

Utilization of Sensory Information for Motor Control

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Introduction

Interactions between perception and action can be considered on various levels, as stressed by Prinz and Sanders (1984), starting with neurophysiological problems and ending with philosophical ones. The problem of how an animal uses information about its own state and about the environment for controlling movement is among the lower-level problems. It is now generally acknowledged that most behaviors arise from a combination of "central" elements which rely on autonomous neural mechanisms and "peripheral" elements which rely on sensory information. Movements are not simply driven by stimuli in a reflex-like manner: in controlling their movements, organisms have some degree of autonomy, that is, some degree of independence from sensory input (von Holst, 1937). On the other hand, there can be no doubt that most movements are influenced by sensory input, despite some opinions to the contrary (e.g., Jones, 1974). Thus, the problem is to determine how sensory input is combined with central or autonomous control. In the combined system, peripheral information can be seen to have three functions: (a) it influences the decision as to what action is to be performed; (b) it participates in adjusting the parameters of the movements required for the action; and (c) it acts

to ensure that the movements are carried out correctly in the face of potential disturbances.

In the present chapter, our first goal is to review several important concepts and experimental findings relevant to understanding the control of movement. We will begin by considering several autonomous mechanisms, but our primary focus will be on how information from the outside world is used for motor control. In discussing the role of sensory input and central control, we will present a model for control mechanisms which shows that an experimental discrimination between a peripheral and an endogenous system is not always easy.

Movement forms the basis of behavior, so it is of interest not only for physiologists but also for psychologists, ethologists, and scientists in various other related disciplines to understand how movements are prepared and performed. Thus, the study of movement is a multidisciplinary endeavor including areas of psychology, biology, medicine, and engineering. Unfortunately, the interaction among the different fields has often been limited. Owing to this separation and to differences in the examples studied, it is not surprising that very different terminologies have arisen in the different fields. As a consequence, one and the same object of research is analyzed not only on many different levels but using a multitude of concepts as well. This diversity can lead to unnecessary controversies: a difference in terminology does not necessarily imply a difference of opinion.

Differences in terminology arise not only from the different fields of investigation but also from the complexity of the subject itself and the number of levels on which it can be studied. Motor control can be investigated by studying the behavior as a whole, the physiology of movement control, or the interaction between motor and perceptual events. In turn, each of these subjects can be further partitioned. For example, the physiology of movement involves two distinct entities: a peripheral skeletomotor system which defines the physical constraints and does the actual mechanical work need for movement to occur, and a neural system which does the planning and coordination. This neuronal system selects movements for performance, sends appropriate commands to the peripheral motor system, and receives information on the state of this system via sensory organs located so that some centers are primarily concerned with global features of a movement, and others are concerned with more specific details such as the activity in a single muscle. Motor behavior can be approached on any of these different levels. One subject of central interest, which is also a source of confusion, is the interaction among the different levels of organization. To avoid confusion, one needs to establish at the outset the unit of analysis and the terminology that will be employed.

Thus, the second goal of this article is to point out some of the unnecessary confusion which arises when common terms are used with different meanings, or different terms are used with a common meaning, and to suggest a set of definitions for a less confusing terminology. We will show that terms such as "feedback", "feedforward", "reference input", "open loop", and "closed loop" are often used in an ill-defined way or not clearly distinguished from one other. For example, performing a movement to a target with the eyes closed is often referred to as an "open loop" condition. However, proprioceptive control loops, which may

also be involved in the action, remain intact or "closed." Thus the kind of signal (or sensory modality) for which the loop is open should always be made explicit. Furthermore, "open loop" is used in two different ways to describe either a control system which does not use feedback or a system in which a normally existing feedback loop has been removed or "opened," usually through an experimental manipulation. A second example illustrates that the appropriate term also depends on the level of analysis. A sensory signal which is part of a "feedback loop" in one context might function as a "feedforward" or "reference signal" in other contexts. Consider the control of movement in a limb with several joints. When externally applied movement at one joint elicits a resistance reflex at this joint, the corresponding sensory signal would clearly be designated a "feedback signal." Assume that this signal also elicits a movement in another joint of the limb as part of a distributed reflex. Then this signal would be called a "feedforward" or "reference signal" when this second joint is the subject of interest. It could also be labeled a "feedback signal" when the whole limb is considered as the unit. Thus, in trying to avoid some of these problems, we will propose a new set of terms which hopefully can be used with less confusion. In this scheme, we consider sensory information as acting in three different ways which subserve the three functions mentioned above. Sensory information can elicit a movement (advance control, type 3); then, during a movement, sensory information can be used for intermittent control (type 2) or for continuous control (type 1).

Motor Control Structures

As a starting point for our discussion of how sensory information is combined with autonomous mechanisms of control, we introduce the concept of a "motor control structure." A motor control structure is here defined in very general terms to include many different aspects of motor control. It is intended as a superordinate term to designate the functional mechanisms involved in controlling movement. Broadly speaking, a motor control structure embodies both the autonomous activity of the nervous system and the rules by which the nervous system handles sensory information. It operates using neural networks which are specified genetically and may be further modified through development and learning. On this neural foundation, the active control structure is established as a pattern of activity from a set of possible patterns generated in response to situational demands communicated by actual sensory information. Thus, the motor control structure emerges from the properties of both the peripheral sensorimotor apparatus and those parts of the CNS which are involved in the control of a particular movement pattern. The former properties include both physical aspects of the skeletomotor elements and physiological characteristics of sensory and neuromuscular function. The latter include the cellular and network properties of a core of anatomical structures centrally involved in motor control, but activity in other CNS centers may be incorporated temporarily as required by the situation. A motor control structure is consid-

ered to be task specific; it is defined as the control mechanism for movements which perform identifiable functions. Thus, individual motor control structures are differentiated at the level of functional movement patterns rather than patterns of motor output in a specific performance. In this sense, one can regard walking or grasping an object or the prey-capture strike of a mantid as under the control of separate motor control structures. In any given performance, the properties of the control structure are instantiated by the task represented by the sensory information about the environment combined, of course, with stored information and autonomous activity. Some elements may be involved in nearly any movement one can think of. The concept is not intended to imply a particular control mechanism: at different levels of analysis a motor control structure may include mechanisms described by more specific concepts such as pattern generator, motor program, coordinative structure, or closed-loop control.

As Poulton (1957) emphasized in his distinction between "closed" and "open" skills, movements differ with regard to the amount of adjustment to the environment that is required. Therefore, different movements require more or less processing of sensory information. Thus, a motor control structure has to subserve two functions: first, the autonomous generation of control signals to the peripheral system; and second, the processing of sensory information. For many years these two functions have been discussed as if they were logical alternatives (e.g., Kelso & Stelmach, 1976). The "open-loop versus closed-loop" debate, however, appears to be fruitless and to distract from the important question of how sensory information is integrated with autonomous control. The main part of this chapter is concerned with this problem. First, however, different conceptions of autonomous control need to be examined.

Autonomous Control

Evidence that autonomous mechanisms, those which operate independently of sensory information, play a role in the control of movements, is available for many species including humans. It has been summarized in several places (e.g., Schmidt, 1982, pp. 237-243; Schmidt, 1988; Heuer, 1988) and will not be repeated here. The major piece of evidence is that limb movements are usually only slightly impaired when sensory information from the limb is not available.

In different fields these autonomous neural mechanisms are conceptualized in different ways. Three of these concepts are reviewed below. They are often seen as logical alternatives, but in our view they can be better described as emphasizing different approaches to the problem of motor control. More complete knowledge of the neural mechanisms should clarify the relationship among these alternative descriptions. For the present, the question should not be whether one concept is "right" and the others are "wrong," but rather which concept is most useful for the purpose at hand.

Central Pattern Generators

The term "central pattern generator" (CPG) is used to describe the control of both rhythmic and nonrhythmic movements. Most often, however, it is used as a synonym for the term "central oscillator"; we will use it in this sense here. This concept comes up whenever the origin of control signals for rhythmic movements such as those of locomotion, respiration, or ingestion is discussed (e.g., Wilson, 1968; Pearson & Iles, 1973; Selverston, 1980; Grillner, 1981). A CPG is thought of as a collection of neurons connected in such a way that they produce an intrinsic oscillation; the neural activity does not depend on sensory information for its pattern, although it may require general excitation from sensory or central sources. Thus the concept of a CPG is intimately related to an analysis of physiological mechanisms on the cellular level. For example, it is applied to neuronal networks that produce simple patterns of alternating activity in antagonistic muscles. The current physiological methodology restricts its use to simple systems and behaviors, like the locomotion of insects or spinal cats, where there is at least a chance of relating behavioral phenomena to details of neuronal networks.

Although we adopt the CPG concept here to designate such neural networks, it should be mentioned that model considerations show that even in very simple networks there may exist a continuum between a pure CPG and a system which is solely driven by sensory signals (Bässler, 1986). Consider the example of the step cycle of a leg. Brown (1911) proposed the simple CPG model shown in Fig. 1a to explain his result with deafferented cats. The two neurons (or sets of neurons) are tonically excited and have mutually inhibitory connections. In addition, they are subject to fatigue. When tonic excitation is present, the less-fatigued neuron will be dominant, and its activity will inhibit the activity of the other. During the inhibition, the inactive neuron recovers from fatigue, while increasing fatigue in the active neuron reduces the strength of the inhibition; these factors combine at some point to allow the previously inactive neuron to become active and rapidly inhibit the previously dominant neuron. The result is a system in which the dominant activity alternates between the two neurons and the switch between the two states is rapid (see Brown, 1911; Wilson, 1968; Pearson & Iles, 1973; Grillner, 1981, p. 1217). In this model, as applied to the example of a walking leg, one neuron might excite the muscles active during the stance phase and the other neuron those active during the swing phase.

