Motor primitives — new data and future questions
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Motor primitives allow integration across scales in the motor system and may link movement construction and circuit organization. This review examines support for primitives, and new data relating primitives to concrete circuit elements across species. Both kinematic motor primitives and muscle synergy/kinetic motor primitives are reviewed. Motor primitives allow a modular hierarchy that may be re-used by volitional systems in novel ways. They can provide a developmental bootstrap for ethologically important actions. Collections of primitives somewhat constrain motor acts, but at the same time sets of primitives facilitate the rapid construction of these constrained actions, and can allow use of simpler controls. Novel motor skill likely requires augmentation to transcend the constraints present in initial collections of low level motor primitives. The benefits and limitations of motor primitives and the recognized knowledge gaps and needs for future research are briefly discussed.

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Introduction
Motor Primitives can be controversial. What is a 'primitive'? The Free Dictionary online (http://www.thefreedictionary.com/primitive) states: *1. Not derived from something else; primary or basic. 2. a. Of or relating to an earliest or original stage or state; primeval. b. Being little evolved from an early ancestral type. 3. Characterized by simplicity or crudity.* These definitions are close to what many of us consider 'Motor Primitives' to be in neuroscience, i.e., *fundamental* building blocks for constructing motion. Motor primitives (MPs) are thus defined here to be compositional elements for movement construction. Assuming more complex motion arises from rearranging and combining MPs, then a subset of fundamental motor primitives should be available to organize initial movements very early in development, and thereby contribute to the ontogenetic and adult construction of more complex motor acts, in one or more ways.

Compositional elements for movement could have various forms. Motor acts comprise overall kinematics, together with force interactions with the environment, and the underlying body kinetics, and regulation of impedance. These in turn depend on patterns of muscle activation and control. At what level should we look for compositional MPs as motor neuroscientist? Different authors have considered MPs at several levels. MPs have been defined as *kinematic elements* (i.e., patterns of motion without regard to force or mass, e.g., strokes [1,2,3•] or cycles [4,5]), or as *kinetic elements* (force-based, e.g., visco-elastic force-field primitives [6–9] and their associated muscle synergies [9–11]), or as neural drive circuits [12•]. Because the nervous system appears to organize both the executed motion as well as prepare the contingent acts and corrections required for any common or unexpected perturbations in any complex body motion, it follows that the most fundamental MPs need to be useful as compositional elements in each of these contexts, i.e., the fundamental MPs must be adequate building blocks to rapidly construct the kinematic, kinetic, impedance and contingent response aspects of a complex movement. Our current computational understanding of motor control likely has a place for both kinematic and kinetic elements [3•,13–15]. However, reconciling the frameworks of kinematic MPs and kinetic/synergy MPs into a unified compositional scheme remains difficult. Explorations that enrich our understanding of movement in important ways continue in both areas as described below. Here I take the kinetic MPs as fundamental building blocks, and take kinematic MPs as more derived, according to the mechanical relations between them, but a satisfying unification of the two in motor neuroscience is eventually needed.

Evidence for kinematic movement primitives
Support for kinematic MPs derives from several methods. Primarily, researchers seek building blocks in complex kinematic patterns, decomposing motor acts at the kinematics level into their constituent elements. Various statistical techniques are available, each with pros and cons, to accomplish this task and break motion patterns into component elements. Early segmentation of kinematics by Viviani and Terzuolo, and by Flash and Hogan [2] has been elaborated today in several further ways. Kinematic segmentation and decomposition has been deepened into a theory of segmentation and of motor invariances based on affine geometries by Flash, Polyakov and colleagues [16]. This framework supports a range of extensions, and novel motion and observation analyses [16,17]. Sosnik and colleagues [18] have shown that learning involves a co-articulation and merging of

primitive strokes. Similarly recovery of function can be couched in these terms [19]. The kinematic MP framework has also been extended effectively to capture soft effector motions, for example in the octopus tentacles [20] (Figure 1, MP1). Unitary kinematic actions allow a common description across species. Kinematic criteria for unitary kinematic strokes, visually acquired, also play a major role in skilled motion tuning and adaptation. In man, fine targeted motor control can be viewed as an accretion of kinematic MPs. Hogan and colleagues also showed that the decomposition into sub-movements is altered during robot rehabilitation of stroke patients [19]. Kinematic MPs can thus capture both skill development and deficit in the clinic. A range of kinematic motor primitive control strategies have been developed in the control of biomorphic robotics, partly inspired by these

kinds of data, and partly from the researchers' first principle analyses of how best to construct robot motion [15]. Load and impedance management in the kinematic robot frameworks is deferred to lower level controllers.

## Evidence for force-field motor primitives and spinal muscle synergies

Support for visco-elastic force fields as kinetic MPs and for their associated muscle synergies as MPs is strong (Figure 1, MP2). These two descriptions (force-field unit and muscle synergy) are equivalent to one another and largely interchangeable (see Figure 2, for more details). Support derives from physiological perturbations, neural recordings, statistical decomposition techniques in animal and human model system data, and more recently from molecular genetics methods and manipulations. Discrete

Figure 1
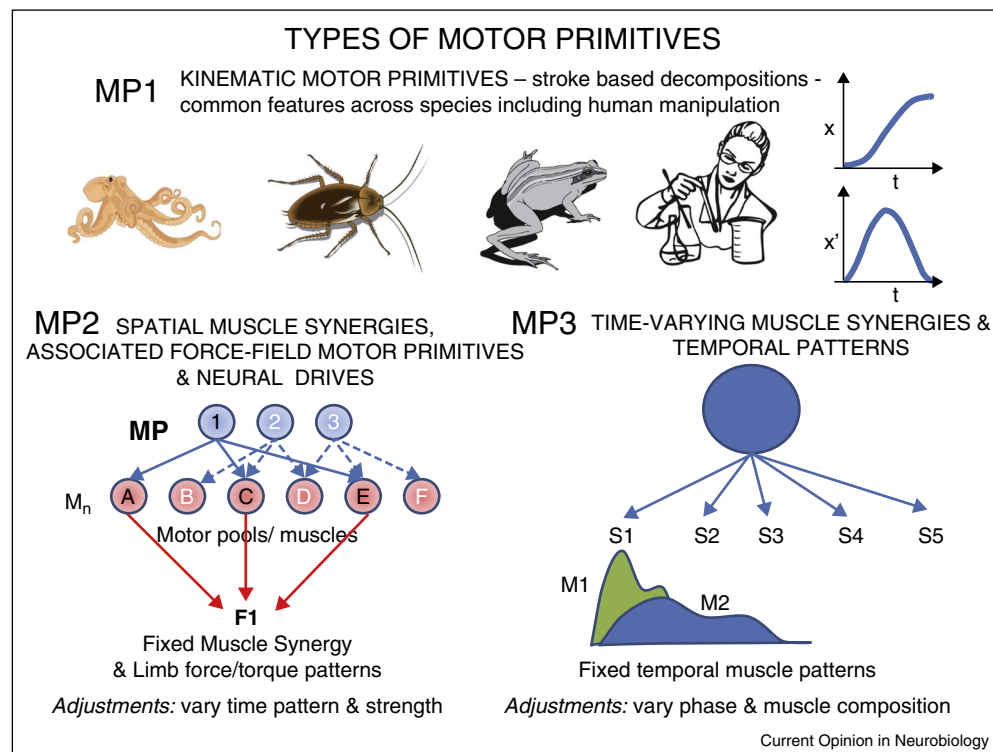
The types of Motor Primitives which have variously been proposed. MP1 — Kinematic motor primitives comprise direct minimum jerk kinematic strokes, and cycles of these. These MPs capture motion independent of effector forces and muscle pattern. They have been identified in octopus, arthropods, frogs and other tetrapods, and they feature strongly in skilled human manipulation and reach behaviors. They have been used very successfully as a generalizing basis in robotics (Schaal, Peters et al.). MP2 — 'Spatial' Muscle Synergies, force-field motor primitives, and synergy neural drives. These MPs represent fixed balances of groups of muscle recruitment over time for each synergy. The spatial muscle synergies' activations translate through muscle properties and limb biomechanics into constant structure viscoelastic force fields relating limb force and torque to limb state (see Figure 2). The fixed muscle recruitment balance of these MPs requires a precisely balanced neural drive to the motor pools. In the example, MP number 1 has a drive which is distributed to three muscles' motor pools (solid blue arrows, to motor pools A, C, and E). These recruited muscle activations acting through the limb geometry and their associated moment arms interact with limb state and the muscle properties cause specific patterns of viscoelastic forces in the limb (F1). Adjustments occur in the timing and amplitude of the drives to motor pools, but not in the relative balance of recruitment by an individual drive across the motor pools. MP3 — Temporal or time varying muscle synergies. Here the primitive is defined by a time varying pattern of muscle activation which can differ among muscles. The relative muscle composition may thus change over time in the temporal synergy. (This is indicated by the different time courses of muscle M1 and M2 for the synergy S1 that is shown. Most data favor MP2 over MP3 [21]. MP1 and MP2 are differing complementary descriptions of motor modularity. A full account integrating MP1 and MP2 seamlessly in either neural implementation or computational theory areas remains to be developed.

