

On the notion of motor primitives in humans and robots

Jürgen Konczak

Human Sensorimotor Control Lab

School of Kinesiology, Dept. of Neurology, University of Minnesota

1900 University Ave. S.E.

Minneapolis, U.S.A.

jkonzak@umn.edu

Abstract

This article reviews two reflexive motor patterns in humans: Primitive reflexes and motor primitives. Both terms coexist in the literature of motor development and motor control, yet they are not synonyms. While primitive reflexes are a part of the temporary motor repertoire in early ontogeny, motor primitives refer to sets of motor patterns that are considered basic units of voluntary motor control thought to be present throughout the life-span. The article provides an overview of the anatomy and neurophysiology of human reflexive motor patterns to elucidate that both concepts are rooted in architecture of the spinal cord. I will advocate that an understanding of the human motor system that encompasses both primitive reflexes and motor primitives as well as the interaction with supraspinal motor centers will lead to an appreciation of the richness of the human motor repertoire, which in turn seems imperative for designing epigenetic robots and highly adaptable human machine interfaces.

1. What constitutes a reflex?

Traditionally a reflex is defined as an involuntary movement which is triggered by a sensory stimulus. That is, a stereotyped motor response is elicited when a particular sensory stimulus is present and the organism cannot voluntarily suppress this response. Some reflexes are responses to avoid a potentially harmful situation for the organism. For example, whenever an aversive stimulus like a drop of water is applied to the human eye, the eyelid reflex quickly closes eye to protect from further exposure. Another function of reflexes is to assure the fast adaptations of motor patterns to maintain or achieve a behavioral goal.

While many animals including humans exhibit motor behaviors that seem strictly stimulus-bound, a large array of motor patterns, which are typically considered to be reflexive, are often not completely shaped by an environmental stimulus but are partially under volitional control. Such volitional influences make it problematic to classify even simple motor patterns as pure reflexes. The quest for an acceptable definition of a reflex is further complicated by the phenomenon of the so-called infantile or primitive reflexes.

These are a set of stereotypic behaviors that can only be elicited *in utero* or in the newborn. That is, a particular motor pattern is only bound to a stimulus for a limited amount of time during early development.

The notion of reflexive motor patterns or motor primitives has been adopted for the engineering of autonomous robots. In the robotic arena reflex-like motor patterns often serve to establish initial sensory-motor relationships that can serve as building blocks for a wider array of desired activities to be acquired after system birth (Metta et al. 1999; Paine and Tani 2004). The issue of reflexes or motor primitives becomes important as roboticists begin to adapt early human development as a model for designing the future generations of autonomous robots. A deeper understanding of the physiological mechanisms of developing human motor control might enhance the features of the design. Conversely, the simplified adaptation of highly complex mechanisms of human motor control might lead to costly design flaws.

2. Spinal reflexes

The link between proprioceptive information from muscles, joints and skin and observable stereotyped movements was established by the English physiologist Charles Sherrington. He investigated the spinal stretch reflex, a response that occurs when the muscles is suddenly lengthened (see Fig. 1). Sherrington found that stretch reflexes were abolished when the ventral or the dorsal roots were cut, which established that they depended on proprioceptive input and an intact return projection to the muscles. He proposed that reflexes constitute the basic units of movement and that complex motor patterns arise from combining or chaining simple reflexes (Sherrington 1906). Today we recognize that many movements can be executed in the absence of sensory information (Lashley 1917; Gandevia et al. 1990), which contradicts Sherrington's reflex-chaining hypothesis. Nevertheless, it is a generally accepted view that reflex patterns are embedded within centrally generated motor commands and play an important part in the regulation of voluntary movements especially when task demands, the behavioral goal or the environment change suddenly (Pearson and Gordon 2000).