The corresponding peripheral oscillator models (Fig. 1b) were based on findings that some sense organs signal the end of each half cycle; in the example of a step cycle (e.g., Bässler, 1977, 1986; Land, 1972; Graham, 1977); some sense organs could signal an anterior leg position appropriate for the end of the swing phase. If one assumes further that these sense organs excite the stance phase muscles, then, upon reaching this anterior position during its swing phase, the leg would switch to stance phase. This switch would not occur if some perturbation during the swing phase prevented the leg from reaching the appropriate end position. An analogous mechanism depending on other sense organs detecting an appropriate posterior position would become active at the end of the stance phase.

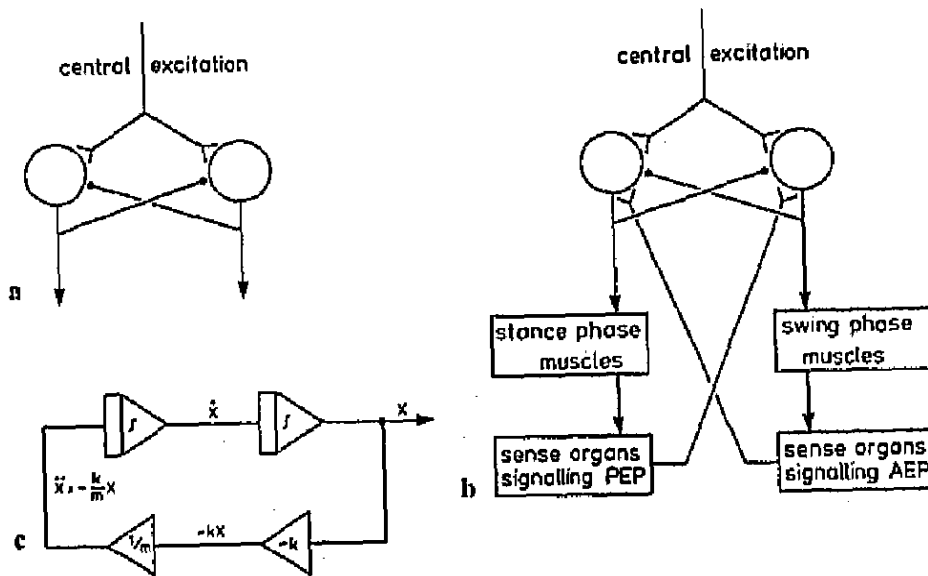


Fig. 1 a-c. Networks illustrating central pattern generators. a Two neurons or groups of neurons are tonically excited and mutually inhibit each other. This inhibition is subject to fatigue. b A peripheral oscillator model applied to the control of walking legs. It is assumed that sense organs which monitor when the leg reaches the posterior extreme position (*PEP*) at the end of its stance phase excite the swing phase motoneurons. Corresponding sense organs detect the anterior extreme position (*AEP*) at the end of the swing phase and excite the stance phase motoneurons. c A simple electronic circuit which is able to produce an oscillating output. (b After Bässler, 1986)

These components of the stepping motor control structure could therefore be described as a reflex chain. Thus, depending on the relative strengths of central and peripheral signals, the combined system can behave as a more centrally or a more peripherally driven oscillator (Bässler, 1986). Similarly, the required tonic excitation might arise from central neural mechanisms as shown in Fig. 1a; it might also arise from sense organs (Fig. 1b). This example shows that the experimental destruction of the sense organs might artificially change the system from a peripheral to a central oscillator. Thus, a clear distinction between central and peripheral oscillators is experimentally difficult.

Central Motor Programs

Central motor programs can be considered as a more general concept which subsumes central oscillators and CPGs. The central motor program idea is related to the CPG concept but it is applied at a higher level of abstraction: it refers more to the functional sequence of movements and less to the neural network in which the motor commands are generated. In addition, it is applied equally to both rhythmic and nonrhythmic movements. It should be noted, however, that if "CPG" is not used as a synonym for a central oscillator, then it is often used in an abstract manner that is equivalent to a central motor program. It should also be mentioned that sometimes, particularly in the biological literature, the term "motor program" with-

out the qualifier "central" is used in the sense of a process controller to describe mechanisms in which data on the actual state of the process, i.e., sensory signals, influence the performance of the program. Used in this way, "motor program" would correspond closely to "motor control structure" as the term is used here.

Central motor programs are usually illustrated using the analogy of a program for a digital computer, but analog mechanisms have also been used as metaphors. For example, Hoyle (1965, 1983) refers to a "motor tape," Schmidt (1988) uses a phonograph record analogy, while Taylor and Birmingham (1948), writing before the advent of modern computers, use the analogy of a mechanical camshaft controlling timing. These different analogies, referring to digital and analog control devices, reflect different ways of thinking about the nature of a central motor program.

The program of a digital computer consists of a series of commands that are performed in sequence at a rate governed by the computer's clock signal. Analogous to this, the "digital" motor program concept considers the content of a motor program as a series of "response commands" that are performed under the control of an internal clock (Rosenbaum, 1985). Setting up a motor program, in this view, involves assigning response commands to clock pulse identifiers; each clock pulse identifier is used to trigger the associated command when the corresponding clock pulse occurs. This digital metaphor is suited to the analysis of movement sequences in which subunits can be meaningfully distinguished. Such subunits, for example, might be the penstrokes in writing, the keystrokes in typing, or the phonemes in speaking. It is, however, also possible to apply the "digital characterization" of a motor program to sequential muscle contractions, e.g., the successive contractions of agonists and antagonists in rapid aiming movements or even to discrete corrections within seemingly continuous movements (see p. 68f).

A rather different way of describing the content of a central motor program is suggested by the analog metaphors (cam control, analog computer, etc.). In very general terms, one can describe a central motor program as a function of time with parameters which are specified by some control signal. The concept of a generalized motor program (Schmidt, 1975, 1988), for example, can be written as:

$$p(t) = A \cdot f(t/T) \quad 0 < t < T \quad (1)$$

The parameters T and A define the movement duration and the amplitude, respectively; $f(\vartheta)$, $0 < \vartheta < 1$, constitutes a "prototypical function" (cf. Meyer, Smith, & Wright, 1982). Position, $p(t)$, is specified as a function of a dummy variable, ϑ , that, for each single movement, is transformed into real time according to $t = T \cdot \vartheta$. The prototypical function is the essence of the central motor program. It defines those temporal and spatial relationships that remain invariant if T and A are varied. In the temporal domain, this mechanism for programming movement leads to phase constancy or invariant relative timing.

It should be noted that Eq. 1 serves as an example of how, in principle, the content of a central motor program can be specified. Starting with von Holst (1939), it has been proposed several times that duration and amplitude can be treated as independent parameters for motor control. During recent years evidence

has accumulated showing invariant relative timing when movement duration (T) is varied (for review see Schmidt, 1985a, 1988), as predicted by the prototypical function concept underlying Eq. 1. Nonetheless, Eq. 1 should be considered as an example only, since invariant relative timing has been shown for some but not all movements.

The relative duration of stance and swing phase in cockroaches, for example, is independent of walking speed (Delcomyn, 1971; see also Carter, 1984) as it is in humans (Shapiro, Zernicke, Gregor, & Diestel, 1981). In contrast, in adult stick insects the absolute duration of swing phase is about the same for all walking speeds, so the relative duration is not constant for these animals (Graham, 1972). This suggests that the hypothesis represented in Eq. 1 may be an appropriate description for some but by no means all movement patterns.

According to the "digital" and "analog" ways of thinking, central motor programs are characterized either as a sequence of commands executed in discrete time intervals or as a signal specified by a continuous function of time. As models for the underlying mechanism, the digital and analog views are not logical alternatives. In the first instance, they are different ways for describing the autonomous functions of a motor control structure with direct reference to the output, i.e., to the spatiotemporal characteristics of the movement. However, they usually differ with regard to the level of description. Analog descriptions are on a low level, referring to the detailed space-time characteristics of a movement. Digital descriptions, on the other hand, are in terms of labels for segments of the space-time characteristics, i.e., for units of the apparently continuous stream of movement (cf. Miller, Galanter, & Pribram, 1960). Initially the definition of units may be arbitrary, but often evidence is sought for their reality (e.g., Monsell, 1986). Reality means that these units are not just units of description, but also units of control (cf. Viviani, 1986).

For both views on central motor programs, the nature of the relationship between kinematic and kinetic characteristics of the movement and the actual parameters of the motor control structure remains unspecified. Motor programs are often discussed as if some kinematic variables, such as movement amplitude or duration, have their counterparts in parameters of the control structure. As a matter of course, the existence of a control mechanism is implied for the kinematic variables that the observer happens to measure or consider important. In general, however, the problem of which kinematic variables are the controlled ones has not been solved (see Stein, 1982). In fact, the controlled parameters may well vary among different types of movements according to the requirements placed on the behavior.