Figure 2
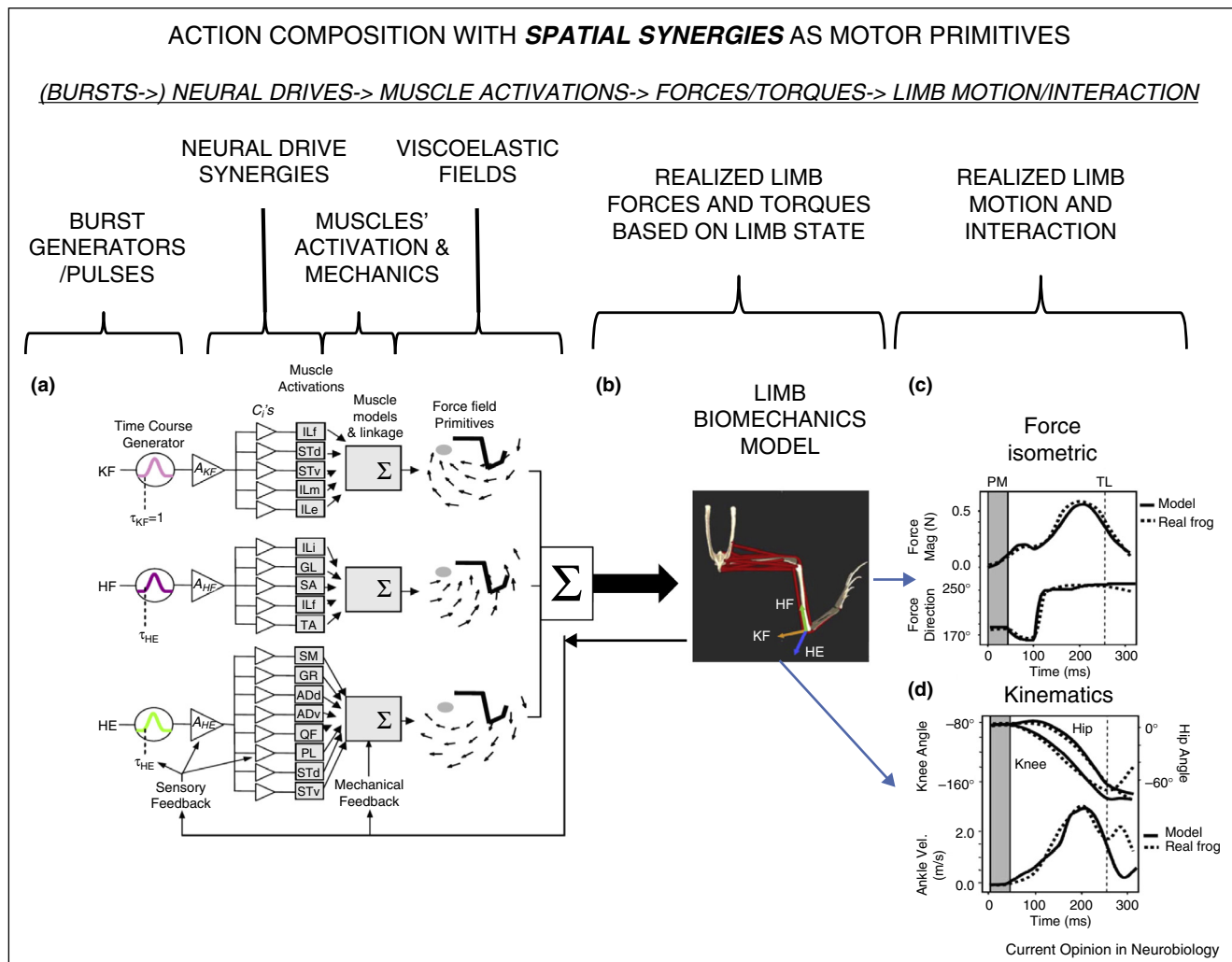
Composition of movement with (MP2) spatial synergies. The causal chain is shown in italics: *bursts* in *neural drives* recruit *specific muscle activations*. These in turn generate state dependent *forces and torques* in the limb (summarized as viscoeleastic fields) which determine *limb motion and interaction*. This framework is elaborated in detail in **a** through **c** below for the hindlimb-hindlimb frog wipe reflex, redrawn from [22]. Each stage is indicated above the diagram. (**a**) Three MPs contribute, KF (knee flexor), HF (hip flexor) and HE (hip extensor), named for their dominant biomechanical actions. Bursts/pulses of activity to neural drives associated with each occur in sequence (staggered with time delays τ_{KF}, etc.). Pulse generation is separated from neural synergy drive, though the two are closely associated. The pulse or burst amplitude is controlled by a simple amplitude value (e.g., A_{KF}). However, each drive has different parameters or weights (C_i) for the level of activation of the motor pools and muscles recruited, (but note that these weights remain fixed over time, and characterize each drive synergy). Motor pools (e.g., ILf — iliofibularis, STd — dorsal semitendinosus, STv — ventral semitendinosus pools and so on) summate the different impinging drives linearly in the model. For example, both KF drive and HF drive impinge on ILf motor pool. Muscle activations will drive forces in their muscles based on muscle and limb biomechanical state. The MP member muscles acting as groups define viscoelastic force-field primitives which include the effects of limb biomechanics and muscle properties as well as the neural drive balance. The forces from these several primitives add and together drive limb motion and interaction biomechanics, here in a biomechanical model (**b**), changing limb state. This scheme of spatial synergies with defined neural drives and biomechanical interactions can in simulation account for measured isometric force if the limb is held immobile in a real frog (**c**) or kinematics of the limb in a real frog when it is free to move (**d**). The close match with the three MPs KF, HF and HE show the MPs are a very compact mechanism to create a limb kinematics with standard bell shaped velocity profiles and kinematic strokes. The MPs capture and summarize in a low dimensional fashion the complex patterns of muscle recruitment and control that are used in frog reflex scratch/wipe behaviors. Reproduced and reorganized from Kargo et al. [22], with permission

