Motor primitives in vertebrates and invertebrates

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In recent years different lines of evidence have led to the idea that motor actions and movements in both vertebrates and invertebrates are composed of elementary building blocks. The entire motor repertoire can be spanned by applying a well-defined set of operations and transformations to these primitives and by combining them in many different ways according to well-defined syntactic rules. Motor and movement primitives and modules might exist at the neural, dynamic and kinematic levels with complicated mapping among the elementary building blocks subserving these different levels of representation. Hence, while considerable progress has been made in recent years in unravelling the nature of these primitives, new experimental, computational and conceptual approaches are needed to further advance our understanding of motor compositionality.

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Introduction

Humans compose words from phonemes, sentences from words, and so on. This ability to combine and reconfigure simple elements in many different ways to build complex patterns, representations and behaviors is crucial, not only for speech and language but also for visual perception, action and cognition. Focusing here on motor control, ample evidence from both higher and lower levels of vertebrate and invertebrate motor systems suggests that voluntary actions are composed of simpler elements that are bonded to each other either simultaneously or serially in time [1,2,3•,4,5].

Such modular organization can account for the richness and versatility of animal and human behavior and for the ability to learn new skills and adapt easily to new environmental conditions. The existence of a large number of redundant modules and the ability to combine them in many different ways might also account for the motor equivalence phenomenon, namely that any single motor task can be performed in many different ways as long as these include some crucial features that enable achievement of the desired goals. More importantly, however, is the assumption that there is a limited vocabulary of primitives. This can alleviate the curse of dimensionality and simplify the complexities associated with the redundancy that exists at all the different levels of the motor hierarchy.

Here, we review recent literature on motor primitives and compositionality. We focus on three aspects. First, how are motor and movement primitives defined? Second, what is the nature of these primitives and how are they internally represented? And third, what rules govern the generation of a large repertoire of movements from a limited set of elements?

Motor primitives

Motor or movement primitives refer loosely to building blocks at different levels of the motor hierarchy. Motor primitives might be equivalent to 'motor schemas' [6], 'prototypes' [7], or 'control modules' [8]. They need not be universal, that is, the same building block need not be used for all possible behaviors or tasks. Instead, they might be specific to only a particular level of representation or task. Their crucial feature is that many different movements can be derived from a limited number of stored primitives through appropriate operations and transformations, and that these movements can be combined through a well defined syntax of action to form more complex actions. Schaal *et al.* [8], Del Vecchio *et al.* [9] and others have recently attempted to better formalize the definition. The term 'movemes' (as the parallel of speech phonemes for movement) was used in Del Vecchio *et al.* [9] to refer to motion primitives.

Methods for extracting and inferring primitives include principal component analysis (PCA), probabilistic PCA, hidden Markov models (HMM), Isomaps, and automatic derivation of primitives based on different similarity measures among, for example, movements or actions (for review see Jenkins and Mataric [10]).

Primitives can be kinematic [1,11], dynamic [4,12] or both. Kinematically defined primitives might be called strokes [1] or submovements [11], whereas dynamic primitives consist of static force fields [2], temporally varying muscle and joint torque synergies [12,13•] or control policies [8].

At the neuronal level, a primitive or a neuronal module corresponds to a neuron assembly, for example, of spinal or cortical neurons [4,14]. In some invertebrates (e.g. *Aplysia*), it might consist of identifiable neurons comprising a central pattern generator (CPG) [15••].

Behavioral level

Since Bernstein [16], there has been a general consensus that we try to follow mental templates of motion when executing motor tasks. For example, reaching movements are composed of straight lines with bell-shaped velocity profiles. These motion primitives can be selected using several optimization criteria [17–19]. During reaching, the shape of the velocity profiles is invariant with changes in speed, unless there are accuracy demands; then the movements obey Fitts' law [20]. Reaching movements appear to be coded in terms of direction and extent [21]. Nevertheless, in spite of their apparent continuity, even pre-planned reaching movements appear to be composed of discrete submovements, all with a similar stereotypical, serially concatenated shape and overlapping in time [22,23,24•].

Submovements are easier to detect during on-line movement corrections, especially when higher end-point accuracy is required [25] or during trajectory modification [26]. Velocity bumps indicate the presence of submovements even in the absence of visual feedback [27]. Movements that are generated by stroke patients [11,28•] or those that are generated during load adaptation tasks [25] show that hand trajectory can be composed of a few velocity primitives, all with similar shapes characterized by a minimum-jerk [17] or log-normal function [29]. These inferred velocity primitives are quite stereotypical, with a well-preserved linear relationship between speed and duration [22]. When stroke patients gain better control over their limb, the number of submovements decreases and their temporal overlap increases, giving smoother trajectories [28•]. Babies learn to generate visually guided reaching by smoothly blending sequential submovements into continuous movements [30].

