# Setting a Framework: Sensory Regulation of Animal and Human Movement

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## Abstract

Sensory control of movement can be loosely categorized into three areas, 1) reflexive driving of a movement for accurate adjustment (reflex servos) or speedy, protective reactions, 2) temporal cueing of an element in a motor sequence (reflex triggers) or entrainment of an oscillatory rhythm, and 3) providing advance information to set such variables as movement direction, amplitude, force, and hand-finger orientation. The gain of sensory pathways is carefully regulated, in many cases on the basis of sensory information to make optimal use of all these benefits. If the neuronal circuitry generating movements is viewed as a system of coupled oscillators, then sensory inputs can be most generally categorized as a peripheral oscillator within the system. Dynamic sensorimotor interaction is viewed as the key to structuring a motor program.

## 1 Introduction

Thirty years ago, concepts of sensory signals used for motor control were constrained to fit a linear feedback loop model. The servo dogma permeated neurobiology as much as engineering. Indeed, biologists were the original culprits in degrading the word *feedback* to refer to any sensory input, whether it was part of a servomechanism or not. Of course, today the word has general coinage, even within dynamic neural networks that have greatly surpassed negative feedback loops. The neurophysiology of motor control is in the midst of a radical shift away from the simplifications of transfer functions and toward the nonlinear dynamics of chaos theory. There is no accepted conceptual foundation other than the nebulous notion of a *motor program*, adapted from computer science. For the purpose of establishing a solid reference, a motor program will be defined here as a set of procedural rules to produce patterns of motor output from the available inputs to the motor centers of the nervous system. A motor program is constructed through practice, using the universal plasticity of the nervous system. The coincidence of sensory signals with a particular motor signal will facilitate the synaptic efficacy of those sensory inputs. Thus the development of a motor program includes replacement of conscious mental effort by reliable sensory data. The program of a cyclic motor behavior such as walking or chewing is embodied in a neuronal circuit known as a *central pattern generator*. In many pattern generators, sensory neurons are physically incorporated into the network structure [1]. In all pattern generators, sensory inputs are a functional part of the structure.

## 2 Motor Set

A major component of any motor program is the setting of gains in sensory channels. Whenever any part of the body is moved, the sensory input originating from that part is subjected to inhibition. The inhibition is elicited by the motor signal itself. Thus stimulation of the arm zone of motor cortex in the cerebral hemisphere results in a suppression of cutaneous input to the arm zone of the somatosensory cortex [2]. Invariably the dynamic conditions associated with suppression are those which stimulate the sensory organs to generate a large burst of

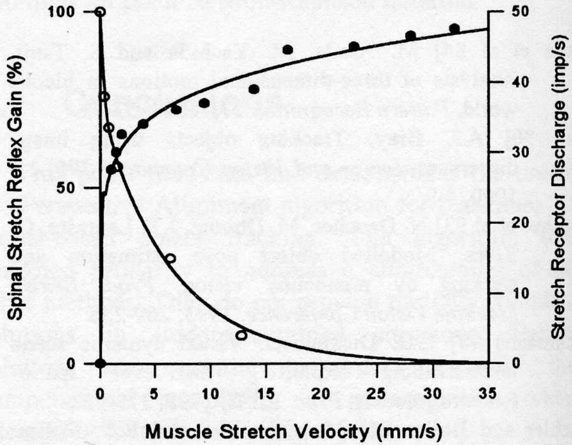

**Fig. 1.** *As stretch receptor discharge (•) increases, the gain in the reflex which it elicits (∘) drops. Receptor data compiled from Windhorst et al., Pflügers Archiv 366: 235 (1976). Reflex data courtesy of J.D. Brooke, U. of Guelph.*

activity. Indeed passively elicited increases in sensory discharge are sufficient to cause inhibition of synaptic transmission for that same sensory channel. For example, Figure 1 compares the discharge of muscle stretch receptors with the gain of the spinal stretch reflex, both as functions of the velocity of passive muscle stretch. The stretch reflex receives its input directly from muscle stretch receptors. The receptor data is from cat and the reflex data from humans, but the shape of the curves is the same across species and muscles. It is reasonable to postulate a general principle: the gain of a sensory channel is reduced in proportion to its mean activity, or anticipated mean activity, in order to maintain a relatively constant influx into the nervous system. This physiological version of automatic gain control may be labelled "homeostasis of the information highway".