pulses of activity found in recordings of electromyograms (EMGs) and electroneurograms (ENGs) in lower vertebrate systems such as frog and turtle show quantal-like deletions, additions, and blending of a small number of pulse types in spinal reflex and patterned behaviors in both moving and fictive preparations [9]. These are consistent with a compositional system of discrete pulses or muscle synergy bursts. Each pulse recruits a specific

grouping of muscles. These same pulses and muscle groupings can be elicited by microstimulation [7], or in perturbations and corrections [9]. These pulsed synergies can be triggered or manipulated as units, with their constituent muscle synergy patterns always remaining intact, under cutaneous and proprioceptive manipulations [21]. Further, the small repertoire of pulses found is sufficient to mechanically drive a complex musculoskeletal limb model in the kinematic patterns closely resembling the reflex behaviors [22]. Figure 2 provides a summary. In deeper mechanical analyses such MPs can be shown to be nearly optimal ways to drive the limb biomechanics in the frog [23]. This can be shown in many synergy-based MP frameworks [24]. These same types of pulsed synergies are seen in mammals. Such synergy pulses have also been described in mammalian fictive preparations during locomotion, where they can be spontaneously deleted from the neural output, without affecting the underlying rhythm generation [25]. This observation of fictive synergy deletion without rhythm change in the cat has led McCrea and Rybak to propose the separation of rhythm generation and pattern shaping in the tetrapod locomotor pattern generation systems [26], and see [27]. Synergy bursts are also seen in intact locomotion by Drew and colleagues and used in accounts of its adjustments [28,29]. These architectural insights have helped structure thought about limb control systems, interlimb integration and limb trunk integration with descending controls and volition in animal model systems for locomotion.

General patterned motor production in animals can be decomposed into motor primitives/synergies in more intact and free moving conditions using a range of statistical and signal processing pattern separation methods. Principle categories among these are Factor Analyses (FA), Non-negative matrix factorization (NNMF), Independent Component Analysis (ICA) methods, and Direct Component Analyses (DCA). These methods largely confirm the construction mechanisms observed in spinal and decerebrate preparation physiology, with data collected in intact animal models and humans in freely moving conditions [30–32]. Use of such methods has shown structural similarities of pattern modularity across species, including man [31–35]. These tools have also been used to examine clinical data [36,37], usually further supporting the framework. At the same time, these decomposition methods require very careful use, as they suffer a range of potential pitfalls, as noted by both critics and proponents [38,39].

Circuit foundations of motor primitives

If MPs reflect an organizational principle in movement construction, we should expect the MP picture to give insight into the underlying circuits, e.g., spinal system architectures, in addition to forming motor pattern and biomechanical building blocks. Strong predictions of an MP framework are that the underlying neural circuitry

should involve interneurons assembling the synergies and driving them as units. The simplest conceptions of these are as simple premotor projection neurons. In the frog, using multielectrode single unit recordings in spinal cord, we have found intermediate zone interneurons that have significant spike triggered average (STA) projections to motor pools (i.e., mono or disynaptic projections). All such cells showed such projections in discrete patterns, each closely resembling one of the synergies or motor primitives found by other means [12]. These data in frogs support the idea that a network of premotor interneurons and projections might be pre-formed by evolution to support the basic protective reflex, grooming, and locomotion operations of the limbs from early stages in development. These crude but effective scaffolds for basic motor function could effectively 'bootstrap' movement systems and provide important early survival functions that are needed in many animals (e.g., the wildebeest calf on the Serengeti, or the hatchling turtle on a Caribbean beach). Similar direct scaffolding of important modular circuits with value for early survival functions is also seen in vestibular and orienting systems [40,41], and in proprioceptive systems.

Recently molecular genetics and optogenetics tools have also been directed at this issue in the segmental motor and premotor drive systems of mammals. Pfaff and colleagues have published direct tests in the mouse, that support the existence of premotor interneuron systems that can potentially mediate synergistic drives of the types seen in lower vertebrates in mammals [42], and thus support the types of drives extracted using various decomposition techniques in animals and man [30–36,37]. To date it is unknown whether these interneuron projections to motor pools occur in specific patterns that cluster into discrete sets, as happens in the frog. Modular networks in mouse clearly exist [43] and in rats [44]. The same gaps exist in the C3–C4 interneuron system characterizations despite recent advances [45,46]. These important aspects of the mammalian data remain to be determined. Further, current data do not inform us whether the MP distribution interneurons are simply summing junctions or have burst-like properties. The distribution circuits for motor primitives/muscle synergies at spinal levels could be intrinsically bursting, or alternatively could be simple passive relays, recruited by burst generators elsewhere in the spinal cord. Hagglund and colleagues [47] have discovered multiple rhythmic populations, comprising activation of extensors and flexors, potentially consistent with different flexor and extensor synergy burst constructions. Synergy burst structures are fairly stereotypic in some animals and are also clearly seen in mammalian locomotion patterning [28,29,48]. These burst elements are usually ascribed to the operation of pattern shaping systems. Figure 3 summarizes possible arrangements of active or passive relay interneurons for MPs in different models hierarchical pattern generation, based on data available at time of