The interaction between descending central commands and spinal reflex activity becomes apparent, if one considers the neural architecture at the spinal level. The alpha motor

neuron pool of a particular muscle receives both sensory input from the periphery via the Ia afferent fibers and input from higher motor centers (e.g., motor cortices and brainstem). That is, peripheral and central inputs can influence the firing behavior of the alpha motor neurons at any given time. In addition, both the peripheral and the descending stream converge on so-called Ib inhibitory interneurons (see Fig. 1A). This architecture allows higher motor centers, involved in voluntary control, to coordinate the action of opposing muscles (antagonists) through a single command. It is essentially responsible for the inhibition of antagonistic muscles - a process that Sherrington called *reciprocal innervation* (see Fig. 1B).

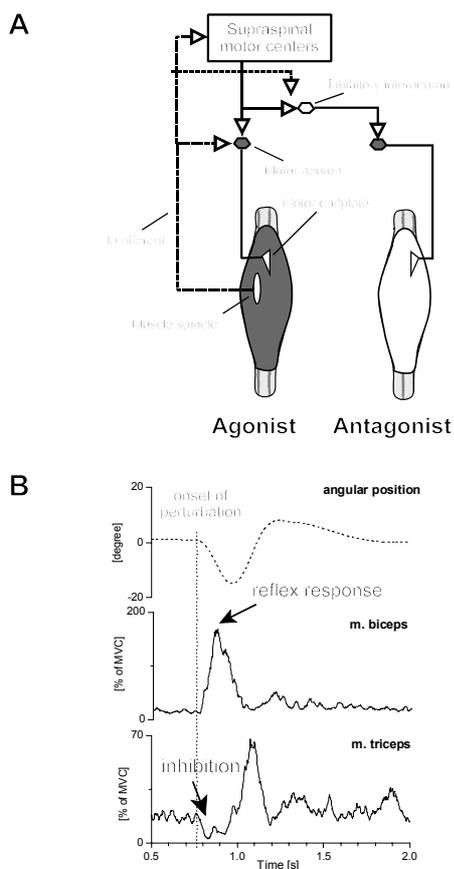


Figure 1: Convergence of proprioceptive signals and descending commands at the spinal motor neuron pools **A**. Efferent projections from supraspinal centers and peripheral signals from muscle proprioceptors converge at the spinal α motor neurons of the agonist muscle as well as Ib inhibitory interneurons, which project to motor neurons of the antagonist. This basic circuitry affords the triggering of stretch responses via the Ia afferents, but also relays commands from supraspinal motor centers. **B**. Electrophysiological response of two muscles to an unexpected perturbation of the forearm by an external force. Within 30–40 ms after the onset of the perturbation the stretched biceps muscle becomes active, while the antagonistic triceps muscle is inhibited. [% MCV: percent of electromyographic activity during maximum voluntary contraction]

There are numerous neurophysiological features other

reciprocal innervation that facilitate the interaction between peripheral and central inputs to the spinal motor neuron pool. The spinal cord circuitry is highly complex, containing additional inhibitory and reciprocal connections not shown in Figure 3A (for an introduction see: Pearson and Gordon 2000).

3. Primitive or infantile reflexes

Reflexive movements can be elicited *in utero* as early as the second or third month after conception. Fetal movements become often quite distinct in the last three months of pregnancy with leg kicking accounting for nearly half of those movements (Walters 1964). At birth, some tendon-stretch reflexes can usually be elicited, indicating that the afferent proprioceptive projections and efferent motor projections from the spinal cord are operational (Myklebust et al. 1986).

Next to stretch reflexes a set of infant reflexes are also observed in the newborn infant. These early reflexes are also sometimes called *primitive reflexes*. They are considered brain-stem mediated, complex automatic movement patterns and are elicited by specific sensory stimuli. These reflexes are fully present at birth in term infants and disappear gradually (Milani-Comparetti and Gidoni 1967; Zafeiriou 2004). For example, the asymmetric tonic neck reflex (ATNR; see Fig. 2) is a likely response to head rotation in the second to fourth months of life. After that time, the ATNR slowly gives way to other behaviors like symmetrical head-lifting, reaching or derotative righting. The other major infant reflex patterns include the Moro response, palmar and plantar grasp, rooting, sucking, placing, the symmetric tonic neck reflex, and the crossed extensor reflex.