Relative gain increases may occur in sensory channels called upon to replace another channel which has been rendered dysfunctional. For example, visually-guided reach to a target normally relies heavily on visual input to both direct the trajectory in space and cue the deceleration to target. If the visual information is lacking, as for example in reaching to a remembered location in the dark, then hand cutaneous information is required to compensate. In the dark, therefore, cutaneous responses to both making and breaking skin contact are greatly enhanced in the somatosensory cortex of the monkey, as shown in Figure 2. Note that this kind of replacement strategy is only possible in a *redundant* system, where there is a good deal of overlap in the information provided by the various channels.

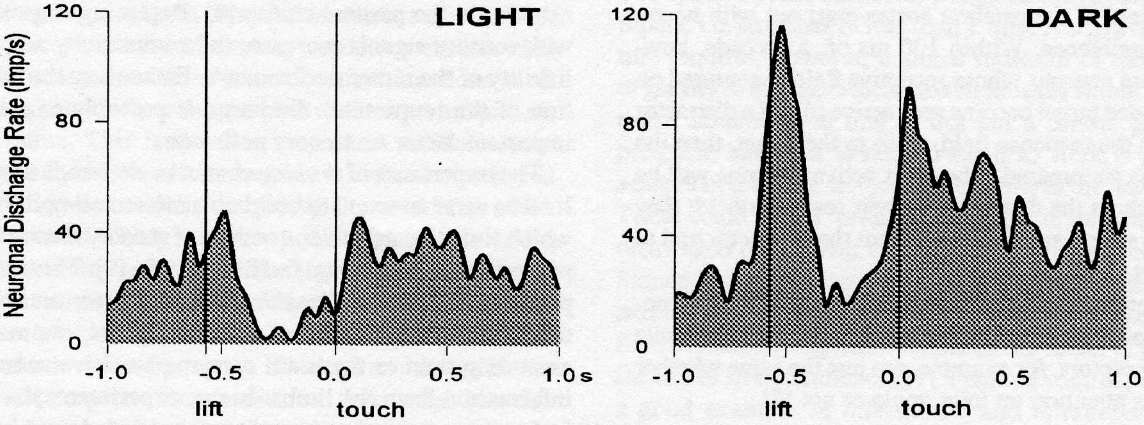

**Fig. 2.** *Increasing responsiveness of a touch-sensitive neuron (receptive field on the fingers and palm) in parietal cortex of a monkey, when a reach task is performed without normal visual feedback (DARK condition).*

## 2.1 Phase-dependent Reflexes

The reflexive sensory driving of movement (see section 4.1) is very useful in certain phases of a movement but not in others. During the step cycle of locomotion, when a leg is bearing weight, stretch of the leg extensor muscles is directly related to the load that they bear. It therefore, makes excellent sense to drive the extensor muscle activity by stretch receptor (load-related) activity for accurate support. Conversely, when the leg is lifted, any stretch of extensor muscles is passive due to limb flexion: stretch reflexes at this point would interfere with the forward swing of the leg. Consequently the stretch reflex gain is tightly regulated by inhibitory processes within the spinal cord. The gain is highest when the leg pushes against the substrate, then drops to virtually zero as the foot lifts into the air [3].

When preparing to catch a ball, the stretch reflex is again called upon, but more than a gain change is made. A task-dependent reflex pattern is assembled. Thus stretch of the arm flexor muscles on ball contact elicits not only a reflex contraction in those flexors, but also in the antagonistic extensors: the latency is 18-25 ms. The cocontraction pattern increases the stiffness of the arm joints to maximize the deceleration of the ball [4].

A central pattern generator manipulates sensory channels as an essential part of the motor pattern. This sets up the paradoxical relationship wherein pattern generators regulate the gains of sensory channels so that sensory input can regulate the pattern generators. To compound the interdependent complexity of the situation, sensory inputs themselves are very capable of modulating the gain in other sensory pathways. For example, passive cyclic movements of one leg modulate the stretch reflex in the other leg [5]. This suggests that pattern generators really make use of sensory input to cue their modulation of reflex gain.