Figure 3
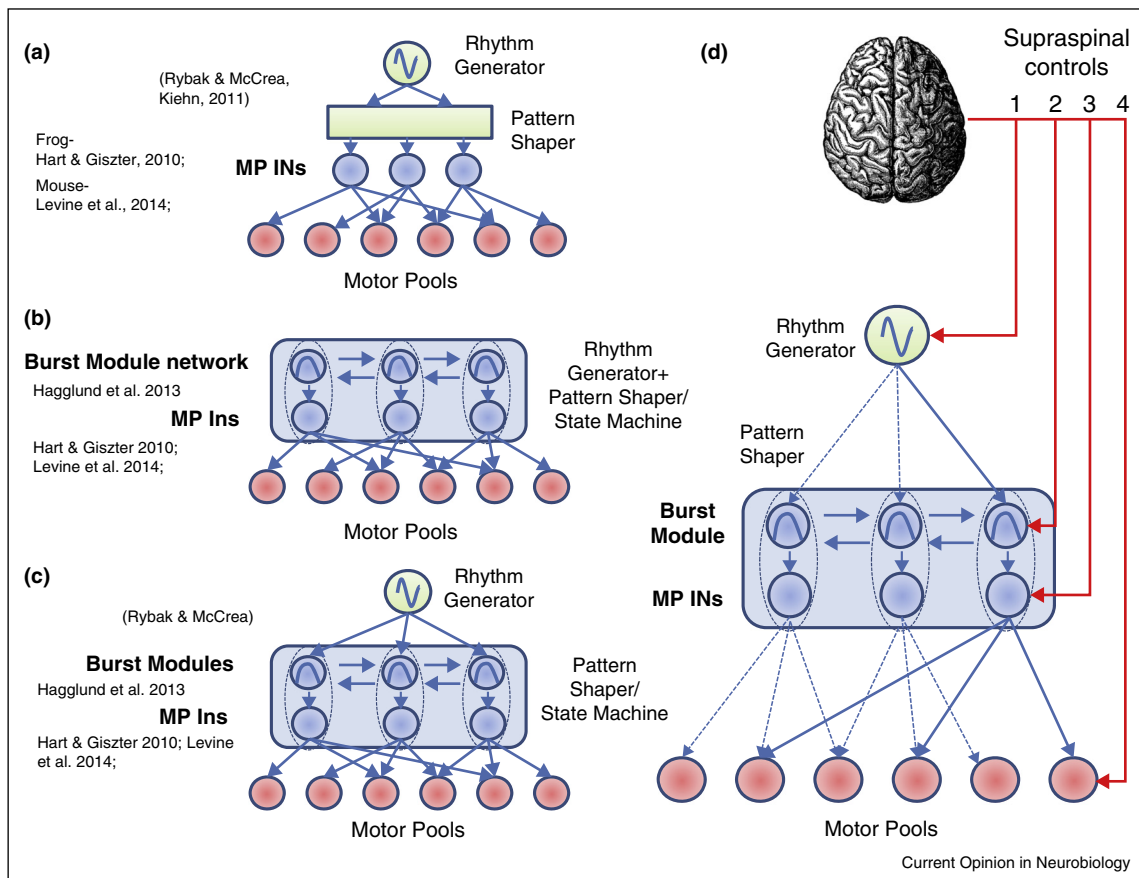
Possible neural structures supporting pattern generation with motor primitives as output elements. (**a**) Neurons suitable for distributing drive to motor pools (MP INs) have been recorded in frogs [10], and neurons able to relay descending drives in related patterns have been identified in mice [42**], in locomotion modules. Drive related MP INs should be excitatory for drive summation to operate linearly and allow easy composition of action. These MP INs would likely be part of, or else targets of the pattern shaping systems, in a layered pattern generator comprising rhythm generator and pattern shaper layers. (**b**) Hagglund and colleagues [47**] have shown bursting and rhythmogenic capacities of both extensor synergies, flexor synergies and some single muscles. These bursting interneurons may associate with the modular drives (indicated by the dashed ovals) or may recruit them depending on the yet to be determined organization of MPs. The bursting systems potentially allow a combined rhythm generation/pattern shaping perspective, resembling the coupled oscillator frameworks proposed by Grillner and colleagues, or a finite state machine model of pattern formation as suggested by Prochazka and colleagues. Whether MP INs are intrinsically bursting in nature or can be simpler relays in mammals remains to be fully understood. (**c**) An alternate scheme avoids choosing between different features of A or B, and combines the data supporting both. The bursting behavior of different muscle groups and synergies in B is combined with the hierarchical rhythm generation and pattern shaping separation in **a**. Both **a** and **b** have attractive features in terms of modular composition of action (e.g., model A. handles deletions and corrections very gracefully). The combined scheme provides a rich variety of ways for descending neural controls to sequence and organize modular activation of the limb. Both burst modules and MP INs could form useful targets for descending controls that re-used spinal primitives in new behaviors or as compositional elements for ethologically important higher order 'motor primitives'. (**d**) Points of descending control to MPs in the more inclusive scheme shown in **c**. 1. Direct control of rhythmogenesis and rhythmic cadence. 2. Direct recruitment of synergy bursts and pulses in pattern shaping systems, independent of overall rhythm generation. 3. Driving of MP IN drive systems independent of the spinal rhythm systems allowing novel usage of available spinal drive synergies. These routes resemble [64•], but may also combine with 4 in novel behaviors. 4. Bypass of the restrictions of modular spinal drive systems by descending systems. Here the descending controls are shown recruiting motor pools in a fractionated fashion directly or via other spinal interneuron targets, in novel ways across many contexts. Likely, to dance the tango or spar in a martial arts contest would require ongoing control by all 4 routes.

writing, and potential sites of descending control in novel movements.

Computational frameworks for motor primitives

Both kinematic and force-field/muscle synergy MPs are currently viewed as rooted in some kind of optimization of movement or an approximation of it [2,15,23,24]. The form of kinematic strokes in movement (i.e., MP1, Figure 1) have variously been attributed to the central nervous system (CNS) minimizing jerk, torque change, muscular effort or some weighted balance of these [2,15,23,24]. Kinematic MPs are seen in a range of animal forms from soft-bodied muscular hydrostat effectors, to

exoskeletons and endoskeletons. The commonalities in the kinematic operations of these very different effectors are likely to be geometric factors in visuomotor integration, see [49,50]. Analyses of the geometric factors continue to be explored, focusing on unifying features of affine geometries and links to dynamics.

Force-field/muscle synergy MPs have been established as supporting compositional movement construction and various optimality criteria in a range of ways. Compositional methods for movement using force-field MPs were explored by Mussa-Ivaldi [51,52]. He demonstrated that arbitrary smooth force patterns are readily approximated with appropriate combinations from discrete sets of static elastic (conservative) and circulating (energy generating and dissipating) force patterns. In other words, the right sets of MPs can generate arbitrary limb force, and ergo arbitrary motion. In practice, in vertebrate movement, in contrast to invertebrates, it is almost impossible to find any strongly circulating force patterns in biomechanical measurements from limbs. Vertebrate basis sets of MPs are limited to the conservative fields (e.g., [6–9]). This limits the possible mechanics that can be composed, but it adds the benefit that biological patterns remain stable in interaction with the normal (passive) environment (e.g., [53]). This also means that MPs must necessarily be sequenced in order to generate cyclic motions, in contrast to if MPs included circulating fields. Cycling through sequences of conservative MPs would be a job for spinal CPGs, managed through their associated rhythm generation and pattern shaping circuitry. Ensemble stability of arbitrary CPG and MPs rearrangements during behavior may also be carefully managed or guaranteed [54,55].

Notions of optimality in motor control have been extremely influential. MPs in simplified frog models can be shown to represent optimal ways of exciting the dynamic modes of the limb [23]. Similarly, MPs identified through both signal processing and physiological testing were shown to be sufficient to support reflex limb behaviors of spinal frogs in simple combinations in a more detailed frog model [22], with similar kinematic features and force patterns to those predicted by the simpler structured optimization model. In human balance, Ting and colleagues showed statistically identified MPs were matched well to model optimal strategies for balance in man [56]. Using an alternate formulation of temporal (time-varying) motor primitives Kuppuswamy and Harris [24] demonstrated competence of the chosen primitives, with emergent kinematic structure resembling that seen naturally. Modular decompositions of movement into MPs may thus frequently be near optimal, and it is also recognized that different optimality criteria may be nearly intersecting in evolutionarily shaped biomechanical systems [57]. Computational criteria alone are thus unlikely to resolve what neural MPs and composition mechanisms operate. The *neurobiological implementation details* of MPs will be

key to understanding how motor primitives operate in practice, and determining whether observed MPs are fundamental elements constructed over evolution, or instead synergies derived from learning under constraints.