Coordinative Structures

Coordinative structures, as defined by Turvey (1977) and Kugler, Kelso, and Turvey (1980, 1982), consist of a set of muscles and limbs which are constrained to act together as a unit. Like the motor program idea, this concept is applied to both

rhythmic and nonrhythmic movements. Another similarity is that the coordinative structure concept is not explicitly concerned with the neural basis; the goal is an abstract formulation of movement characteristics including responses to disturbance. The role of peripheral influences is not explicitly addressed in this theory. Instead, the concept is applied to a state of the organism. Therefore, we have included it under autonomous control, although it seems obvious that proprioceptive mechanisms contribute to the dynamic properties present in specific formulations.

Compared to motor program approaches, more emphasis is placed on physical and dynamic features of movement and less emphasis on representations or information processing in the nervous system. However, the constraints present in a coordinative system must arise from a combination of physical and neural factors. At the physiological level, the muscles require neuronal activity to perform their tasks, so we consider coordinative structure formulations to represent implicitly the properties of those neuronal subsystems which control the set of muscles involved (cf. Kelso, 1986).

One of the important problems that the concept of coordinative structures addresses is the "degrees-of-freedom problem" first discussed by Bernstein (1957, 1975). He postulated that movement can only be efficiently controlled if the nervous system has some way of mastering the enormous number of variables (each representing a degree of freedom) inherent in the numerous joints, muscles, and motor units making up the motor system and in the many gravitational and dynamic configurations under which it acts. Bernstein applied the word "coordination" to the mechanisms performing this task. Reducing the number of variables is one possible solution. Here, "reduction" is meant in a mathematical sense. It does not mean that a real degree of freedom is simply held constant - for example, by fixation of a joint.

However, if two joints are constrained to flex with proportional angular velocities, only one central control signal is required, and the number of degrees of freedom is thereby reduced. Coordination among the various degrees of freedom is one focus of the coordinative structure approach, although, as discussed below, this feature is also implied in the concept of generalized motor programs.

The notion that the role of coordination is to reduce the number of independently controllable muscles might suggest that coordination is always absolute, but this is not the case. The classic example of "relative" coordination was described by von Holst (1939) in his study of the coordination of fine movements in fish. The fins behave like weakly coupled oscillators; each strives to impose its own rhythm or a specific phase relation on the rhythm of the other fins (the "magnet effect" of von Holst) but does not succeed in establishing a rigid coordination. Relative coordination has also been described for walking legs of insects (Wendler, 1964) and lobster (Clarac, 1981), as well as for human arm movements (Gunkel, 1962).

A magnet effect is also illustrated by more recent data on intermanual coordination. Kelso, Southard, and Goodman (1979) studied aimed movements performed simultaneously with the two hands. When performed separately, the test move-

ments of different amplitudes to targets of different sizes showed different movement times according to the well-known Fitts' law, which predicts a logarithmic relation between the ratio of amplitude and imposed accuracy on the one hand, and movement time on the other. When the two movements were performed simultaneously, however, movement durations for left and right hands became nearly identical. This could be taken to suggest one and the same temporal control signal is used for both hands, and only the amplitude parameter is varied to produce movements of different amplitudes. However, the synchrony of the movements was not perfect. Although the durations became more similar, the movement that was of shorter duration when performed in isolation was still of shorter duration when performed in combination. This residual difference is stressed, for example, by Marteniuk and MacKenzie (1980) and by Marteniuk, MacKenzie, and Baba (1984). Its existence points to the danger of over-simplification in describing complex, coordinated movements in terms of a single coordinative structure (cf. Heuer & Wing, 1984) which neglects a more detailed account of the underlying mechanisms.

Theoretically, coordinative structures can be described using linear or nonlinear differential equations. This theoretical approach is restricted explicitly to the macroscopic level of behavior. No attempt is made to detail the network that generates this behavior. As an example, consider the model of Saltzman (1986) and Saltzman and Kelso (1987) for aimed movements. The starting point of this model is Feldman's equilibrium-point concept (Feldman, 1966, 1974 a,b, 1986) – sometimes referred to as the mass-spring model (see, for example, Schmidt, 1987, 1988). However, this model is applied to an abstract "task space" which is defined by two axes, the one running through the initial and target positions, and the second orthogonal to the first. Movement along both axes is governed by linear second-order differential equations. Thus, the "physical" mass-spring model becomes a "metaphysical" mass-spring model.

Movement along the two axes of the task space, according to this model, is "uncoordinated," that is, independent. Coordination arises only when the real movement is considered. This requires coordinate transformations, which, in moving from the abstract task space to the actual joint movements, are fairly complex. The basic principle, however, by which coordinated joint movements can arise from uncoordinated movements in the abstract task space, is simple. Imaging a movement along the x -axis of a coordinate system; as soon as the coordinate system is rotated, the same movement requires a "coordinated" change of x' and y' values in the new coordinate system. The transformation from task space to joint space has a similar consequence for a two-joint arm; moving the end of the arm along a straight line forces "coordinated" rotations at the two joints.

The simple principle of deriving coordination from coordinate transformations fails as soon as coordination is not completely determined by task demands. This, for example, is the case for planar aiming movements with a three-joint arm. Here the redundancy problem can be solved by assuming additional constraints. In one example, these constraints have been described as cost functions defined at each joint. Adding a constraint that the total cost be minimized provides solution for

this redundancy problem (Cruse, 1986). In this case, a description by nonlinear equations without derivative terms was shown to be appropriate. The corresponding kinematic model also shows the property of immediate reorganization after blocking an angle (Cruse & Brüwer, 1987).

A somewhat different approach to the coordination problem is presented by Haken, Kelso, and Bunz (1985) and Schöner, Haken, and Kelso (1986). The phenomenon studied has been described by Cohen (1971): it is easy to oscillate both wrists symmetrically (flexion and extension of the two wrists are in-phase), but it is harder to oscillate them alternately (anti-phase). When the frequency of anti-phase oscillations is increased, it becomes impossible to maintain them, and a shift to symmetric oscillation can be observed (see Kelso, Schöner, Scholz & Haken, 1987). This phenomenon can be conceived as a shift between two modes of coordination, comparable for example to the transitions among walk, pace, trot, and gallop observed in quadrupeds as a function of speed. The wrist system has been modeled using coupled nonlinear oscillators. The interesting feature of the model is that it mimics the observed phase transitions when the frequency of oscillation is increased. Moreover, it duplicates the instabilities occurring in the range of frequencies in which the transition occurs. Here there is nothing like a qualitative shift from one motor program to the other in changing from anti-phase to in-phase; rather, the shift between modes of coordination arises from the intrinsic properties of the motor control structure when frequency is increased.

The "dynamic approach," with its emphasis on an abstract description at a macroscopic level by way of differential equations (e.g., Kelso & Kay, 1987), is not the only approach to the coordinative structure problem. An information-processing or cybernetic approach aims at specifying the computations required within the structure rather than simply describing its global behavior. For example, coordination may be interpreted as arising from information exchange between the various segments of the limb(s) involved. The focus here is on the kinds of signals indicating the states of the various segments or articulators and on how these signals are used to achieve coordinated control of different segments. For example, in locomotion studies, a basic question is how information on the state of one leg is used to "convince" another leg to behave in a certain way. In the crayfish, two such influences have been found (Cruse & Müller, 1986). First, for as long as a leg is in stance phase, the next anterior leg is held in swing phase; second, a leg which is near the end of the stance phase sends a signal to its posterior neighbor to elicit the start of a stance phase in this leg: in this way the swing phase of this leg may be shortened. This type of conditional coordinating influence can more easily be described by means of a digital computer program than by differential equations. A description of the wrist phase transitions by means of the motor program concept has not yet been attempted. As related to the above discussion, the dynamic approach provides an interesting quantitative description of this phenomenon and therefore leads to testable hypotheses.

Multiple Characterizations of the Autonomous Functions of Motor Control Structures

As mentioned above, we consider CPGs, motor programs, and coordinative structures to be complementary concepts that focus on different aspects of the autonomous function of a motor control structure. This position may appear awkward in view of the ongoing controversies. These arise in part from the discrepant theoretical frameworks in which the motor program and coordinative structure concepts in particular are embedded. The motor program concept generally uses an information-processing framework, while the coordinative structure concept (associated with a dynamic description) arose from the ecological framework of Gibson (Turvey, 1977). However, these different associations may simply reflect historical development rather than logical necessity.

It should be stressed that we are not arguing that CPGs, motor programs, and coordinative structures are identical concepts - a number of differences have been described in the preceding sections. What we are arguing is that the concepts are complementary rather than logically exclusive. They refer to the same thing, that which we labeled a "motor control structure," but they focus on different aspects of it. They can be likened to the descriptions of the sea provided by a chemist, a physicist, and a poet, or the description of an airplane provided by an engineer, a pilot, and a passenger.