## 2.2 Focusing Attention

In general, movements are initiated to attain a goal. Often the goal is out of sensory range, specified at the conscious level of behavior, e.g. driving home from work. The subconscious goal of each elemental movement, however, is definable in concrete sensory terms. Normally, the process of preparing the movement includes a relative facilitation of the sensory field which will be activated with respect to the suppression of competing fields in the immediate surroundings. For example, during visual search of a scene, visuomotor neurons in the frontal eye field of the cerebral cortex start out with no response preference. Within 100 ms of a saccade, however, those neurons whose receptive field is centered on the intended target become very active [6]. If a distractor is also in the response field, close to the target, then the activity is suppressed. The most active neurons will be those without the distractor in their response field: they can help steer a saccade away from the distractor and to the target.

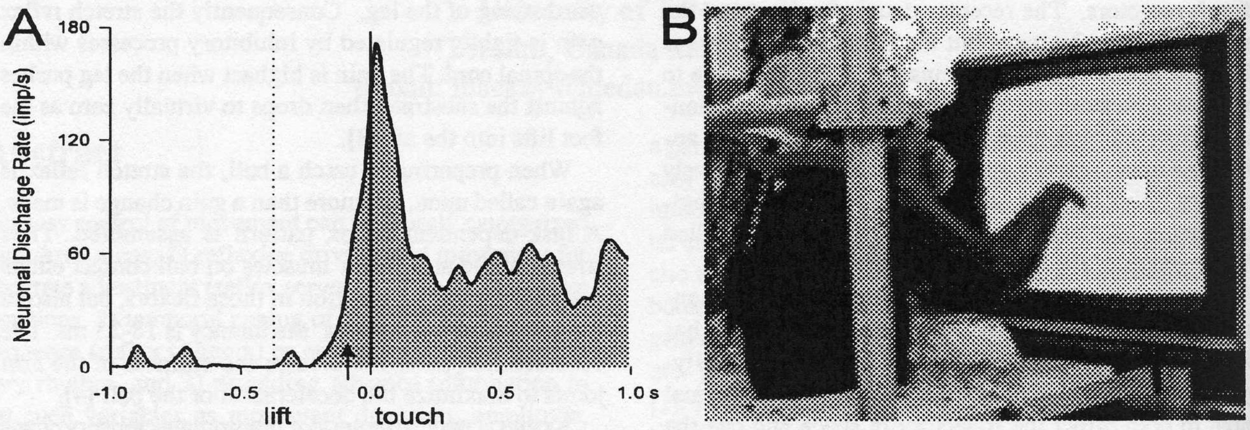

**Fig. 3**. *Increase in activity of a touch-sensitive neuron in parietal cortex prior to contact with target. Video frame in* **B** *captures arm position at the time during reach indicated by an arrow in* **A**.

Attention does not increase discharge out in the periphery at the sensory receptor. Responses of muscle stretch receptors, for example, are just the same whether you focus attention on joint angle or not [7].

## 2.3 Expectation

In many movements important sensory cues can be anticipated hundreds of milliseconds before the stimulus occurs. During reach to a target, contact with the endpoint may elicit a grasp, terminal deceleration and/or whatever else may be appropriate. Neurons in the parietal cortex which respond to hand contact start to discharge before contact is made. This is evident in Figure 2, but is further detailed in Figure 3 which shows the arm position at the time of the increase in discharge rate (the arrow in Fig. 3A). The fingers are just starting their extension which will continue until the hand is flattened: the tips are still 5-10 cm from the screen.

One can argue that this is not sensory expectation but direct stimulation by active stretching of the palm and finger skin from finger extension. Functionally the two may be synonymous. Cognitive expectation which is invariably linked to a synchronous sensory event will soon be vicariously replaced by that event given the processes of neuronal plasticity. Both sensory stimulation and cognitive expectation of that stimulus influence the same neurons in the parietal cortex [8]. Replacing cognition with sensory signals increases the automaticity and reliability of the motor performance. Either way the function of the 'expectant' discharge is probably to prime important motor or sensory pathways.

The importance of *priming* cannot be overemphasized. It takes up to a second to build up a motor volley, during which time the continuous receipt of sensory data is hypothesized to play a vital facilitatory role [9]. This interpretation is supported by the effects on motor anticipation of lesioning the dorsal columns in cats, the major ascending tract to the brain carrying sensitive somatic information from the limbs. In one experiment, the cat had to jump over a barrier as it was carried along a conveyor belt. Intuitively one would regard this as a purely visual problem of judging when to initiate the leap. Not so. The sense of contact with the substrate, and probably load on the limbs, is just as important. The lesioned cats tended to do nothing until they actually brushed against the barrier, at which time it was too late to produce an effective jump [10].