Traditionally, the disappearing of primitive reflexes is thought to be the result of brain maturation (Gesell 1946; McGraw 1946). As higher cortical centers mature, they begin to inhibit the brainstem mediated responses and thus allow for the emergence of postural responses and volitional movement. The major premise of this maturational viewpoint is that the successive myelination of specific brain regions give rise to new sensory, motor and cognitive functions (Myelination is the process of depositing myelin to nerve fibers. Myelin acts as an electric insulator and improves nerve conduction velocity and signal strength). In recent years, the maturational view has been criticized for primarily using myelination as an index of brain maturation, since it does not correlate well with the onset of new behaviors. For example, at the onset of walking, which typically occurs between 12 to 15 months in term infants, less than half of the corticospinal fibers that innervate the leg muscles are myelinated (Brody, Kinney, Kloman and Gilles, 1987). Other research in kittens shows that the myelination of the corticospinal tract, which is a major projection of motor commands from the brain to the spinal cord, correlates lower with improved limb motor control than changes in axon terminal morphology of the same tract (Li and Martin 2002). These findings indicate that myelination alone cannot account for the emergence of new behaviors and that additional factors of neural development must also play a role in shaping behaviors.

Moreover, these findings speak against the notion that cortical inhibition first needs to subdue no longer wanted spinal reflexive patterns to make room for volitional motor control. Knowing that at a time when infants achieve major motor milestones like sitting, reaching and walking they still show a substantial lack of myelinated fibers, implies that supraspinal signals terminating at inhibitory spinal neurons may be as noisy as those signals that reach excitatory neurons. Thus, it remains at least questionable how the “noisy” cortical inhibition of spinal motor drives can be causal to the disappearance of primitive reflexes.

An alternative view contends that growth-related, biomechanical changes contribute to the disappearance of certain infantile reflexes. For example, Thelen and Fisher (1982) demonstrated that babies, who had lost their stepping reflex, showed coordinated stepping when their legs were submerged in water. The conclusion was that the rapidly increased leg inertia had mechanically “inhibited” the appearance of stepping motion, which was then being compensated by the buoyancy of the water. That is, the reflex had not disappeared, but the activation of appropriate motor units had not kept up with increases in leg mass. Against the notion that growth related factors may play a major role in the suppression of reflexive behavior are findings showing that kinematic differences in pre-term versus full-term babies are not explained by differences in leg volume (Geerdink, Hopkins, Beek and Heriza 1996).

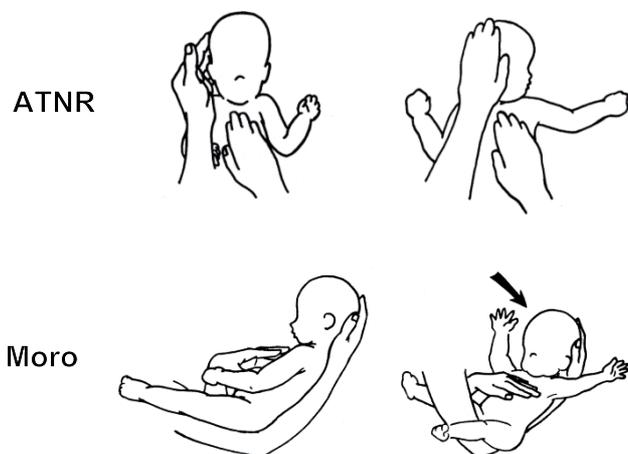


Figure 2: Primitive reflexes in human infants. **A.** Asymmetric tonic neck reflex (ATNR). Turning of the head elicits extension of the arm in view and flexion in the opposite arm. The baby assumes a “fencer” position. **B.** Moro reflex. Named after Ernest Moro who first described the reflex in 1918. Sudden lowering of the head or body elicits extension in all four limbs. Modified from: Milani-Comparetti (1967).

A third view, in line with the view on the embedding of stretch reflexes into voluntary behavior is that as the higher brain centers mature and the corticospinal projections find their motor neuron targets within the spinal cord, the spinal motor center and the motor centers in the brain can begin to interact in such a way that goal-directed action becomes more

reliant and successful (Johnson 2001). Within such framework the development of specific motor functions involves the union of many specialized areas in the brain and spinal cord. The onset of new behaviors or the disappearance of previous behaviors is thus not the result of a top-down modulation, but needs to be understood as the result of associated and parallel changes in several regions of the motor system (e.g., cortex, cerebellum, brainstem and spinal cord).