The view that the concepts are complementary is supported by the fact that the different descriptions applied to one system can often be transformed into one other as can be illustrated by the following simple example. Figure 1c shows a simple electronic circuit that exhibits essentially the same behavior as the neural oscillator of Fig. 1a. In this example we consider the output of the circuit to represent the position of the moving limb rather than neural activity. We can describe this system in three ways. First, the physical components and their connections can be specified: this corresponds to the description of a CPG. Second, we note that Fig. 1c is a wiring scheme for an analog computer to solve the following linear differential equation.

$$m\ddot{x} + kx = 0 \quad (2)$$

Tracing around the circuit, we see that the output value, x , is multiplied by a constant, $-k$, and then by a second constant, $1/m$. The result, $-x \cdot k/m$, is integrated twice to give the value of \ddot{x} . The input to the second integrator is labeled the first derivative of x because integration of \dot{x} yields x . By the same argument, the input to the first integrator is \ddot{x} . Therefore this circuit corresponds to the equation, $\ddot{x} = -x \cdot k/m$, which is equivalent to Eq. 2. This equation represents a description of the system that corresponds to the dynamic approach to motor control. The equation does not explicitly specify the space-time characteristics of the movement; that is, it does not specify " $x(t) = \dots$ ". Instead these characteristics are implicitly specified.

The third kind of description makes the space-time characteristics explicit by solving Eq. 2. According to the rules of calculus, the general solution can be written as shown in Eq. 3.

$$x(t) = C \cdot \sin (\omega t - \varphi) \quad \text{for } \omega = \sqrt{k/m} \quad (3)$$

where φ is a constant determined by the initial conditions. This description of the system corresponds to a motor program for a harmonic movement. The complementarity of a CPG on the one hand and a central motor program on the other is quite obvious: the first emphasizes anatomy and physiology, the second emphasizes function. As soon as the CPG is used in an abstract manner without reference to its physical instantiation, CPGs and central motor programs become virtually equivalent terms.

The complementarity of Eqs. 2 and 3 is obvious as well. There seems to be no reason to ascribe a higher degree of "reality" to one equation or the other, or to consider the one as being a consequence of the other. Both equations describe the system in equivalent ways, but for particular purposes one may be better suited than the other. For example, the wiring diagram can easily be derived from Eq. 2 but not from Eq. 3. On the other hand, what the output, $x(t)$, really looks like can easily be seen in Eq. 3 but not in Eq. 2.

Although a dynamic approach, focusing on the global description of the behavior of coordinative structures, and a motor program approach, focusing on the temporally ordered motor commands and their generation, can be considered as being complementary, major differences appear as soon as these formal descriptions are discussed in the context of possible mechanisms. For example, an obvious question is how systems described by equations like Eqs. 2 or 3 come into being. As pointed out by Schmidt (1987), a motor program is generally considered as some kind of central representation of the movement, while advocates of the dynamic approach deny the existence of such a representation. It is worth noting, however, that a differential equation like Eq. 2 "represents" a movement described by Eq. 3 in that a system described by Eq. 2 produces the output given by Eq. 3. Only if the equations are reified, could one say that Eq. 3 is a representation of a sinusoidal movement but Eq. 2 is not. Reification of functional or abstract descriptions is, of course, completely unjustified. It could be that the general orientation of the dynamic approach differs from more concrete formulations with regard to the representation issue.

The fundamental equivalence of these different ways to describe the autonomous function of motor control structures should not obscure the fact that the concepts are of different value for different purposes. Because of the different levels of abstraction, this is clear for the central pattern generator concept on the one hand and the central motor program and coordinative structures concepts on the other. At present, however, we feel that dynamic descriptions of coordinative structures have some strength in modeling transitions between modes of coordination. However, they are necessarily global and neglect the "mechanisms inside the box." Therefore, motor program descriptions appear to be more powerful as far as the details of motor control structures are concerned.

The Role of Sensory Input in Motor Control Structures

Motor control structures usually contain more than just autonomous central mechanisms; they also incorporate peripheral mechanisms dependent on sensory input. The problem here is to identify how autonomous control mechanisms are integrated with those that depend on sensory input. In what is to follow we will describe various modes of integration. The exposition is organized around what we will consider as three different types of such integration, somewhat arbitrarily defined according to the temporal relation between the sensory information and the motor act it affects. As already mentioned, there is often ambiguity in identifying units of motor output. Similarly, the coding of sensory information in a frequency code and the delays inherent in processing complex information limit the ability to attribute sensory information to discrete, precisely defined points in time. Despite these difficulties, we propose to distinguish the following types.

At one extreme is continuous control or, more accurately, "quasi-continuous" control within the limits of temporal resolution (type 1). Here sensory information is continuously used to influence motor output. (When the sensory information is frequency coded, the control cannot be strictly continuous, since the code itself is extended in time.)

The next type (type 2) refers to intermittent use of sensory information for motor control. In this case, there are clearly identifiable periods where sensory input is not incorporated into control. Although the sensory signal may be continuously monitored, it affects motor commands only when the signal exceeds a certain threshold, at certain times, or at certain intervals. Whether or not a particular input is processed during a particular time interval is a feature of the motor control structure and may depend on the requirements placed on the action.

The final type (type 3) is advance processing. Again, sensory information is not continuously used. In advance processing it is incorporated into motor control before execution of the movement. In this case, sensory information is used to set up a motor control structure and to specify initial values for parameters rather than to modify an ongoing movement as is the case in intermittent and continuous processing.

In discussing motor control, it is particularly important to distinguish signals that indicate the current states of a terminal device or the joints controlling the terminal device from signals that indicate what these states should be. The former are feedback signals, while the latter are reference signals. Although, at first sight, type 1 and type 2 influences seem to refer to feedback signals and type 3 influences to reference signals, it will be shown below that this distinction is only sensible when the system is well defined in the sense that its input and output channels are clearly identifiable (see also "Introduction"). Therefore, although we will partly distinguish between feedback and reference signals, we realize that in practice an unambiguous classification is often impossible.

Type 1: Continuous Incorporation of Sensory Information into Motor Commands

Feedback Signals

Thinking in terms of closed-loop systems dominates the cybernetic approach to motor control. There are two ways to verify that a particular signal is used as a feedback signal: (a) the signal can be eliminated; and (b) it can be distorted. Either manipulation should result in gross malfunctioning of the system if the control system depends only on servo-mechanisms relying on feedback. A remarkable finding about motor control is that elimination of sensory input that presumably acts as a feedback signal has only minor effects on motor behavior, but distortion of the very same signal has drastic effects. We will first consider this evidence and then present a design principle for motor structures that exhibits these characteristics.

In insects and crustaceans, minor effects of eliminating sensory input that presumably serves as feedback have been found. Destroying different sense organs that signal leg position produces only small changes in the movement of a walking leg. The same is true for ablation of strain-sensitive proprioceptors (for review see Bässler, 1983; Graham, 1985).

Findings reported for deafferented mammals are basically similar. After dorsal root section, monkeys show only small motor deficits, provided that they use the deafferented limbs at all (for review see Taub & Berman, 1968; Taub, 1976). Taub, Goldberg, and Taub (1975) investigated the accuracy of aiming by a deafferented limb. Although other sensory input that could replace the missing proprioceptive input was carefully excluded, deafferented animals exhibited better performance in their "good" sessions than intact animals in their "bad" sessions. Thus, while deafferented animals were less accurate on the average, the distributions of session means for intact and deafferented animals showed considerable overlap (see also Polit & Bizzi, 1978). In humans, corresponding results we have been reported by Lashley (1917) and Laszlo (1967).

Minor effects on motor performance are found not only when proprioceptive input is eliminated, but also - as is perhaps more familiar - when other sources of feedback are eliminated. We are able to point to a target without seeing our hand. If the movement takes longer than 100-200 ms, accuracy is slightly reduced compared to conditions where visual information is available (Carlton, 1981; Keele & Posner, 1968; Zelaznik, Hawkins, & Kisselburgh, 1983), but these are not gross disturbance. The view of the hand can be obscured through the first half of the path to the target without any detectable effect on accuracy or movement time (Carlton, 1981). Also, we are able to speak without gross disturbance when we cannot hear our own voice.

Elimination of potential feedback signals, in summary, has astonishingly little behavioral effect. This finding has been the major reason for attributing primary importance to autonomous CNS activity in the control of movement (Delcomyn, 1981).

If, as the evidence above suggests, the various potential feedback signals are not used for feedback, then disturbing them should also have minor effects. This, however, is not the case. Distortion of a sensory signal can result in drastic changes, even when completely eliminating the same signal has little effect. When joint proprioceptors in a walking insect are not ablated but fixed so that they constantly signal a forward leg position, the leg rarely starts a swing movement (Bässler, 1977; Dean & Wendler, 1983). More drastically, when an internal proprioceptor (the femoral chordotonal organ) is operated on in such a way that its position signal is inverted (i.e., extension is reported as flexion and vice versa), the leg is hindered from completing a normal step movement: it remains in the air at the endpoint of the swing phase (Bässler, 1977; Graham & Bässler, 1981). Corresponding effects are found when the strain-sensitive proprioceptors are stimulated so that they always signal the leg to be under load (Bässler, 1977).

Distortion of proprioceptive input has gross effects in humans as well. Goodwin, McCloskey, and Matthews (1972) disturbed proprioceptive input by vibrating muscle tendons at the elbow joint. One of the effects of vibration appears to be a tonic excitation of the muscle spindles. The message contained in this hyperactivation is that the length of the corresponding muscle is greater than its true length. When the biceps tendon is vibrated, the elbow angle should be registered as being too large. In accord with this prediction, the extension of the elbow joint was too small when subjects had to match the position of the vibrated arm to passive movements of the other arm (see also Sittig, 1986).