Valero-Cuevas and colleagues have argued strongly that while MPs manage degrees of freedom issues, and may simplify or bootstrap behaviors, they also limit options [58]. The muscles we have and their tendon mechanisms provide both affordances and mechanical limitations. Similarly, any neurally defined MPs will then further limit these sets of options and reduce motor capacity if used alone. Valero-Cuevas and Kutch [59] have explored the extent to which such neural constraints are detectable in patterns of fluctuation in force and electromyography. In some instances they have uncovered such constraints in skilled hand use [60••,61]. In human dexterity, they argue, the problem the CNS faces is to fully explore the biomechanical options, and furthermore to transcend any neural constraints due to MPs. Individual muscles exist and were likely retained under selective pressures in order to support individuated use. MPs therefore cannot capture the range of skilled behavior, but instead likely capture the most common patterns of use in a species in a 'broad strokes' fashion, and learning beyond these is needed to achieve the full motor capabilities that are possible.

Development, skill and plasticity in relation to Motor Primitives in humans

The concept of MPs raises a range of questions in human development. What collections of MPs are available in man, based on our current understanding, and do they constrain our options for human movement? Do skilled biped primates still continue to utilize the 'built-in' MPs seen in other specie? Are human and primate MPs constructed de novo in novel tasks, or for bipedal locomotion? Do neocortical representations replace or incorporate the evolutionarily older systems in skilled novel movement? Likely the answer is a mixture of these. Data are available for locomotion, upper limb and grasp actions, and these suggest at least some incorporation occurs (Figure 4).

Dominici and colleagues [31] have shown significantly conserved MP structure across species, but also the possibility of significant plasticity in man. In clinical settings Cheung, Bizzi and colleagues [36,37•] have shown data supporting retention of synergies after stroke, but disorderly use of these in the affected limb, fitting with a framework of re-use. Similarly, Clark and colleagues [62] have shown changes in stroke affecting the lower limb that are consistent with collapses of timing of synergies, then followed by a re-separation of synergies in rehabilitation and recovery. Fox and colleagues [63•] have shown modular structures in muscle patterns across different tasks in spinal injured children which resemble able-bodied intact patterns. Taken together, these data and other work [19,28,29,48,61,64•] support re-use of

Figure 4

Motor Primitive Re-use and Plasticity Issues
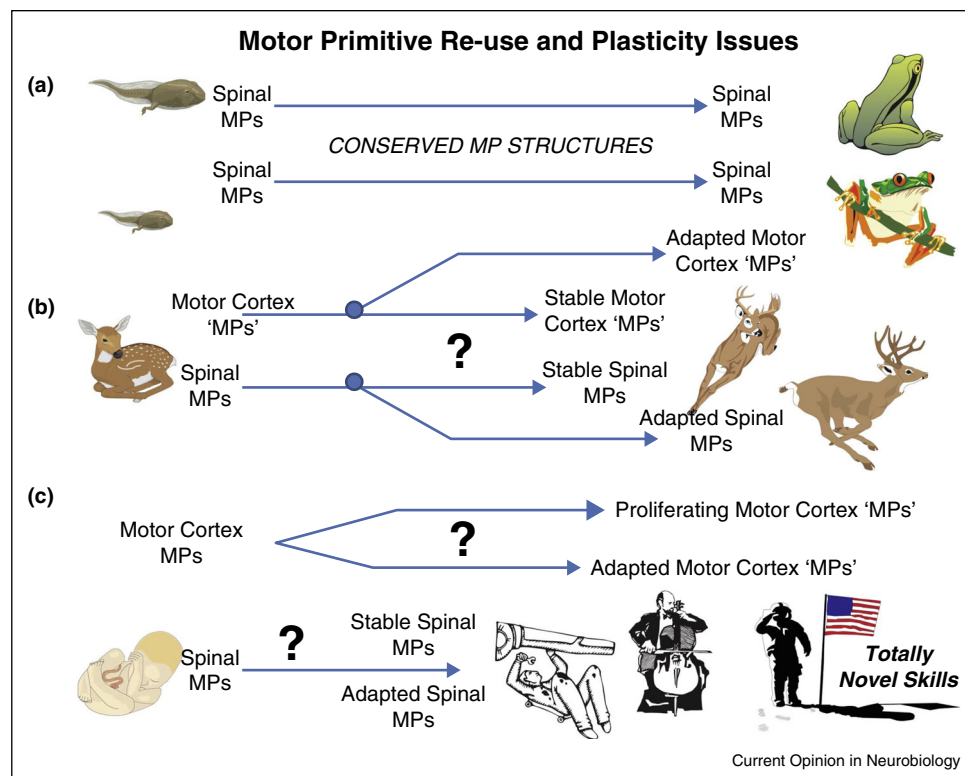
Open questions and issues in motor primitive plasticity and reuse. (**a**) In amphibia it seems conserved sets of motor primitives that are similar among individuals and likely across related species are conserved and reused in adult voluntary behaviors such as prey strike. (**b**) In mammals there is evidence for similar motor primitives. However, the extent to which these are stable elements through development, and the degrees of plasticity in spinal motor primitives and any coupled cortical mechanisms are still largely open questions. It is also unclear how similar the overall operation of any new cortical modularity developed by mammals may be to the modes of use of spinal primitives. (**c**) In humans the degree of stability and plasticity of motor primitives defined in spinal cord/brainstem, and the relations of these with cortical modularity are controversial. Further, there is the suggestion that totally novel skills for technology-enabled affordances may require innovation and generation of novel patterns and libraries of 'novel motor primitives' that have perhaps never before been used in evolutionary history. Whether these libraries of motor bases should be termed 'primitives', is unclear. They violate the initial definition of primitives used here as 'primary', 'basic', 'ancient' and 'not derived' although they may form re-usable building blocks.

motor primitives in skilled behaviors rather than replacement and suppression of these elements. Early ethologically important motor primitives in man clearly exist, and are certainly persistent into adulthood-observations of some of these out of context are usually taken as signs of cortical damage [65]. Recent research in humans also supports cortical representation of some of these early patterns for re-use in the adult [66]. However, we do not yet understand whether re-use also involves, or could sometimes involve, significant plastic modifications of the original spinal MPs through development and into adulthood. This may be of special concern in man.