When a cat lands from a jump, anticipatory activity appears in the forelimb extensor muscles about 70 ms prior to ground contact [11]. This is true for all jump heights. Since the onset is fixed relative to anticipated contact, it must be triggered by behaviorally conditioned, non-vestibular cues. These are most likely visual , possibly features of optic flow. To summarize, the preparatory *motor set* of gains in sensory channels is essential for prompt, effective actions and reactions. The most cogent definition of set [12] covers most of the points made above. "*A sensorimotor set is a state in which transmission parameters in various sensorimotor pathways have been adjusted to suit a particular task or context. This includes parameter adjustments evoked by conditioning, and parameter schedules in stereotyped tasks such as gait.*"

# 3 Entrainment

Periodic sensory signals which interact with a central pattern generator can successfully entrain the generator rhythm to their own frequency. Thus periodic hip rotations of 2-30° rhythmically drive step pattern generators in the spinalized cat [13]. Passive flexion of the hip reinforces flexor motor activity whereas extension blocks it. Sensory driving of the stepping rhythm in the cat occured over the frequency range 0.13-2.2 Hz.

On the ski slopes of Lillehammer, the spatial frequency of the moguls and mass-spring properties of the body virtually dictated the frequency of knee-bending in Jean-Luc Brossard's legs. There would have been no Olympic gold, but a trip to the hospital, if some central oscillator paced the rhythm at its own whim. The strong influence of somatosensory input on spinal oscillators and the high dynamic sensitivity of sensory receptors ensures that motor interaction with the environment functions as an external oscillator pulse coupled to the internal pattern generators. This is the most important oscillator coupling in the whole system because it forces motor signal generation to match the frequency characteristics of the environmental/body machinery. Riding a bicycle would be an exercise in futility if the leg flexor muscles contracted as the cycle started a phase of leg extension. Every time a gear change is made the central oscillators are jostled into a new frequency. If central oscillators had to guess appropriate frequencies on their own, bicycles would have been abandoned as soon as invented (not to mention bodies).

Typing provides another example of entrainment wherein the keyboard is turned into an interactive oscillator by keystrokes eliciting phasic responses in skin pressure receptors. Finger contact with the key helps to sharpen up the rhythm which becomes quite irregular if the same motions are duplicated in the air [14].

Typing and other ballistic repetitive movements are normally performed in the frequency range 4-7 Hz, whereas exploratory finger movements in which one tries to determine object shape or texture are performed at rates of 0.8-2 Hz [13]. Far more than temporal cues are being extracted in the latter case, whereas rhythm would be the major feature of sensory input in the former.

# 4 Reflexes

Reflexes are the most obvious use of sensory input in motor control. The sensory signal directly influences motor output.. This tight sensorimotor coupling has several unrivalled advantages, namely speed and precise matching to peripheral conditions. Therefore reflexes are indispensable for fine adjustment and protective responses. Reflexes can be broadly divided into *servo* and *trigger* categories. The former drives motor output in proportion to the intensity of the sensory input. The latter provides a pulse to cue transitions between movement phases.

## 4.1 Direct Sensory Drive

The classic example of servomechanistic reflex action is postural support in which a muscle contraction is tonically maintained against gravity. The gain in the stretch reflex is close to maximum, because the ultra-sensitive muscle stretch receptors are ideal for detecting the minute stresses exerted by deviations in the center of gravity. Stretch receptor activity elicits a muscle contraction which is graded according to the degree of muscle stretch. The spinal stretch reflex has a high sensitivity for small inputs, i.e. stretches of less than 1 mm. Antigravity posture requires, however, a global indicator of the center of gravity to modulate local stretch reflexes within a functional scheme. It is fine to trot out a central postural program, but what is needed for it to work is gravity sensors in the body, not just the otoliths in the head [16]. These could be the pressure receptors in joint capsules distributed throughout the limbs and vertebral column. Stance is also regulated by vision. Subjects orient body axis to visual verticals, and the subtle motion of the visual field accompanying disturbances of the center of gravity facilitates stretch reflexes [17]. Postural control provides a good example of *interaction* and *interdependence* among sensory channels.