A nice example involving visual feedback was reported by Nielsen (1963). The subject's task was to move one hand along a vertical line. The gloved hand which the subject could see was not his own but that of the experimenter. The visible hand followed a curved path rather than the straight line. This visual signal was processed to correct the apparent error, causing the subject's hand to deviate from the straight line in the direction opposite to the deviation of the observed hand. In spite of the obvious discrepancies between intended movement and visual feedback, it required large deviations and several trials before subjects gave up the search for magical explanations and realized that the gloved hand they were watching could not be their own. This appears to be a rather dramatic case of "visual capture" (see also Jordan, 1972).

Closing the eyes does not prevent humans from maintaining a vertical stance: body sway may increase, especially if we imagine we are falling, but the mean is still vertical. However, presenting a distorted visual stimulus by moving the visual surrounding induces activity in the leg muscles that would be appropriate if the visual input were a result of body movement (Berthoz, Pavard, & Young, 1975; Lee & Lishman, 1975). If the amplitude of the forward-backward oscillation of the walls is sufficiently large, this distorted feedback about the orientation of the body can induce falling. The effect is stronger in children; they exhibit greater body sway and also a larger effect of lack of visual information (Shumway-Cook & Woollacott, 1985). This particular effect of distorted feedback is exploited for fair attractions like the "haunted swing" (where the walls swing rather than the people). The latencies of compensatory responses to distorted visual information can be as

short as 100 ms (Nashner & Berthoz, 1978), less than the usual latencies for responses to visual stimuli (Zelaznik et al., 1983). Thus, a disturbed signal again produces a strong effect, whereas completely removing the input elicits only minor alterations.

In speech production the presence of delayed auditory feedback induces hesitations and repetitions which are similar to stuttering. The maximal effect is found at a delay of about 200 ms (see, for example, MacKay, 1986). This speech disturbance can be avoided at least partly if attempts to neglect the auditory feedback are successful (see Roeck, 1977). Similar effects of delayed auditory feedback have been observed when finger tapping is accompanied by tones and these are delayed (Wing, 1977; see Chase, 1965). Again, although we need to hear neither our own voice speaking nor auditory feedback for tapping, if these signals are present and distorted they have gross effects on behavior.

How can the apparently discrepant results obtained from elimination and distortion of various sensory signals be reconciled? The minor effects of elimination indicate that these signals are not continuously processed as feedback, while the strong effects of distortion indicate that they are. We shall outline a design principle for a motor control structure that can show these different effects of elimination and distortion of sensory signals. This design can be identified with physiological mechanisms on lower levels of the motor system; we suggest that it might be repeated on higher levels.

The basic scheme is shown in Fig. 2a. We will use the muscle spindle system as an illustration. Through the alpha-gamma linkage, the supraspinal movement command is fed onto alpha and gamma motoneurons roughly simultaneously. The direct signal to the alpha motoneurons is amplified by a factor A and sent to the muscle, where it causes a change in muscle length according to the factor M . Muscle length (y) is measured by the muscle spindles, which effectively measure the difference between the setpoint determined by the gamma motoneuron discharge and actual muscle length. The error signal, with gain S , is added to the alpha control signal. The essential feature of this scheme is the parallel arrangement of the open-loop control of muscle length via the alpha motoneurons and the closed-loop control via the muscle spindles. The reference signal for the feedback loop is provided by the gamma motoneuron activity, so it is linked to the open-loop control signal.

With appropriate values for M , A , and S , a system of the kind shown in Fig. 2a will show only minor changes in its output when the feedback loop is opened. The controlled variable, y , can be written as a function of the input signal, x , as follows:

$$y = \frac{MA + MS}{1 + MS} x \quad (4)$$

Opening the feedback loop by cutting the dorsal roots is equivalent to setting $S = 0$, so that the contribution of the loop to the controlled variable, y , becomes zero. If the gain, A , is chosen properly so that $MA = 1$, then $y = x$ for all values of S including $S = 0$. If the gain is not properly chosen, then eliminating the feedback

will produce smaller or larger effects depending on the extent to which A deviates from the reciprocal of M .

Although such a system is insensitive to elimination of feedback, it will be affected by distorted feedback. In this case the disturbance, d , is added to y before the error is computed. Then the controlled variable is given by:

$$y = \frac{MA + MS}{1 + MS} x + \frac{1}{1 + MS} d \quad (5)$$

Even if $MA = 1$, so that feedback will be ineffective in the "normal" case, a disturbance will reveal that it is processed. It will induce a change in y that increase according to the gain (MS) of the feedback loop, but always remains smaller than d itself.

Before generalizing the design-principle of Fig. 2a to higher levels of motor control, some remarks on its advantages are appropriate. First, the redundancy in the system makes it less prone to failure. Second, and more important, it combines the merits of closed-loop and open-loop control. The advantage of an open-loop system is that it responds rapidly to an input signal and cannot become unstable like a closed-loop system subject to a delay in the feedback signal (Cruse, 1981, pp. 66-67). The disadvantage, however, is that it is unable to compensate for disturbances. In the example, A has to be properly adjusted to M so that a desired output, y , can be achieved. Even in the absence of outside disturbance, A or M may vary due to fatigue and cause errors in a pure open-loop control. (In the generalized case, where the simple gain factor M has to be replaced by complex transfer characteristics – i.e., when the dynamic properties of the elements are taken into account – this problem becomes even more serious.)

A closed-loop system in parallel with the open-loop system will compensate for the weaknesses of the latter: it will serve to reduce the errors that occur through variation in A or M or through external disturbances. Owing to the operation of the open-loop system, the closed-loop system only has to deal with small error signals, so the gain (S) can be relatively low, which helps avoid instability. The actual gain of the spinal reflex loop does appear low; the system can only partially compensate for gross disturbances (e.g., Bizzi, Polit, & Morasso, 1976; Hopf, Handwerker, & Hausmanns, 1967). In addition proper design of the dynamic properties of S could further reduce stability problems (Cruse, 1981, pp. 69-72). In summary, the design principle of Fig. 2a amounts to adding the advantages of open-loop and closed-loop control while eliminating their disadvantages.

We now have to consider the case of a feedback loop in which the sense organ, unlike the muscle spindles, is not under efferent control. This is shown in Fig. 2b (solid lines); S is considered to be 1 and is therefore omitted in this drawing. In this circuit the interruption of the feedback loop by ablation of the sense organs cuts the loop at another position. It corresponds to $F = 0$ in Fig. 2b. In this case, as long as we consider only linear systems, cutting the feedback loop always produces major differences in the behavior of the system compared to the intact situation.

