and Neuroscience Advances* **3**, 239821281983714 (2019).
25. Kawasawa, Y. I. *et al.* Control of species-dependent cortico-motoneuronal connections underlying manual dexterity. *Science* **357**, 400–404 (2017).
26. Murabe, N. *et al.* Higher primate-like direct corticomotoneuronal connections are transiently formed in a juvenile subprimate mammal. *Scientific Reports* **8**, 1–10 (2018).
27. Cheney, P. D. & Fetz, E. E. Functional classes of primate corticomotoneuronal cells and their relation to active force. *Journal of Neurophysiology* **44**, 773–791 (1980).
28. Griffin, D. M. & Strick, P. L. The motor cortex uses active suppression to sculpt movement. *Science Advances* **6**, eabb8395 (2020).
29. Rathelot, J.-A. & Strick, P. L. Subdivisions of primary motor cortex based on cortico-motoneuronal cells. *Proceedings of the National Academy of Sciences* **106**, 918–923 (2009).
30. Griffin, D. M., Hoffman, D. S. & Strick, P. L. Corticomotoneuronal cells are "functionally tuned". *Science* **350**, 667–670 (2015).
31. Takei, T., Confais, J., Tomatsu, S., Oya, T. & Seki, K. Neural basis for hand muscle synergies in the primate spinal cord. *Proceedings of the National Academy of Sciences* **114**, 8643–8648 (2017).
32. Dum, R. P. & Strick, P. L. The Corticospinal System: A Structural Framework for the Central Control of Movement. in *Comprehensive Physiology* (John Wiley & Sons, Inc., 2011). doi:10.1002/cphy.cp120106.
33. Furuya, S. & Altenmüller, E. Flexibility of movement organization in piano performance. *Frontiers in Human Neuroscience* **7**, (2013).
34. Carroll, T. J., McNamee, D., Ingram, J. N. & Wolpert, D. M. Rapid Visuomotor Responses Reflect Value-Based Decisions. *The Journal of Neuroscience* **39**, 3906–3920 (2019).
35. Weiler, J., Gribble, P. L. & Pruszynski, J. A. *Spinal stretch reflexes support efficient control of reaching.* (2020) doi:10.1101/2020.01.06.896225.
36. Pruszynski, J. A., Omrani, M. & Scott, S. H. Goal-Dependent Modulation of Fast Feedback Responses in Primary Motor Cortex. *Journal of Neuroscience* **34**, 4608–4617 (2014).

37. Sussillo, D., Churchland, M. M., Kaufman, M. T. & Shenoy, K. V. A neural network that finds a naturalistic solution for the production of muscle activity. *Nature Neuroscience* **18**, 1025–1033 (2015).
38. Graziano, M. S. A. *The intelligent movement machine: An ethological perspective on the primate motor system*. (Oxford University Press, 2009).
39. Ebina, T. *et al.* Arm movements induced by noninvasive optogenetic stimulation of the motor cortex in the common marmoset. *Proceedings of the National Academy of Sciences* **116**, 22844–22850 (2019).
40. Watanabe, H. *et al.* Forelimb movements evoked by optogenetic stimulation of the macaque motor cortex. *Nature Communications* **11**, 3253 (2020).
41. Wiltschko, A. B. *et al.* Mapping Sub-Second Structure in Mouse Behavior. *Neuron* **88**, 1121–1135 (2015).
42. Berger, D. J., Masciullo, M., Molinari, M., Lacquaniti, F. & d’Avella, A. Does the cerebellum shape the spatiotemporal organization of muscle patterns? Insights from subjects with cerebellar ataxias. *Journal of Neurophysiology* **123**, 1691–1710 (2020).
43. Bahl, S., Mukadam, M., Gupta, A. & Pathak, D. Neural Dynamic Policies for End-to-End Sensorimotor Learning. 5 (2020).
44. Ijspeert, A. J., Nakanishi, J., Hoffmann, H., Pastor, P. & Schaal, S. Dynamical Movement Primitives: Learning Attractor Models for Motor Behaviors. *Neural Computation* **25**, 328–373 (2013).