Precise manipulation of objects requires a refined coordination of forces exerted on the object by the finger tips and thumb. The balance of forces is adapted to the friction between the skin and the object, providing a relatively small safety margin to prevent slips. Reflex adjustments of the force balance occur in response to small slips revealed as vibrations in the object which stimulate cutaneous mechanoreceptors [18]. The use of reflexes for grip maintenance is energy efficient: tonic muscle activity is kept to a minimum with increases exactly timed and matched to need. The reflex delay is 60-80 ms, indicative of cerebral cortical involvement. Sensitivity is high enough that corrections are made long before serious errors develop. Not only grip force but accurate positioning of the fingers relies on ascending somatosensory input to the cerebral cortex [19].

When a cat's footpads are anesthetized, it can no longer leap reliably from one platform to another over 2m away. The development of adequate extensor thrust in the limb muscles requires the facilitatory drive from cutaneous pressure receptors in the paws. The angle and force of takeoff is inaccurate such that the landing platform is entirely missed or the cat ends up dangling from the edge by its claws.

There is a great variety of stereotyped protective reflexes designed to guard against injury. These include flexion withdrawal from painful stimuli and postural support reflexes to restore body equilibrium. When the body starts falling to one side, the otolith organs of the inner ear are activated. Vestibulospinal drive from the otolith organs in the inner ear to leg extensor muscles on the same side has a latency of 75 ms [20]. Forward falling is braced by a reflexive step, which differs from volitional steps in lacking the preparatory phase of leg unloading on one side. The sensory volley elicited by falling short-circuits the pattern generator network to force the leg out after 160 ms rather than 1 s [W.E. McIlroy, personal communication]. There is no motor set here, but unbridled dictatorial rule by a specific pattern of sensory inputs which the nervous system is permanently programed to obey.

### 4.2 Phase Cueing

The sight of an approaching ball elicits visuomotor reactions in the arm muscles. An immediate response starts at 130 ms in elbow and wrist flexors and extensor muscles to stiffen the arm. This is later intensified starting approximately 100 ms before anticipated contact [4]. The precise trigger for the latter has been difficult to pin down: it may be related to optical flow expansion, but certainly it is different for every situation. The intensity of muscle activity is linearly proportional to the momentum of the ball.

The swing phase of the walking step cycle is triggered by two sensory signals: 1) unloading of leg extensor muscles, and 2) hip extension [1]. If these conditions are not met, the step pattern generator hangs up. Similarly, the inspiratory phase of the respiratory cycle is terminated by pulmonary stretch receptor activity which elicits the Hering-Breuer reflex [1], well known to practiced breath-holders.

Humans are innately capable of using purely kinesthetic cues to trigger hand opening at a specific elbow angle in a movement sequence similar to throwing [21]. It is likely, therefore, that sensory phase cues are used ubiquitously in motor sequences, but they are very task-specific and difficult to identify. That difficulty may be due to the plurality of participating components. All elements, visual, kinesthetic, auditory, etc., which are normally coincident with the critical moment will be consolidated into the motor program for use as a phase cue.

## 5 Advance Information

Almost every aspect of a movement is preset by bits of information from the environment and from the body itself, all of which must be transmitted by the sensory pathways and extensively processed. The visually-guided reach is typical. There are processes of target selection, specification of target location relative to the hand and the initial setting of reach direction and amplitude. In addition the form of the object is classified for appropriate preshaping/orientation of the fingers.

A reach can be subdivided into an initial transport mechanism which moves the hand to the appropriate spatial location, and a grasp requiring alignment of the fingers with the target object. The two processes overlap extensively in time, and rely on advance information, visual and proprioceptive [22]. Once started a trajectory can be promptly rerouted if the target is moved: the minimal delay to the start of a correction is 90-100 ms.

Many neurons in the parietal cortex are involved in the analysis of the advance visual and somatic information to guide a reach. Some are specific to the orientation of hand grip required [23], and others respond preferentially to targets in a specific territory relative to the body [24]. This is visual input processed into a motor format. Other neurons in parietal cortex monitor the current position of the limbs [25]. From knowledge of current position and intended destination, the motor system can compute a signal proportional to direction and amplitude of the reach. One device that helps to spatially relate a target to the arm, is to make visual target responses within the parietal cortex dependent on arm position [24].