Simple curved motions containing several velocity peaks are regularly observed during curved or obstacle-avoidance movements. Such continuous two-dimensional trajectories follow the two-thirds power law [31] with a piecewise constant gain factor. Thus, drawing movements, in spite of their apparent continuity, also appear to be constructed of individual segments or strokes, which are either straight or consist of curved segments, for example parabolic segments, as was shown recently on the basis of the use of differential geometrical tools [32]. The two-thirds power law was recently shown to be compatible with a model assuming an underlying objective of generating maximally smooth hand trajectories. Movement segmentation based on the existence of a piecewise constant velocity gain factor might be an epi-

phenomenon of trajectory optimization, rather than a reflection of an underlying segmented control [33,34].

The existence of motor primitives has also been examined for human and monkey grasping and object manipulation movements. Prehension, such as lifting a full cup, is composed of reaching, orienting the hand and grasping. Although these components can be combined in all possible ways, the three actions are executed as a unified well-coordinated complex act [35]. In compliant tasks such as grasping, not only must the positions of the fingers and motions be appropriately selected and preplanned but the forces exerted on the object must also be controlled to achieve the goal of the task while securing a stable grasp [36]. Finger movements and forces have been decomposed into basic synergies based either on the idea of uncontrolled manifold [37] or on inverse dynamics computations [12]. Complicated hand gestures, such as typing and finger spelling [38], also consist of primitives or more complicated sequences that can be decomposed into a series of elementary units of action.

In the field of invertebrates with hard exoskeletons, locust reaching movements during grooming have been analyzed. The reaching movement is controlled in joint space [39], but it is not clear whether movement primitives and force field summation are involved. By contrast, in the octopus, the totally flexible arm enables the control system to use a unique space for constructing movement primitives. During reaching or fetching movements, the arm is stereotypically configured to fit the task using a minimal number of degrees of freedom [40,41••].

When fetching a grasped object to the mouth, the octopus arm is configured into a quasi-articulated structure with three segments and three rotary joints. Joint positions are adjusted to the site of grasping along the arm, giving a geometry resembling that of vertebrate arms and some arthropod appendages. This structural primitive enables the octopus to have precise control of point-to-point movements [41••].

Muscle level: synergies

Co-activation of several muscles, a 'synergy', produces a torque about a joint or a force in a particular direction. Only a few of all possible 'synergies' are used [42]. Electromyographic (EMG) recordings from frog hind limb muscles have been computer analyzed to test whether natural behavior shows synergies among groups of muscle activities for an entire set of natural behaviors [4,13•,42–44]. Similar attempts have been made to find muscle synergies during human posture and locomotion [13•,45•,46].

Originally, each muscle was assumed to take part only in one particular synergy. Such over-simplified attempts failed, throwing the existence of muscle synergies into

doubt [45•]. More recently, however, muscle synergies during a postural task in the cat [45•] have been successfully identified based on the use of non-negative matrix factorization (a linear non-negative approximate data representation), a technique that was first used in Tresch *et al.* [47] for the identification of muscle synergies. Because several synergies were assumed to act on a given muscle, the net activation of that muscle is the sum of activations due to all the synergies.

d'Avella and Bizzi [13•] have employed a similar approach to extract invariant amplitudes and timing relationships among muscle activations during more natural behaviors in intact animals. A combination of synergies that were shared across behaviors and those that were for specific behaviors captured the invariance across the entire observed dataset. These results support a modular organization of the motor controller and that the motor output of these modules is combined to control a large set of behaviors. A similar approach was applied to human locomotion [46].

Neural level
Frog wiping behavior is an ideal model for investigating how a sensory map is transformed into a well-coordinated motor output (for a review see Tresch *et al.* [47]). Microstimulation of an interneuronal region in the spinal cord showed that microcircuits are organized into discrete modules, each generating a specific force field [2,3•]. Although movements are generated by centrally organized synergies, sensory feedback adjusts the motor output of complex movements [44]. In the turtle, the motor output of the spinal cord in deafferented preparations is similar to that of intact animals [5,48], also indicating the existence of a CPG, and these appear to be relatively independent modules [48,49]. Some identified temporal relations among muscle and motor nerve activities appear common to several behaviors, whereas others are behaviorally specific. Single unit recordings support the modular organization of spinal neurons at the neural network level: some neurons are active during several movements, whereas others are active only during a certain movement [49]. Similar results have been obtained from single identified neurons in the feeding system of *Aplysia* [15••].

In the locust, the specific pattern of motor activity during grooming can also be generated in deafferented preparations, suggesting that this motor output also is generated by a CPG [50].