Modular representations in motor cortex of primates have been argued using various approaches, including microstimulation and recording [67,68•]. Long stimulus trains have been used to elicit complex motions of controversial interpretation [69]. In non-human primates, use of STA in

spinal recordings during hand tasks suggest combined re-use of spinal synergies and interneuron systems together with other controls [70,71]. The control of the patterns and strengths of any projections to spinal MPs and their plasticity through CST developmental pruning and reorganization [72] must be better understood in terms of MP related interneurons and other spinal systems' plasticity [44]. The degree of preservation into adulthood, and extent possible modification of low level primitives by the descending systems remain to be fully determined. Further, to transcend the limitations of restricting actions to re-use of MPs that were noted above, it is likely that motor cortex and CST projections must also construct new collections of synergies or 'novel MPs' in mammals. These 'novel primitives' (note the possible oxymoron here) may be necessary to learn unusual and highly novel skills and to support major motor innovations such as novel tool use, technological augmentations, and so on, in

man. Thus it has been argued that it is possible that human movement is built on a small collection of spinal, brainstem and cortically defined MPs available at birth, then augmented by optimal controls mediated by cortical and other descending systems, see [73]. An increasing library of 'primitives' for new controls to transcend initial limitations of MPs might thus be constructed throughout life for novel skills. This library's 'primitives' might perhaps then exceed the number of muscles by orders of magnitude.

Berger, D'Avella and colleagues [74**,75] have addressed the issue of re-use and innovation in human motor acts. They tested how easy it may be to replace or augment MPs during learning. They did this with series of elegant learning experiments using virtual reality and myographic controls in the upper limb. They explored whether human learning is easier or harder when learning is confined to the statistically identified and observed MP framework, compared to when deviations from the MP 'constraints' are demanded. Their results match with both a degree of initial constraint and with the ability to learn to transcend some of the limitations associated with MPs. Recent experiments with transiently induced deltoid pain in adult human reaching also showed significant preservation of synergy structure, despite the perturbation [76].

Conclusions — Major issues for the future

Motor Primitives at a low level in the CNS can provide an animal with initial simplified control of movement, and can bootstrap development of movement using information captured and 'baked in' by many prior generations of evolutionary selection pressure, forming modularity that is closely matched to the biomechanics and standard movement repertoire. MPs may thereby almost immediately provide near optimal patterns of muscle activation in some species with high early motor demands. MPs also form a theoretical framework that can unify neuroethological, kinesiology/biomechanics and neurobiological perspectives on movement and can simplify integrated analysis of circuitry and movement composition, thus facilitating cross-level transfer of information in neuroscience. Such lofty goals demand very careful work. To further an understanding of the MP framework in the future, it will be necessary both to drill down further into the spinal underpinnings of built-in MP structures, and also to better understand how such spinal structure is utilized and augmented in mammalian skilled movement and by cortical controls. In amphibia it may be possible for built-in structure with very limited augmentation to be sufficient for the operations of daily living within their niche, and plasticity may be limited to maintenance of MPs and flexible rearrangements of MPs. However, in mammals this seems highly unlikely. Although interneuron systems associated with drive that could support MPs have been identified in mammals [42**], we do not know if these systems show the discrete groupings of different patterned projections to motor pools seen in recorded

limb-related interneurons in frogs. Likely there are commonalities across tetrapods, but this is an assumption that must be carefully tested. We also do not know in sufficient detail whether spinal structures observed and characterized in neonatal mammals are preserved relatively intact and untouched into adulthood, or whether and how they are significantly modified and reshaped through interactions with descending systems, for example, in developing bipedal locomotion in man. The similarity and difference of the spinally organized circuitry and MPs among adult mammals compared across species and individuals hinge on such issues. These issues are also at the crux of determining the overall utility of MPs and associated circuitry as a potentially useful therapeutic basis to be applied in clinical settings.

Acknowledgments

References and recommended reading
Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Hogan N: **An organizing principle for a class of voluntary movements**. *J Neurosci* 1984, **4**:2745-2754.

2. Flash T, Hogan N: **The coordination of arm movements: an experimentally confirmed mathematical model**. *J Neurosci* 1985, **5**:1688-1703.

3. Hogan N, Sternad D: **Dynamic primitives of motor behavior**. *Biol*
• *Cybern* 2012, **106**:727-739.
This article seeks to provide a unified conceptual account of human motor skills and tool use using three types of primitives: kinematic strokes, kinematic oscillations, and impedance primitives. These types of elements emerge repeatedly across the motor literature and have significant data support.

4. Sternad D, Marino H, Charles SK, Duarte M, Dipietro L, Hogan N: **Transitions between discrete and rhythmic primitives in a unimanual task**. *Front Comput Neurosci* 2013, **7**:90.

5. Hogan N, Sternad D: **Dynamic primitives in the control of locomotion**. *Front Comput Neurosci* 2013, **7**:71.

6. Bizzi E, Mussa-Ivaldi FA, Giszter S: **Computations underlying the execution of movement: a biological perspective**. *Science* 1991, **253**:287-291.

7. Giszter SF, Mussa-Ivaldi FA, Bizzi E: **Convergent force fields organized in the frog's spinal cord**. *J Neurosci* 1993, **13**:467-491.

8. Mussa-Ivaldi FA, Giszter SF, Bizzi E: **Linear combinations of primitives in vertebrate motor control**. *Proc Natl Acad Sci U S A* 1994, **91**:7534-7538.

9. Kargo WJ, Giszter SF: **Rapid correction of aimed movements by summation of force-field primitives**. *Journal of Neuroscience* 2000, **20**:409-426.

10. Hart CB, Giszter SF: **Modular premotor drives and unit bursts as primitives for frog motor behaviors**. *J Neurosci* 2004, **24**:5269-5282.

11. Saltiel P, Wyler-Duda K, D'Avella A, Tresch MC, Bizzi E: **Muscle synergies encoded within the spinal cord: evidence from focal intraspinal NMDA iontophoresis in the frog**. *J Neurophysiol* 2001, **85**:605-619.

12. Hart CB, Giszter SF: **A neural basis for motor primitives in the**
  • **spinal cord**. *J Neurosci* 2010, **30**:1322-1336.
This article uses spike triggered averaging of electromyograms from interneuron recordings to show that interneurons in the frog spinal cord act on discrete groups of motor pools. Further, the groups and projection weights match the muscle synergies (MP2 motor primitives in Figure 1) discovered by other means, such as perturbations [9,21] and signal decomposition methods [10]. The results thus strongly support a specific neural basis for some types of motor primitives.

13. Flash T, Hochner B: **Motor primitives in vertebrates and invertebrates**. *Curr Opin Neurobiol* 2005, **15**:660-666.

14. Schaal S, Schweighofer N: **Computational motor control in humans and robots**. *Curr Opin Neurobiol* 2005, **15**:675-682.

15. Ijspeert AJ, Nakanishi J, Hoffmann H, Pastor P, Schaal S: **Dynamical movement primitives: learning attractor models for motor behaviors**. *Neural Comput* 2013, **25**:328-373.

16. Polyakov F, Stark E, Drori R, Abeles M, Flash T: **Parabolic movement primitives and cortical states: merging optimality with geometric invariance**. *Biol Cybern* 2009, **100**:159-184.

17. Abeles M, Diesmann M, Flash T, Geisel T, Herrmann M, Teicher M: **Compositionality in neural control: an interdisciplinary study of scribbling movements in primates**. *Front Comput Neurosci* 2013, **7**:103.