4. Human motor primitives

The term *motor primitive* is used by researchers in biological motor control to indicate "building blocks of movement generation" (Peters and Schaal 2004). However, *motor primitives* should not simply be equated with *primitive reflexes*. A motor primitive is defined as a set of force-fields that are generated by muscle synergies (Mussa-Ivaldi 1999). It may encompass reflexive activity, but it is not necessarily stimulus-bound like a palmar-grasp reflex in newborns. In this view, motor primitives are not restricted to early motor development, but are also part of an adult motor system.

Researchers that work within the framework of equilibrium point control (Berkinblit et al. 1986; Bizzi et al. 1992; Mussa-Ivaldi and Bizzi 2000) have proposed that the brain may control complex movements through flexible combination of motor primitives, where each primitive is an element of computation in a sensorimotor map that transforms desired limb trajectories into motor commands (Thoroughman and Shadmehr 2000). In this view, a small set of basis vector fields generate an entire motor repertoire from appropriate combinations of these basis vectors (Fod et al. 2000). Rather than explicitly planning the trajectory of motion of a limb for each movement, equilibrium point control theories suggest that higher animals and humans chose from a limited repertoire of such movement primitives. In support of such view are experiments, where goal-directed multi-joint movements (such as reaching and wiping) were produced by electrically activating distinct regions of the spine of spinalized frogs (Fukson et al. 1980; Berkinblit et al. 1986). These movements are considered to be primitives for two reasons: First, similar movements are exhibited by different frogs for similar activations of the spine. Second, supra-spinal inputs co-activate and thus superimpose multiple primitives in an additive fashion, resulting in a potentially large repertoire of meaningful movements.

It is known that motor primitives are present in spinalized animals, that can no longer receive descending inputs from the brain and brainstem. The presence of motor primitives in spinalized animals implies that an intact spinal motor system is sufficient to generate the respective force fields. However, this does not imply that such motor primitives are based on the chaining or layering of spinal stretch reflexes.

On a physiological basis, we may conceive spinal motor primitives not as chain of stretch reflexes, but as sets of fixed duration motor unit bursts or pulses that can be assembled by the motor system to compose voluntary or reflexive actions (Bizzi, Giszter, Loeb, Mussa-Ivaldi, & Saltiel 1995; Hart and

Giszter 2004). These burst patterns are distinct from each other and are reused in multiple behaviors. For example, only six such burst patterns explained 80% of the electromyographic activity of decerebrate frogs (“brainstem frogs”) during kicking, jumping, locomotor and wiping behaviors (Hart and Giszter 2004). When comparing the burst patterns of spinalized frogs with brainstem frogs, it became apparent that both shared motor primitives, but brainstem influence shaped and refined these burst patterns, improving movement smoothness and reducing co-contraction.

In summary, there is evidence from human and animal experiments suggesting that motor primitives build the basis for volitional motor control. The notion of motor primitives is appealing, because it does not rely on inverse dynamics computations to generate the appropriate joint torques for a given trajectory. Given that the equations of motion for inverse dynamics computations of multi-joint movements are very complex, avoiding such calculations potentially reduces the computational load of the control system. However, one also needs to acknowledge that it is still a matter of debate, whether the nervous system uses equilibrium point mechanisms for controlling limb motion. Critics of the approach have pointed out that during multi-joint movements the construction of a virtual trajectory of equilibrium points might be as challenging computationally as calculating the appropriate inverse dynamics (Gomi and Kawato 1996).

5. The non-reflexive infant

The human newborn can hardly be considered to be a reflexive animal. Next to the early reflexes that seem so characteristic of this developmental period, infants show a wide variety of spontaneous motion and even early goal-directed behaviors. For example, infants as young as three weeks will track a bright moving object with their eyes and make swiping motions with both arms in an attempt to catch it (von Hofsten 1980; Trevarthen 1984). Like many animals humans exhibit coordinated movement patterns that are not stimulus-bound nor are they necessarily acquired. Ethologists have described such movements as inborn and speak of inherited coordination (*Erbkoordination*) (Eibl-Eibesfeldt 1987). For example, a newborn gnu, an African antelope, will walk next to its mother within minutes after birth.