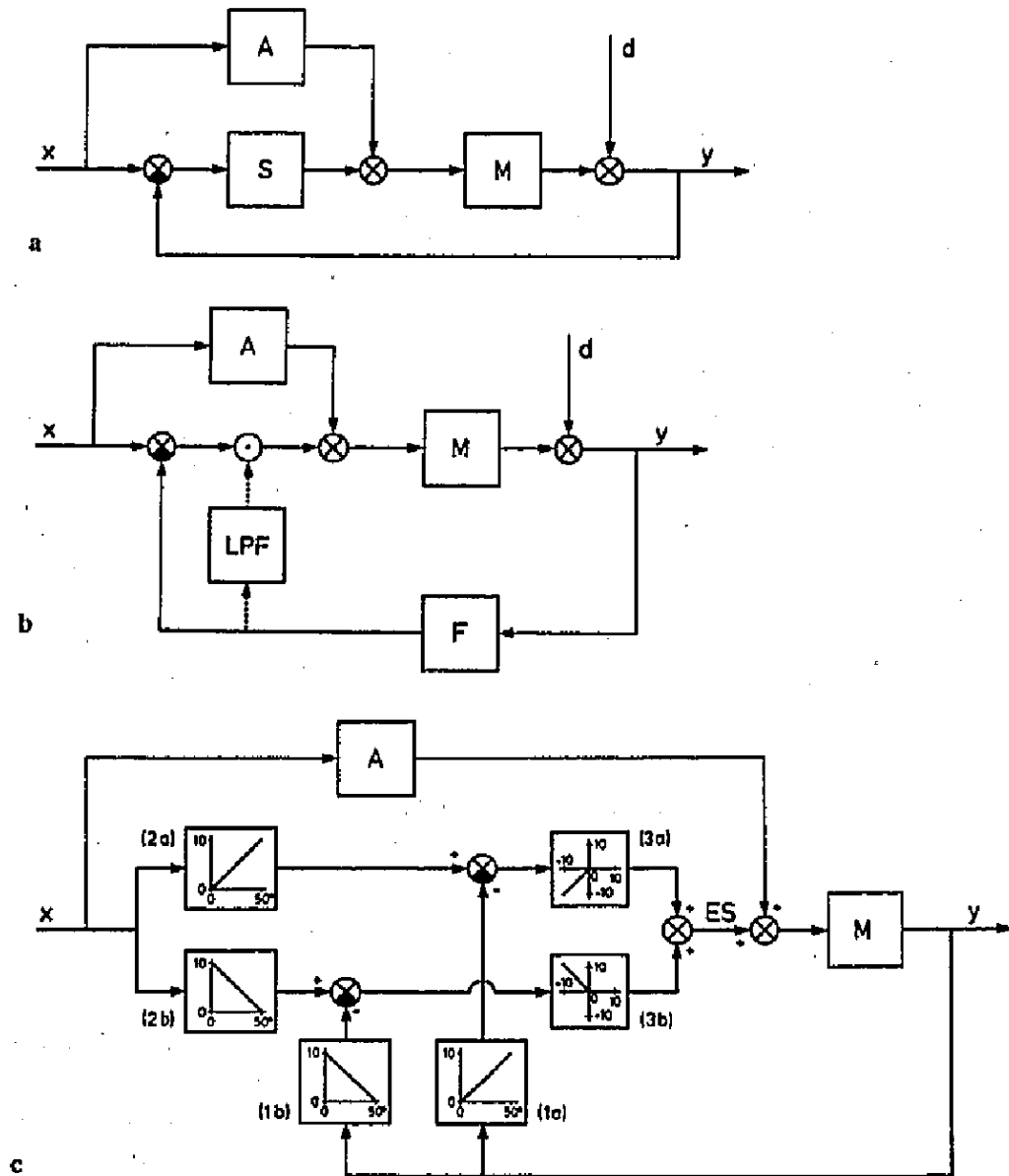


Fig. 2. a A basic scheme describing the control of skeletal muscles in vertebrates and the role of the muscle system. The amplification factor of the channel directly influencing the alpha motoneurons is A , that of the muscle spindle is S , and that of the muscles is M . Muscle length, y , is controlled via a reference input, x ; and a disturbance signal, d . b A feedback system in which the sense organ (F) is not efferently controlled. The interruption of the feedback loop by ablation of the sense organ does not significantly influence the behavior of the system with respect to the reference input, x , because the nonlinear influence of the low-pass filter (LPF) cancels the effect of the error signal. c A corresponding result is obtained by another system using antagonistically arranged parallel channels (a, b). Each channel contains a feedback transducer (I), a characteristic producing the reference value (2), and a rectifier (3). Summation of the outputs of the latter gives the final error signal (ES) (Cruse, 1980). The disturbance input is omitted for sake of simplicity. (a After Cruse, 1981)

The gain of the system, $y/x = (M + MA) / (1 + MF)$, is different according to whether $F = 0$ or $F \neq 0$.

However, two nonlinear systems can be constructed, which have the property that cutting the feedback does not change the output of the system. As shown in

Fig. 2b by dotted lines, we now add a low-pass filter with a very long time constant (in the order of hours or days) which receives the signals from the sense organs as input. The output of this low-pass filter will provide a sort of long-term mean value of the sensory input which, due to the long time constant, will be a relatively constant value. Assume that this mean value is normalized to have a numerical value of about 1. When the error signal is multiplied by this constant value, the resulting system behaves essentially like the linear system with no low-pass filter. However, if the sensory input is zero for a long time due to destruction of the sense organs, then the output value of the low-pass filter will also decay to zero and the action of the error signal is removed.

Another circuit which shows invariant output characteristics when sensory feedback is destroyed occurs if the sense organs are organized antagonistically (Fig. 2c). Joint position, for example, is often measured by two groups of sensory cells which are increasingly excited by joint flexion or extension, respectively. Assume that the joint angle can adopt values between 0° and 50° , and the excitation can vary between 0 and 10 in arbitrary units which may correspond to spike frequency. The antagonistic responses of the two sense organs are represented in Fig. 2c by the two response characteristics yielding increasing (1a) or decreasing (1b) excitation when the joint angle increases. For the respective comparison with the reference value these proprioceptive signals also require antagonist characteristics (2a, b); then the results are passed through separate rectifiers (3a, b). For positive input values, both rectifiers produce zero output; for negative input values, the upper one (3a) produces negative output values, whereas the lower one (3b) produces positive output values. The intact system behaves like the linear system shown in Fig. 2a, as can be verified by some simple calculations. Assume, for example, that the actual position is 25° , and the reference value is 0° thus demanding a movement with a negative sign. The error signal in the lower channel will be $10 - 5 = 5$ which is made to zero by the rectifier (3b); that in the upper channel will be $0 - 5 = -5$ which is not changed by the rectifier (3a). The total error signal, ES, will be -5 . In the same way a reference value of 50° , produces a final error signal of 5. If the sense organs are destroyed, there will be no activity at their output (a value of zero). Therefore the input values to the rectifiers in each pathway will be greater than zero - yielding a zero output. Thus the total ES becomes zero and, if $AM = 1$, it follows that $y = x$ even when the sense organs are ablated. This system shows a normal response immediately after sensory ablation, whereas the system described earlier (Fig. 2b) adapts slowly due to the long time constant of the low-pass filter.

Generalizing the design principle to higher levels of motor control requires some minor changes (Fig. 3) but retains the parallel arrangement of open-loop and closed-loop control. The scheme has as its input two (or more) variables. The one called "autonomous control signal" corresponds to a movement command. The "feedback reference" corresponds to a sensory representation of the expected feedback for the intended movement. There may be different reference signals for different types of feedback. It should be noted that these two inputs are equivalent to

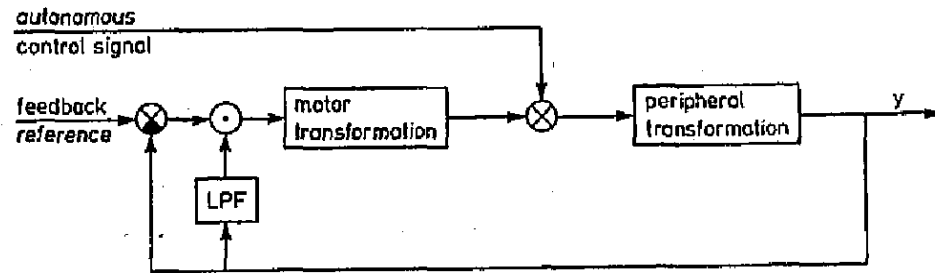


Fig. 3. The control principle shown in Fig. 2b generalized for higher levels of motor control. *LPF*, low-pass filter with a very long time constant. See text for further explanation

the representations postulated by Adams (1971) and Schmidt (1975). Hoyle (1964) proposed a similar distinction in his use of motor and sensory tapes.

The autonomous control signal affects the controlled variable, y , via the "peripheral transformation." If, for example, y is the position of the hand, then the peripheral transformation includes all transformations that central commands undergo due to mechanical characteristics of the muscles and the limbs (see Partridge, 1979). If y is the position of a terminal device, such as a part of a tool, then the peripheral transformation also includes the transformations added by the tool. It should be noted that to adequately control y , the generation of the autonomous control signal has to take the peripheral transformation into account (see Heuer, 1983, pp. 15-16).

The sensory feedback is processed in parallel with the open-loop system. The "sensory error" is transformed into a corresponding motor command and added to the autonomous control signal. For this transformation, the motor control structure must select motor commands which are suited to cancel the "sensory error." More generally, the use of sensory error signals for motor control requires that their "motoric meaning" is known. As one way to solve this problem Hein and Held (1962) postulated the existence of a correlation storage which assigns motor commands to sensory signals. Transforming the sensory error into motor commands does not require that the peripheral transformation be taken exactly into account.

What arguments justify this generalization of the design principle of parallel open-loop and closed-loop control to higher levels of motor control? First, the evidence reviewed above for sensory signals processed either at the spinal level or at higher levels shows that distorted input produces stronger effects than complete removal. It should be noted that the case where removal of the feedback signal produces no effect at all is only a limiting case of the design that will be observed if the autonomous control signal is exactly adapted to the peripheral transformation. Whenever the peripheral transformation is not taken into account exactly – and this will be common in biological systems – elimination of the feedback signals will produce some small effects. Second, as will be discussed in the next paragraph, the scheme allows correct predictions as to when the elimination or the distortion of feedback signals will produce greater or lesser effects. Finally, there is evidence that separable motor and sensory representations do indeed exist.

If the peripheral transformation is unusually complex or only partially known, then it may be impossible to generate an autonomous control signal that takes this transformation into account. (If, in the simpler scheme of Fig. 2a, M is unknown, then A cannot be adjusted such that $MA = 1$). In this case, the output, the controlled variable y , varies according to the presence or absence of feedback. Such situations arise when complex tools are added to the peripheral transformation. One example is a tracking task where the position of the follower is the controlled variable. If the only feedback from the controlled variable is visual, then performance should depend more strongly on visual feedback as the peripheral transformation becomes more complex. This dependence was confirmed by varying the peripheral transformation and by measuring the performance decrement when the follower is occasionally extinguished for a few seconds (Heuer, 1988). The increasing importance of visual feedback with increasing complexity of the peripheral transformation is also indicated by the fact that quasi-linear, closed-loop models are reasonably successful with highly complex tracking tasks (Poulton, 1966).

Postulating separable motor and sensory representations of a movement implies that it should be possible to modify one without changing the other. There are some data from prism adaptation experiments which suggest that this may happen. Bailey (1972) examined slow and rapid movements to a target during prism adaptation and also during pre- and posttests. If subjects pointed slowly at the target while wearing the prism, then the after-effect - a systematic bias in pointing after removing the prism - was much larger for this slow movement than for the fast movement. This finding suggests that during prism adaptation the kinesthetic representation of the visual target was changed, giving rise to the bias in slow pointing, but the motor representation, which is the major determinant of rapid aiming movements was unchanged. Also Schmidt, Christenson, and Rogers (1975) showed that delaying knowledge of results (KR) during learning affected the development of memory for movement recognition, but did not affect the memory of movement production. This result again supports the separation of sensory (recognition) and motor (production) representations (see also Schmidt, 1975).