18. Sosnik R, Hauptmann B, Karni A, Flash T: **When practice leads to co-articulation: the evolution of geometrically defined movement primitives**. *Exp Brain Res* 2004, **156**:422-438.

19. Rohrer B, Fasoli S, Krebs HI, Volpe B, Frontera WR, Stein J, Hogan N: **Submovements grow larger, fewer, and more blended during stroke recovery**. *Motor Control* 2004, **8**:472-483.

20. Zelman I, Titon M, Yekutieli Y, Hanassy S, Hochner B, Flash T: **Kinematic decomposition and classification of octopus arm movements**. *Front Comput Neurosci* 2013, **7**:60.

21. Kargo WJ, Giszter SF: **Individual premotor drive pulses, not time-varying synergies, are the units of adjustment for limb trajectories constructed in spinal cord,**. *J Neurosci* 2008, **28**:2409-2425.

22. Kargo WJ, Ramakrishnan A, Hart CB, Rome LC, Giszter SF: **A simple experimentally based model using proprioceptive regulation of motor primitives captures adjusted trajectory formation in spinal frogs**. *J Neurophysiol* 2010, **103**:573-590.

23. Berniker M, Jarc A, Bizzi E, Tresch MC: **Simplified and effective motor control based on muscle synergies to exploit musculoskeletal dynamics**. *Proc Natl Acad Sci U S A* 2009, **106**:7601-7606.

24. Kuppuswamy N, Harris CM: **Do muscle synergies reduce the dimensionality of behavior?** *Front Comput Neurosci* 2014, **8**:63.

25. Lafreniere-Roula M, McCrea DA: **Deletions of rhythmic motoneuron activity during fictive locomotion and scratch provide clues to the organization of the mammalian central pattern generator**. *J Neurophysiol* 2005, **94**:1120-1132.

26. Rybak IA, Shevtsova NA, Lafreniere-Roula M, McCrea DA:
  • **Modelling spinal circuitry involved in locomotor pattern generation: insights from deletions during fictive locomotion**. *J Physiol* 2006, **577**:617-639.
This article uses data from burst deletions in fictive cat locomotion to elaborate a model of locomotion that separates rhythm generation and pattern shaping. Modular burst structures and primitives would likely be elaborated as parts of the pattern shaping circuits.

27. Kiehn O: **Development and functional organization of spinal locomotor circuits**. *Curr Opin Neurobiol* 2011, **21**:100-109.

28. Drew T, Kalaska J, Krouchev N: **Muscle synergies during locomotion in the cat: a model for motor cortex control**. *J Physiol* 2008, **586**:1239-1245.

29. Krouchev N, Drew T: **Motor cortical regulation of sparse synergies provides a framework for the flexible control of precision walking**. *Front Comput Neurosci* 2013, **7**:83.

30. Overduin SA, d'Avella A, Roh J, Bizzi E: **Modulation of muscle synergy recruitment in primate grasping**. *J Neurosci* 2008, **28**:880-892.

31. Dominici N, Ivanenko YP, Cappellini G, d'Avella A, Mondi V, Cicchese M, Fabiano A, Silei T, Di Paolo A, Giannini C et al.: **Locomotor primitives in newborn babies and their development**. *Science* 2011, **334**:997-999.

32. d'Avella A, Lacquaniti F: **Control of reaching movements by muscle synergy combinations**. *Front Comput Neurosci* 2013, **7**:42.

33. Lacquaniti F, Ivanenko YP, d'Avella A, Zelik KE, Zago M: **Evolutionary and developmental modules**. *Front Comput Neurosci* 2013, **7**:61.

34. Torres-Oviedo G, Ting LH: **Muscle synergies characterizing human postural responses**. *J Neurophysiol* 2007, **98**:2144-2156.

35. Torres-Oviedo G, Ting LH: **Subject-specific muscle synergies in human balance control are consistent across different biomechanical contexts**. *J Neurophysiol* 2010, **103**:3084-3098.

36. Cheung VC, Piron L, Agostini M, Silvoni S, Turolla A, Bizzi E: **Stability of muscle synergies for voluntary actions after cortical stroke in humans**. *Proc Natl Acad Sci U S A* 2009, **106**:19563-19568.

37. Cheung VC, Turolla A, Agostini M, Silvoni S, Bennis C, Kasi P,
  • Paganoni S, Bonato P, Bizzi E: **Muscle synergy patterns as physiological markers of motor cortical damage**. *Proc Natl Acad Sci U S A* 2012, **109**:14652-14656.
Cheung and colleagues [36] in both this and their preceding article show that the same sets of modules can be seen in both affected and unaffected limb after stroke, but modules are more uncoordinated in their use in the affected limb. The disorder includes collapse or merging of modules usually staggered in time (see also [62]). Degree of change relates to deficit and recovery, as also seen with kinematic primitive analyses of stroke, see [19].

38. Steele KM, Tresch MC, Perreault EJ: **The number and choice of muscles impact the results of muscle synergy analyses**. *Front Comput Neurosci* 2013, **7**:105.

39. Steele KM, Tresch MC, Perreault EJ: **Consequences of**
  •• **biomechanically constrained tasks in the design and interpretation of synergy analyses**. *J Neurophysiol* 2015 http://dx.doi.org/10.1152/jn.00769.2013.
This article is a thorough analysis and discussion of the pitfalls and cautions needed in using statistical signal decomposition methods to identify primitives in motor patterns. It is essential reading for the novice considering the use of these techniques and designing experiments around them.

40. Straka H, Simmers J: **Xenopus laevis: an ideal experimental model for studying the developmental dynamics of neural network assembly and sensory-motor computations**. *Dev Neurobiol* 2012, **72**:649-663.

41. Straka H, Fritzsch B, Glover JC: **Connecting ears to eye muscles: evolution of a 'simple' reflex arc**. *Brain Behav Evol* 2014, **83**:162-175.

42. Levine AJ, Hinckley CA, Hilde KL, Driscoll SP, Poon TH,
  •• Montgomery JM, Pfaff SL: **Identification of a cellular node for motor control pathways**. *Nat Neurosci* 2014, **17**:586-593.
Levine and colleagues here identify classes of interneurons in the mouse spinal cord that could support motor primitives in mammals. The precise projection patterns compared to motor primitives identified in behavior are not established yet, but the means now clearly exists to attack this issue.

43. Talpalar AE, Bouvier J, Borgius L, Fortin G, Pierani A, Kiehn O: **Dual-mode operation of neuronal networks involved in left-right alternation**. *Nature* 2013, **500**:85-88.

44. Schouenborg J: **Action-based sensory encoding in spinal sensorimotor circuits**. *Brain Res Rev* 2008, **57**:111-117.

45. Azim E, Jiang J, Alstermark B, Jessell TM: **Skilled reaching relies on a V2a propriospinal internal copy circuit**. *Nature* 2014, **508**:357-363.

46. Azim E, Alstermark B: **Skilled forelimb movements and internal**
  • **copy motor circuits**. *Curr Opin Neurobiol* 2015, **33C**:16-24.
This very readable article reviews the C3–C4 interneuron contributions to skilled forelimb use and techniques recently brought to bear on the analysis of these. Precise effects are identified and discussed. As in [42••], as yet the degree of discreteness in projections vis a vis muscle synergies remain to be elaborated.