With respect to reflexes, we need to realize that even simple stretch reflexes are not completely autonomous but are influenced by supraspinal motor centers in humans. In addition, reflexes are not necessarily restricted to a single-muscle or a single-joint. They may involve complex patterns of innervation leading to the coordination of several limbs. Lastly, motor primitives of biological systems are considered to be a set of basis force fields generated through muscle synergies. They are viewed by some as building blocks of voluntary motor control in humans. Whether these motor primitives are inborn or acquired has not been addressed in biological motor control. However, it is clear that motor primitives are thought to be present in adults and are not considered to be exclusive to early ontogenesis like primitive

reflexes. In contrast, primitive reflexes are often viewed as relicts of our evolutionary past (e.g., crossed extensor reflex) or are said to serve a specific, yet limited role in development by enabling infants to establish rudimentary forms of sensorimotor experience.

At this point, no theory of motor development has attempted to link motor primitives and primitive reflexes. Based on the current developmental and neurophysiological research it seems not warranted to claim that the early primitive reflexive motor patterns somehow need to be inhibited at a neuronal level to allow for the emergence of motor primitives. That is, a viewpoint that propagates early motor development as a transitory period from primitive reflexes to motor primitives is unwarranted.

I would put forward the more plausible view is to conceive early human motor behavior as being based on a rudimentary set of inborn spinal motor primitives. These primitive receive peripheral as well as central inputs and likely interact with each other? In this scenario, at least a limited number of functioning motor primitives are present at birth. They serve as output modules for generating limb dynamics. They are loosely assembled and, depending on their input, give rise to either spontaneous, early goal-directed or reflexive movement patterns.

Within such framework, several factors may then contribute to the presence or absence of primitive reflexes:

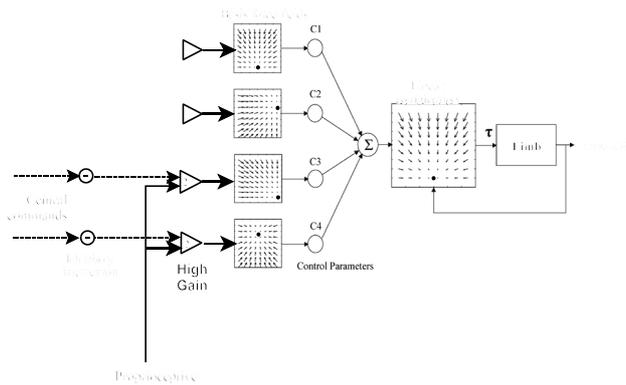
- 1) Since the connectivity between supraspinal areas and spinal neurons is not fully established in early infancy, supraspinal influence on the spinal motor neuron pool is not refined. Although the stimulation of descending motor pathways influences the excitability of large number of neurons in the spinal gray matter (Meng and Martin 2003), such stimulation is minimally effective in producing muscle contraction in newborn kittens and monkeys (Armand, Olivier, Edgley and Lemon, 1997).
- 2) In the absence of supraspinal influence the spinal cord is in a generally more excitable state (Fitzgerald et al., 1988), which makes it easier for peripheral input to trigger motor responses (see Fig. 3A).
- 3) With increasing age neurons in the brainstem and sensorimotor cortex increasingly modulate spinal cord activity (Porter & Lemon, 1993). Through elimination and addition of corticospinal axon terminals the response of spinal motor neurons to cortical stimulation becomes more refined (Kuang & Kalil, 1994; Meng & Martin, 2003).

In summary, as excitation thresholds of spinal neurons heighten and supraspinal communication with spinal neuron becomes more succinct, proprioceptive inputs from the periphery that used to trigger primitive reflexes may increasingly fail to elicit such responses (see Fig.3B).