In the octopus, arm extension in reaching movements (Figure 1a) is controlled by a simple wave of muscle stiffening propagating along the arm [51,52]. This stiffening wave can be viewed as a basic muscle synergy of simultaneous activation of all arm muscles. A central command is needed to initiate and scale the movement parameters [53]. During octopus fetching (Figure 1b), two

waves of muscle activation propagate along the arm towards each other. These stiffen the proximal and medial segments of the quasi-articulated arm, their collision point setting the medial joint location. This is a remarkably simple peripheral mechanism for adjusting segment lengths according to where along the arm the object was grasped (Sumbre G, Fiorito G, Flash T, Hochner B, unpublished).

In monkey cortex, electrical microstimulation in primary motor and premotor cortex evokes complex purposeful movements involving many joints and even several body parts [54]. These actions were very similar to gestures included in the monkey's natural repertoire. Microstimulation at each site caused the arm to move to a specific final posture [55]. There, thus, appears to be a cortical map of joint angles.

Neural recording studies have shown that arm motion can be reconstructed from the firing of a population of neurons in the motor areas of the vertebrate cortex [56]. Although earlier reports indicated that neural populations mostly code instantaneous time-varying kinematic or dynamic variables (e.g. movement direction and velocity or force), analyses of both single neurons and neural assemblies have provided evidence for cortical coding also of more global features, such as a segment geometrical shape [57] or the order of the segments within the sequence [14,58].
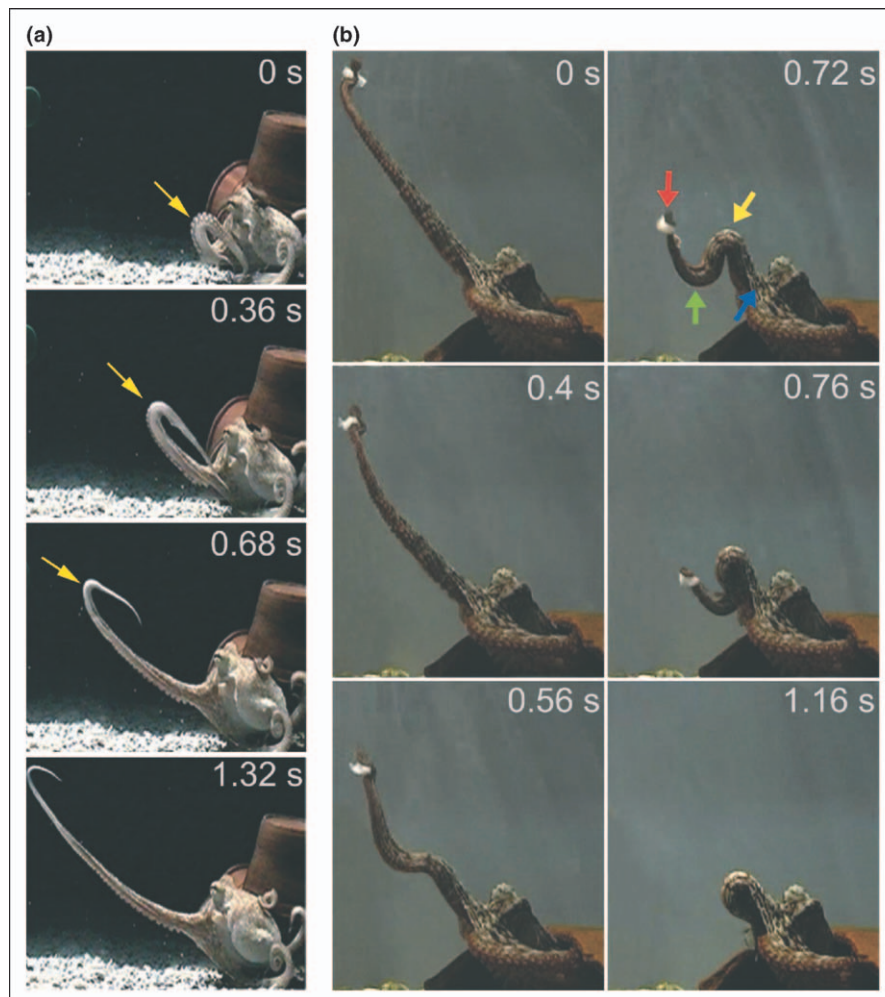
Syntax of action
Components can be strung together serially in time or in parallel. Not all possible combinations are utilized. The syntax of action is constituted by rules, such as which stroke can be combined with which. Different syntactic rules, identified at different levels of the motor hierarchy, consist of, for example, linear superposition of movement segments [26], vector summation of spinal force fields [2,3•], and weighted summation of muscle activities [13•,42,46]. Syntactic rules in the temporal domain involve simple linear temporal scaling of velocity profiles and their superposition [24•], or more complicated nonlinear time warping or co-articulation between consecutive elements [59].