### 5.1 Coordinate Transformation

Sensory information is monitored within a framework which is rarely (muscle receptors being possibly the sole exceptions) applicable to driving motor output without a "coordinate transformation". For example, visual stimuli on the retina must be transferred into some body-centered spatial scheme before they can be used to guide any movement other than an eye saccade. It appears that the neuronal activity associated with the collection of visual information is used to organize the visual data into a motor-relevant format. An interactive modulation among sensory channels is involved. Visual neurons in the parietal cortex code target position with respect to the head by modulating their sensitivity to a specific receptive field as a function of eye position [26]. Similarly, finger cutaneous input is put into a spatial context by interaction with arm position information. Thus touch of an object located on one side of the body may elicit a response in parietal cortical neurons, but not if it is located on the other side [27].

Infant monkeys cannot visually, or even tactually, guide a reach with accuracy if they are raised without sight of their arms [27]. It is necessary to see the consequences of a movement in order that visual input may be used to control it. Consequently, "*the ability to guide the hand visually ... requires mapping of the coordinates of motor response onto the space for vision*" [28]. This would occur in the posterior parietal cortex where they converge, during motor learning. Sensory signals from the neck muscles, which monitor head position with respect to the trunk, are especially important in the visual guidance of reaching. Local anesthesia of the neck muscles on one side of the neck results in misreaching toward that side. Conversely, vibration of the muscles on one side of the neck (which strongly stimulates the stretch receptors) causes misreaching to the contralateral side [22].

Environmental objects are coded with respect to one another in memory, the *allocentric* spatial map organized by the hippocampus. That map is built up from the experience of moving within the environment, not from one or two retinal snapshots. Thus it has the motor perspective built in as a storage code. Inevitably the representation of the immediate extrapersonal space, explored by eye/head and arm movements, is different from the larger space requiring ambulatory cognizance.

Realistically, movements are probably not planned in a spatial domain at all, but in the sensory realm. This is the essence of motor set. Thus finger-thumb contact in a prehensile grip consistently excites a limited set of peripheral receptive fields, whereas the spatial coodinates of the finger trajectories vary significantly [29].

## 6 Motor Learning

It is frequently claimed that once a skill is learned, i.e. a motor program is created within the nervous system, the dependence on sensory information is attenuated. To cite one case, monkeys need the somatosensory cortex in order to learn a novel catching task, but once the new skill is learned it is not abolished by ablation of the somatosensory cortex [30]. Of course other sensory channels are still present to compensate in a redundant system, but also, one only sees what one looks for. With proper testing it can be shown that even tiny lesions in somatosensory cortex disrupt shaping of the fingers for challenging prehensile tasks [31], in spite of the fact that they are well learned. No matter how overtrained a movement may be, sensory areas are always very active during its performance. This has been dramatically clear in human PET records. Furthermore, all cellular mechanisms of learning require continuous reinforcement, or the substrate of synaptic enhancements gradually fades. Where sensory regions provided the motor cortex with the original 'learning signal', they must continue to supply it if the motor memory is not to disappear.

Development of a fine motor skill can lead to plastic changes within sensory systems. Training of a monkey in a task requiring constant finger pressure on a slowly rotating, fluted disk results in an enlargement of the finger representation in somatosensory cortex [32].

So pervasive is the influence of sensory input that animals will not volitionally use a limb which has been deprived of sensation by cutting all of the sensory axons. The animal may then be laboriously *trained* to use the limb for a variety of purposes, but that just proves the point. A new program must be structured which replaces all of the lost sensory bank with substitutes. For example, a monkey with an arm deprived of sensation will develop the habit of slapping his side before any reach. The trunk can still feel the arm pressing against it, so the slap serves to initialize the motor control system for arm position.

## 7 Conclusions

Sensory inputs provide the information for preparing any movement, which may include assembly of appropriate program elements, and certainly variable specification such as direction, distance etc. During performance, sensory cues trigger key phases of a sequence and drive episodes of fine adjustment to peripheral conditions. Every instant of a motor act is accompanied by a rich influx of sensory data. That which is consistently synchronous with a given motor signal will inevitably increase its influence over the signal and become part of the motor program. The mutual interaction between sensory and motor activity within the nervous system has profound implications for the problems of motor sequencing and sensory reference frames. Because the sensorimotor flow is *dynamic* and ever-changing in detail, it embodies all of the information necessary to cue motor program elements as they are executed. To be frank, there is not anything else that will suffice. In order to be employable in this manner, sensory data must be gathered in the context of the motor behavior for which they will be used. Thus the movement itself is the reference frame for the sensory input, not any mathematical abstraction. Ultimately motor routines are planned in terms of a specific dynamic flow of sensory signals.

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