I put forward that on the basis of behavioral as well as neurophysiological findings the view of flexibly assembled

motor primitives is attractive, since it could explain early reflexive as well as non-reflexive motor behaviors without exclusively relying on mechanisms of myelination or inhibition to account for the “disappearance” of reflexes. It would imply that these primitive reflexes never really disappear, since the underlying motor primitives do not disappear. According to this view, primitive reflexes would just be temporal assemblies of motor primitives that serve a purpose for a limited time during development.

Early spinal motor system



Mature spinal motor system

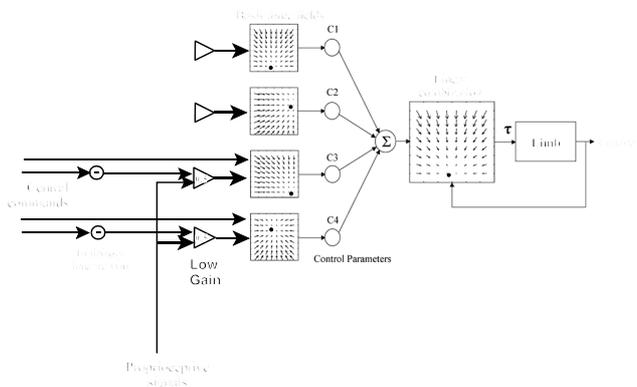


Figure 3: Motor primitives during development. Both diagrams show four motor primitives (basis force fields). Each basis field is weighted (control parameters C1-C4) and combined linearly. Activation of the basis fields will give rise to a specific limb motor pattern. **A.** Early motor systems are characterized by input high gain. Even weak proprioceptive inputs from the periphery will activate the basis fields. The actual movement patterns is determined by the “synaptic” weights. The central commands coming from the brain are noisy or non-existent. Supraspinal motor centers cannot activate the basis fields directly (missing connectivity) or such activation is too unspecific (not shown here). **B.** In a mature spinal motor system central commands can activate the basis fields as well as inhibit proprioceptive input. In addition, input gain to the basis fields is

lower. As a result, peripheral stimuli will no longer trigger a reflexive response. Note: This schema only represents part of the intraspinal connectivity. Connections to basis fields 1 and 2 were omitted for clarity. [τ : joint torque]. Modified from Metta et al. (1999).

6. Implications for robotics

Robotics is still an emerging field. In some respect, its evolution mimics the development of psychology as a discipline. Psychologists in the 19th and early 20th century were foremost interested in perception and motor behavior. In the last decades cognition has dominated the field of psychology, portraying an image that the major questions of perception and action have been solved. In designing autonomous robots, engineers faced similar problems like psychologists. They first needed understand how to control the motor plant of the robot, and how create sensory systems that could be integrated with the motor system to enable it to perform independent, goal-directed behaviors. In a subsequent phase, the engineering of cognitive functions like decision making or motivation received widespread recent attention. In addition, roboticists have examined whether human development can be used as a framework for designing autonomous robots.

This review addressed a special aspect of human motor development. It focused on what some consider to be rudimentary motor functions in early human ontogenesis. It outlines how the immature spinal motor system already provides opportunities for young infants to explore their environments. This “primitive” motor system is not suppressed during later development as the disappearance of primitive reflexes might suggest. Instead its functions are being integrated with later maturing supraspinal motor centers to give rise to complex motor behaviors that allow for rich interactions with the environment.

For robotic engineers several notions of neural development might be of interest:

First, the notion of pruning and adding connectivity between sensory and motor systems. Changes in connectivity can be based on gaining a certain level of sensory experience (sensory memory) or could be triggered by an endogenous rhythm of the system (internal clock mechanism). There is evidence that both mechanisms are used in biological development.

Second, a set of predefined motor patterns that are available at system birth to perform basic exploratory or life sustaining functions (e.g. grasp reflex in monkeys). These functions do not have to be hard wired, but can be “soft assembled” upon need. They can be turned off by changes in reflex gain or through the interaction with other motor centers.

Third, such interaction between several motor and sensory centers can be accomplished via inhibitory and excitatory connectivity. This does not imply the necessity of competing excitatory or inhibitory control systems.

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