In co-articulation, the position of an effector is affected by the previous and/or following element. With practice, smoother blending of units can evolve and new chunks or movement primitives might emerge [60,61•]. Learning to generate a series of handwriting-like trajectories through a series of targets shows that co-articulation in hand movements can reflect the global optimization of a segment [25,34,61•]. Co-articulation between sequential elements has also been reported for finger spelling and sign language gestures [38].

Possible neuronal mechanisms for stringing together or blending different elements have been described for the

Figure 1

Two examples of stereotypical unconstrained octopus arm movements. **(a)** Snapshots taken during a reaching movement towards a target (arm extension). A dorsally oriented bend in the arm (yellow arrow) propagates toward the tip of the arm. In this configuration the suckers are pointing up-front and only 3DOFs are controlled (Reprinted with permission from [53]. Copyright 2001 AAAS). **(b)** Fetching movements whereby a grasped object (red arrow) is brought to the mouth. To achieve this accurate point-to-point movement, the octopus reconfigures its arm into a quasi-articulated structure in which the two proximal segments (the segments bounded between the blue–yellow and yellow–green arrows) are of similar lengths. The segments then rotate about the medial 'joint' (yellow arrow) to bring the food to the mouth. This movement involves one DOF for each joint.

turtle spinal cord [5]. Stimulating the dorsolateral funiculus elicited forward swimming patterns combined with specific scratch movements triggered by a mechanical stimulation [62]. Thus, different movements can be organized by reconfiguring a small number of motor output units, some of which are shared, whereas others are task specific.

The cortical synfire chain was conceived to explain precise spike patterns in multiple single unit recordings. The so-called 'binding mechanism' was proposed for binding the elements of a composite object to each other. Given that activities in synfire chains might bind and form a hierarchy of representations as required for language [63],

they might also offer a unique neural mechanism for compositionality of motor elements [64].

Motor learning and robotics

Using a small set of modifiable and adjustable primitives tremendously simplifies the task of learning new skills or adapting to new environments. Constructing internal neural representations from a linear combination of a reduced set of basis functions might be crucial for generalizing to novel tasks and new environmental conditions [65]. Particular choices of basis functions might further reduce the number of functions required to represent learned information successfully [66]. These basis functions undergo tuning with learning [67] and might depend

either on velocity [68] or on both position and velocity and be gain modulated [69]. Particular choices of variables or the use of contraction fields can yield more stable representations [70].

Using a reduced set of movements, control policies or actuator synergies have attracted great interest in robotics research [8,71–73]. A limited set of primitives can considerably reduce the high dimensionality and complexity associated with robot control problems. Thus, several robotic studies have focused on, for example, what is a good set of primitives, how they can be mathematically extracted [10] and formalized [8,9], and how they can be used for robot learning by imitating human movements [7,72,73]. Schaal *et al.* [8] used point attractors and limit cycles based on non-linear dynamic descriptions and suggested a repertoire composed of both discrete and rhythmic movements, similar to vertebrate and invertebrate motor pattern generators. Recent brain mapping studies have also shown that the generation of discrete movements involves a greater number of cortical areas than the generation of rhythmic movements [74].

The language connection

How did humans evolve their remarkable ability to communicate in words? One theory is that language might have evolved from the use of gestures rather than vocalizations [75••]. This idea is supported by the discovery of mirror neurons in monkeys [76,77] and of a similar system in humans [78]. This theory is also supported by the following three observations: first, the availability of a neural system participating in both action production and observation, second, the analogy between Broca's area and F5 in the monkey brain, and third, the coding for nonlinguistic actions in Broca's area [79]. Nowhere is there a tighter connection between hand movement and language than in sign language. A recent study of the hand movements in Nicaraguan sign language describes the emergence of discreteness and a combinatorial linear structure within motion event expressions, particularly in later learners [80•]. Children possess the learning abilities that give language its structure. A study involving the analysis of babbling-like hand movements in sign-exposed hearing children claims that babbling is fundamentally a linguistic [81] and not a motoric activity in contrast to the claim made by MacNeilage [82].

Conclusions

We have reviewed recently published studies that aim to extract, characterize and model motor and movement primitives at different levels of the motor hierarchy and to seek the principles underlying motor compositionality. Although recent studies have been successful in extracting muscle synergies and decomposing point-to-point movements into stereotypical submovements, further mathematical tools and more advanced approaches are needed to segment continuous trajectories into basic elements. Further neurophysiological studies are also needed to unravel the neural representations used for encoding whole strokes or primitives and the mechanisms used for the concatenation of these 'movemes' (primitives of motion in analogy to phonemes, see [9]) into motor words and sentences. Some of the laws regulating movement production might also be responsible for action perception. Hence, further advances in our understanding of motor compositionality might shed new light not only on motor production, learning and skill acquisition but also on motor imitation and perceptual learning, and might advance our ability to develop versatile and adaptive robotic systems.

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