47. Hagglund M, Dougherty KJ, Borgius L, Itohara S, Iwasato T,
•• Kiehn O: **Optogenetic dissection reveals multiple rhythmogenic modules underlying locomotion**. *Proc Natl Acad Sci USA* 2013, **110**:11589-11594.
This article shows bursting capacity to be available in the mouse in extensor synergies, in flexor synergies and perhaps single muscle 'modules'. The data thus provide the potential for a scheme like Figure 3b or c with coupled oscillator or finite state machine like pattern and rhythm generation. The authors favor Figure 3b which also has resemblance to the frameworks of localized oscillators suggested by Grillner and colleagues.

48. Yakovenko S, Krouchev N, Drew T: **Sequential activation of motor cortical neurons contributes to intralimb coordination during reaching in the cat by modulating muscle synergies**. *J Neurophysiol* 2011, **105**:388-409.

49. Wolpert DM, Ghahramani Z, Jordan MI: **Perceptual distortion contributes to the curvature of human reaching movements**. *Exp Brain Res* 1994, **98**:153-156.

50. Maoz U, Flash T: **Spatial constant equi-affine speed and motion perception**. *J Neurophysiol* 2014, **111**:336-349.

51. Mussa-Ivaldi FA, Giszter SF: **Vector field approximation: a computational paradigm for motor control and learning**. *Biol Cybern* 1992, **67**:491-500.

52. Mussa-Ivaldi FA: **From basis functions to basis fields: vector field approximation from sparse data**. *Biol Cybern* 1992, **67**:479-489.

53. Colgate JE, Hogan N: **Robust-control of dynamically interacting systems**. *International Journal of Control* 1988, **48**:65-88.

54. Slotine JJ, Lohmiller W: **Modularity, evolution, and the binding problem: a view from stability theory**. *Neural Netw* 2001, **14**:137-145.

55. McIntyre J, Slotine JJ: **Does the brain make waves to improve stability?** *Brain Res Bull* 2008, **75**:717-722.

56. McKay JL, Ting LH: **Optimization of muscle activity for task-level goals predicts complex changes in limb forces across biomechanical contexts**. *PLoS Comput Biol* 2012, **8**:e1002465.

57. Collins JJ: **The redundant nature of locomotor optimization laws**. *J Biomech* 1995, **28**:251-267.

58. Valero-Cuevas FJ: **A mathematical approach to the mechanical capabilities of limbs and fingers**. *Adv Exp Med Biol* 2009, **629**:619-633.

59. Kutch JJ, Valero-Cuevas FJ: **Challenges and new approaches to proving the existence of muscle synergies of neural origin**. *PLoS Comput Biol* 2012, **8**:e1002434.

60. Racz K, Brown D, Valero-Cuevas FJ: **An involuntary**
•• **stereotypical grasp tendency pervades voluntary dynamic multifinger manipulation**. *J Neurophysiol* 2012, **108**:2896-2911.
In this article and in [61], Racz and colleagues show that stereotypic patterns not expected under strict optimization are seen in manipulation. They attribute these to brainstem projections, and the effects they see are consistent with primitive contributions to manipulation tasks.

61. Racz K, Valero-Cuevas FJ: **Spatio-temporal analysis reveals active control of both task-relevant and task-irrelevant variables**. *Front Comput Neurosci* 2013, **7**:155.

62. Clark DJ, Ting LH, Zajac FE, Neptune RR, Kautz SA: **Merging of healthy motor modules predicts reduced locomotor performance and muscle coordination complexity post-stroke**. *J Neurophysiol* 2010, **103**:844-857.

63. Fox EJ, Tester NJ, Kautz SA, Howland DR, Clark DJ, Garvan C,
• Behrman AL: **Modular control of varied locomotor tasks in children with incomplete spinal cord injuries**. *J Neurophysiol* 2013, **110**:1415-1425.
Fox and colleagues examine modularity in spinal injured children in a wide range of locomotor tasks and show common modular structure, matching with the cross-species examinations in [31] and stroke effects in lower limb in adults [62].

64. Drew T, Marigold DS: **Taking the next step: cortical**
• **contributions to the control of locomotion**. *Curr Opin Neurobiol* 2015, **33C**:25-33.
Drew and Marigold provide a thorough summary of the modular burst structures in locomotion, forelimb controls, and their voluntary cortical control and adjustment.

65. Tremolizzo L, Susani E, Lunetta C, Corbo M, Ferrarese C, Appollonio I: **Primitive reflexes in amyotrophic lateral sclerosis: prevalence and correlates**. *J Neurol* 2014, **261**:1196-1202.

66. Desmurget M, Richard N, Harquel S, Baraduc P, Szathmari A, Mottolese C, Sirigu A: **Neural representations of ethologically relevant hand/mouth synergies in the human precentral gyrus**. *Proc Natl Acad Sci U S A* 2014, **111**:5718-5722.

67. Overduin SA, d'Avella A, Carmena JM, Bizzi E: **Microstimulation activates a handful of muscle synergies**. *Neuron* 2012, **76**:1071-1077.

68. Overduin SA, d'Avella A, Carmena JM, Bizzi E: **Muscle synergies**
• **evoked by microstimulation are preferentially encoded during behavior**. *Front Comput Neurosci* 2014, **8**:20.
This article examines both microstimulation and nearby neural recordings and shows that stimulation recruitment effects closely match neural correlations to modules in reach, grasp and carry tasks in primates. The data are consistent with modular control, possibly through lower level primitives.

69. Graziano MS, Taylor CS, Moore T: **Complex movements evoked by microstimulation of precentral cortex**. *Neuron* 2002, **34**:841-851.

70. Takei T, Seki K: **Spinal premotor interneurons mediate dynamic and static motor commands for precision grip in monkeys**. *J Neurosci* 2013, **33**:8850-8860.

71. Takei T, Seki K: **Synaptic and functional linkages between spinal premotor interneurons and hand-muscle activity during precision grip**. *Front Comput Neurosci* 2013, **7**:40.

72. Martin JH: **The corticospinal system: from development to motor control**. *Neuroscientist* 2005, **11**:161-173.

73. Todorov E: **Efficient computation of optimal actions**. *Proc Natl Acad Sci U S A* 2009, **106**:11478-11483.

74. Berger DJ, Gentner R, Edmunds T, Pai DK, d'Avella A: **Differences**
•• **in adaptation rates after virtual surgeries provide direct evidence for modularity**. *J Neurosci* 2013, **33**:12384-12394.
Berger and colleagues demonstrate using myographic controls of a VR display that virtual surgeries that force subjects to control away from the modularity observed in baseline conditions are more difficult than those allowing use of baseline modules. They see this as direct evidence for modular controls. The constraints are not absolute, but impede other solutions, or facilitate use of existing modules when possible.

75. Berger DJ, d'Avella A: **Effective force control by muscle synergies**. *Front Comput Neurosci* 2014, **8**:46.

76. Muceli S, Falla D, Farina D: **Reorganization of muscle synergies during multidirectional reaching in the horizontal plane with experimental muscle pain**. *J Neurophysiol* 2014, **111**:1615-1630.