So far our discussion has been simplified by considering only a single controlled variable - e.g., the position or velocity of the terminal device. Control of the terminal device, however, usually requires coordinated control of many muscles and joints. In general, there are many inputs to the box labeled "peripheral transformation" in Fig. 3, so a network has to be postulated that "distributes" the global control signal referring to the controlled variable among the various muscles involved. The function of this distributing network is partly constrained by how the peripheral transformation combines the various inputs to determine the single controlled variable, y . But partly its function seems to be arbitrary or the product of habit (cf. MacNeilage, 1980). Some arbitrariness in the function of the distributing network is possible when various input patterns to the peripheral transformation produce one and the same output value (c.f. "Coordinative Structures").

What is the role of sensory input for the distributing network? As an example, consider lip closure when speaking. A lip closure of amplitude a can be achieved by various combinations of movements by the upper lip (a_u), lower lip (a_l), and

jaw (a_j). The task of the distributing network is to insure that $a = a_u + a_1 + a_j$. One way of doing so is to use constant weights, setting $a_u = w_u \cdot a$, $a_1 = w_1 \cdot a$, and $a_j = w_j \cdot a$ with the weights adding to 1. This would specify a rigid pattern of the three articulators, which runs counter to experimental findings. In fact, in a sequence of utterances with constant a the contributions of the various articulators vary, so that sometimes the one and sometimes the other contributes more to lip closure (e.g., Hughes & Abbs, 1976). Thus, instead of setting a rigid distribution, the function of the distributing network is to specify the required covariation. One of the oldest reports of such covariation concerns the task of throwing a ball a certain distance: the initial velocity of the ball and the deviation of the initial trajectory from 45° are negatively correlated, which corresponds to the physical fact that these two variables have to be negatively correlated if distance are to remain constant (Stimpel, 1933).

So far the distributing network could be considered as being a pure output device. Perturbation experiments, however, show that its function depends on sensory input. For example, interfering with the movement of one of the articulators during speech elicits rapid compensatory movements in remote articulators (for review see Abbs, Gracco, & Cole, 1984). If an unexpected state of one of the articulators is signaled via sense organs, then other articulators take over to achieve the desired state of the controlled variable, which in this case is the task-related variable lip closure. The occurrence of remote compensation in the case of perturbations implies that the covariations defined by the distributing network are formed at least partly in sensory terms and not just in motor terms.

Should the sensory inputs to the distributing network be called "feedback"? If one focuses on individual articulators, then proprioceptive signals from the perturbed articulator clearly have feedforward effects when they modify the movement of other articulators, as well as probable feedback effects onto the perturbed articulator to resist the perturbation (see Abbs et al., 1984). But if the total system is considered with respect to the task variable lip closure, or the sensory signals themselves relate to this variable, then it is justified to talk about feedback.

One final aspect of the scheme of Fig. 3 as amended to include a distributing network should be mentioned. If one and the same autonomous control signal can be channeled through different distributing networks to activate different effector groups, then this could explain the phenomenon of motor equivalence. The most common example is the observation that a person's handwriting retains many common features when written small on paper or large on a blackboard. Therefore it is reasonable to think that these common features are part of a higher level control structure, organized above the level of the specific muscle groups. This effectively means that different motor control structures may share the higher levels of control related to their respective controlled variables (e.g., position of a pen on paper or a piece of chalk on a blackboard), but use different distributing networks to translate the control signal into the pattern of neural activity necessary to coordinate the different effector muscles.

Reference Signals

Reference signals indicate what the state of a moving limb should be. Thus they include both the "autonomous control signal" and the "feedback reference" of Fig. 3. Often, however, reference signals are produced not just by autonomous processes but also by sensory input. These sensory inputs may derive either from sense organs which are unaffected by the motor system using the reference signal - in which case the sensory signal serves as feedforward - or they may derive from sense organs which are affected by the system for which they provide reference information. In the latter case it may be difficult to distinguish between feedback and feedforward: a sensory signal relating to the controlled variable can provide feedback as outlined in the scheme of Fig. 3 and at the same time participate on a higher level in the production of the reference signal.

It is a rather trivial observation that sensory reference signals can define the desired positions of a terminal device. For example, in a continuous tracking task, the reference signal provides an exact prescription for the position-time curve of the follower. In a discrete tracking task, where the reference signal consists of a series of steps, the movement of the follower is incompletely specified. (As we will discuss on p. 68f, discontinuous or intermittent processing of sensory information may occur even when the target is continuously present.) In both cases the afferent information is used to update reference values incorporated into autonomous control mechanisms, even if this updating does not occur continuously.

In some movement patterns, a more complex integration of sensory reference signals and autonomous control functions can be observed. For example, consider a central pattern generator producing a harmonic oscillation. On a more abstract level, this mechanism can be described as a motor program with a sine wave as the prototypical function and the amplitude and frequency as parameters. It is possible that a sensory reference signal continuously controls one or the other parameter. An example is the control of wing beat amplitude by a flying insect, in which an optomotor turning response is induced by rotating the insect's visual surroundings. A similar optomotor response can be elicited from the stick insect during walking: the rotation of the visual field induces changes in amplitude or frequency of leg movements or both, causing the insect to walk in curves (Jander, 1985).

The role of this afferent information as a reference signal might also be called feedforward but, as mentioned above, the distinction between feedforward and feedback depends on the definition of the system and on the selection of the variable considered to be the controlled variable. As long as the movement defined as the output does not directly influence the sense organ considered, the afferent activity should be regarded as providing a reference signal.

As outlined above, a central motor program can be described using a prototypical function. So far, we have considered the transformation of the dummy variable ϑ into real time by a simple scaling operation, $t = T \cdot \vartheta$, to obtain an actual movement of duration T , but we have not discussed how this might occur. Lashley (1951) outlined a simple mechanism for generating a temporal series of events from a nontemporal representation. According to his hypothesis, a spatially orga-

nized representation is read out sequentially. This is what actually happens in stepping through the "spatially" organized command sequence for a digital computer. If the same mechanism applies to the execution of a central motor program, then the relative timing should remain invariant, as is often the case. This kind of design might require some internal clock mechanism that determines how fast the program is executed. Alternatively, a chain reflex mechanism which allows the movement velocity to be varied would also show invariant relative timing or phase constancy.

Whether something like "metering out of time" does occur in motor control has been a subject of debate (e.g., Schmidt, 1980, 1987; Kelso, Holt, Kugler, & Turvey, 1980; Kelso & Kay, 1987). The experimental results seem to depend on the nature of the movement studied (Schmidt, 1980; Schmidt, McGown, Quinn, & Hawkins, 1986). To answer the question by "always" or "never" probably underestimates the versatility of motor control structures. An internal clock mechanism which can run at different rates would represent an internal time base for the motor program, providing a signal that replaces the dummy variable ϑ . But an autonomous, clock-like signal is not the only candidate for replacing the dummy variable. In fact, the motor control structure may use several different signals: some of them internally generated, others possibly derived from sensory signals. In some sense, these signals can be considered equivalent to "time," but they do not measure time itself and they may represent different functions of real time.

Lee, Young, Reddish, Lough, and Clayton (1983) describe a case where a sensory reference signal seems to fulfill this timing function. The task for the subject is to time a jump so as to punch a falling ball at the apex of the jump. This task requires preparatory flexion of the knees followed by rapid extension to propel the body. The hypothesis explored was that the timing of the preparatory movements is coupled to a stimulus variable called τ . τ is defined as $\alpha/(d\alpha/dt)$, where α is the visual angle of the approaching object and $d\alpha/dt$ is its first derivative with respect to time. This variable is directly related to the time that remains until the object collides with the observer, given that it approaches with constant velocity. Since a falling ball has a constant acceleration, its velocity increases during the approach. When the ball falls from different heights, different functions for τ as a function of time to contact can be obtained. From these functions, specific predictions can be made as to how the anticipatory movement pattern should depend on the height from which the ball is dropped, given the assumption that the movement is temporally coupled to τ .

Lee et al. (1983) confirmed these predictions. The timing of the preparatory movements for striking a ball dropped from different heights varies when knee angle is plotted as a function of time, but these differences vanish when the data are plotted as a function of τ . This finding strongly suggests that the dummy variable ϑ of a motor program is replaced by the sensory variable τ . Here we have a case of what Lee and Young (1983) call extrinsic timing; in this case the extrinsic timing is continuous. It is not hard to imagine other instances where a sensory reference signal may be processed in the manner described here for τ .

Type 2: Intermittent Use of Sensory Information

The continuous stream of movement can often be segmented into units. In the computer program analogy, the autonomous control mechanisms for such units are often referred to as subroutines. It is not always clear whether the units used in the description of behavior have a counterpart in separate units of control, but in some instances a division of the apparently continuous flow of movement into subunits seems realistic (e.g., swing phase and stance phase of legs walking, in Grillner, 1981; Bässler, 1983; see also Viviani, 1986; Monsell, 1986; Schmidt, 1985b). Unfortunately, the criteria for defining units are unclear.

Sometimes it can be shown that sensory information for motor control is only used at discrete points in the movement rather than continuously. This could provide one criterion for dividing a complex movement into subunits. In this section we will consider this intermittent processing of sensory information, focusing on the question of when and how sensory information is used. It is again possible to classify signals as feedback and reference signals. However, as mentioned above, the distinction varies according to how the units of control are defined. This problem is particularly acute for intermittent processing, so we will discuss both types together in this section. The problem is acute because the effect of intermittent processing can either be related to the immediately preceding movement segment, in which case it serves as feedback, or to the succeeding segment, in which case it serves as feedforward or as a reference signal.

Updating Parameters

The points in the time at which a sensory signal is processed need not depend on the signal itself; they can be specified either through autonomous mechanisms or other sensory inputs. This, for example, is the case in an intermittent servo-system that samples the error signal at a fixed rate. Such a system served as the model for Craik's (1947) description of human operators in manual control tasks. Craik's model is based on the following observation: when inexperienced subjects have to track a ramp, their movement is uneven and oscillates around the target ramp. The response looks more like a sequence of small, discrete aiming movements than like a smooth ramp movement. Therefore, Craik postulated that the movement consists of a sequence of ballistic corrections occurring approximately every 0.5 s. In Craik's model of manual tracking, the visual stimulus, in this case a deviation from the target, is sampled according to some kind of internal clock and used to adjust the parameters of a motor program for the corrective movements. During programming and execution of the corrections the system is thought to be refractory and insensitive to sensory input. Since the frequency of the intermittent corrections was not affected by amplification of the error signal, the conclusion was that the sampling rate is internally determined and independent of the amplitude of the error signals itself. However, it was shown later that the start of the first correction

is triggered by the error signal (Navas & Stark, 1968). Brooks, Cooke, and Thomas (1973) found very similar discontinuities in arm movements of monkeys.

There is another type of internal specification of the times at which a sensory signal is used for motor control. In some behaviors, particular sensory signals need to be processed only at certain points associated with particular states of the movement. Different sensory signals may be used in different parts of a movement cycle. The fact that a certain signal is not incorporated into the control of movement during some part of the movement, of course, does not imply that the sensory input is not monitored during this time.

As an example, consider the human stride length in running. This depends mainly on the flight distance of the trunk (see Lee, Lishman, & Thomson, 1982). If the trajectory of the trunk is approximated as a parabola, then this distance is given by

$$s = \frac{2 v_x v_y}{g} \quad (6)$$

where v_x and v_y are horizontal and vertical velocity at takeoff, respectively, and g is the acceleration due to gravity. There is evidence that the horizontal velocity is roughly constant during a step cycle. Hence, distance is proportional to the flight duration as given by

$$t = \frac{2 v_y}{g} \quad (7)$$

Since v_y is proportional to the vertical impulse, this impulse has to be adjusted according to an estimate of how long it will take - given a certain horizontal velocity v_x - to reach the position for the next footstep. This "time estimate" is available through the variable τ that we have discussed on p. 67 (see also Warren, Young, & Lee, 1986).

In this example, there are "time windows" in the continuous run during which a visual variable is used for the adjustment of certain parameters of a central motor program. The time windows are imposed by the intermittent opportunity for making corrections - i.e., during contact with the substrate. These properties are presumably incorporated into the motor control structure so as to determine when and how different signals are processed in the course of a periodic movement.

Other examples where the use of afferent information for motor control depends on the state of the system are the so-called phase-dependent reflex reversals or "program-dependent reflexes," which occur in walking movements of crustaceans (DiCaprio & Clarac, 1981), insects (Bässler, 1974, 1977; Graham, 1979), and cats (Forssberg, Grillner, & Rossignol, 1975). In these examples, sensory signals lead to different responses depending on when they occur in the step cycle.

Stick insects show a reflex which prevents the hind leg from standing on the tarsus of the adjacent anterior leg. If the hind leg lands on the forward leg, it is briefly lifted and moved to a more posterior position. The trigger for this reaction is a tactile stimulus to the forward leg. Touching this leg with a brush will do, but

this stimulus is only effective during part of the hind leg's step cycle (Graham, 1979). The full reaction only occurs for stimuli during the beginning of the stance phase. Stimuli in the second half of the swing phase cause the hind leg to shorten its swing. When the hind leg is in the second half of its stance phase or in the first half of the swing phase, no reaction of the hind leg is observed. Similar effects have been described for cats (Forssberg et al., 1975). Stimulating the dorsal part of the paw causes the leg to flex when it is in swing phase, whereas the same stimulus elicits increased extensor activity when applied during the second half of the stance phase. Z. Hasan (1986, personal communication) has suggested, however, that instead of being program dependent, the response may vary simply as a function of the position of the leg which of course covaries with the phase of the locomotor cycle.

So far we have considered instances in which processing of sensory information for adjustment of motor program parameters is determined internally or by other sensory input. It can, however, also depend on the sensory information itself. This seems to be the case in an experiment by Pew (1966). In this experiment subjects had to center a marker on a screen by pressing two keys alternately. Pressing a key resulted in a constant acceleration of the marker in one or the other direction. Early in practice, key presses were rather slow. It seemed as if subjects pressed a key and then waited until the marker changed and crossed the center line of the screen before they pressed the other key.

In the course of prolonged practice, subjects learned rapid key press sequences that held the marker approximately stationary with only small oscillations. However, the marker remained completely stationary only for identical transition times between the two keys. This the subjects were unable to obtain. Because the ratio of transition times was not equal to 1, the marker drifted slowly across the screen. At this stage of practice subjects seemed to neglect the small oscillations and only to process the drift. Corrections occurred when the drift became too large. These corrections revealed two different strategies. Some subjects changed the durations of a few key presses, bringing the marker quickly back to the center. Other subjects used a more elegant strategy. They changed the ratio of transition times and thus altered the direction of the drift. This suggests that in both groups - but in a different way for each group - the visual signal itself influences the parameters of the motor control structure when a certain threshold was exceeded.

Triggering Transitions

In the following examples the sensory information itself is assumed to be continuously monitored. In these motor control structures, however, only the transitions from one subroutine to the next appear to depend on critical values of the monitored variables and there is no obvious processing of these signals with regard to parameter adjustment within a subunit. Consider the transition from the stance phase to the swing phase in the stick insect. When the movement of a leg in stance phase is prevented, one might still expect that the swing phase would be initiated

as soon as the normal duration for the stance phase is reached. This is true for monkeys trained to make oscillating arm movements: obstructing the movement in one direction does not alter the time at which the antagonists become active to initiate the movement in the opposite direction (Conrad & Brooks, 1974). The situation for the stick insect is different: the leg continues its stance phase. During this stance phase continuous feedback systems which apparently control velocity are active. Proprioceptive information on position does not appear to be incorporated into motor commands. Nevertheless, position information is monitored and used to trigger the transition from the stance to swing phase. This transition occurs only if a given position threshold is reached (Cruse, 1985a, 1985b; Dean & Cruse, 1986). In this way a continuous afferent signal is only used for motor control at particular points which are dependent upon the actual position of the leg.

Similar trigger functions have been reported for the variable τ (see, for example, Lee & Young, 1986). The forceful leg extension of ski jumpers is probably initiated when a certain value of τ is reached. Similarly, the gannet which plummets toward the sea seems to streamline its wings when a τ threshold is reached.

To summarize, there are two basic functions for intermittently processed sensory signals: (a) triggering transitions from one movement phase to another; and (b) updating parameters. The triggering function implies that the signals are monitored continuously. The motor control structure defines a threshold for the transition from one subroutine to the next, and the transition occurs as soon as the threshold is exceeded.

The updating function can be performed at internally or externally determined points in time. Externally determined updating again requires continuous monitoring of the afferent signals. Updating occurs as soon as a certain threshold is exceeded. Thus updating is similar to triggering except that in triggering the monitored signals have no influence on the parameters of the triggered subroutine, while in updating there is a systematic relation between at least one sensory signal and the parameter change. Internally determined updating, in contrast, is completely defined by the requirements of the motor control structure. Certain information may be needed only at certain times, so it can be processed for parameter adjustment during preset time windows.

Type 3: Advance Use of Sensory Information

The third role is played by sensory information which is used prior to or at the start of an action. Sensory information of this type is used to elicit movements, selecting motor programs, and specifying parameters. It is hard to make a cogent distinction between type 3 and type 2 functions in the general case, but in practice the distinction is usually clear. The problem is similar to that of distinguishing between feedback and feedforward: it arises in deciding just what entity is taken as the unit for analysis. When an entire tracking task or a complete step cycle is defined as the action, then the error signals eliciting correction movements in the first

case or the transition signals in the second are type 2 - intermittent influences occurring within the movement. However, one might also consider each correction movement or the separate swing and stance phase as the units of organization, in which case the same signals would be considered as type 3, advanced processing influences.

It is rarely the case that an external stimulus is the only determinant of a movement. (Exceptions in humans might be eye movements toward a moving peripheral stimulus or withdrawing a hand in response to pain.) The more frequent condition for elicitation of a movement pattern appears to be a conjunction of internal "drive" and external stimulus. This formulation, of course, is reminiscent of Hull's (1952) theory of behavior. A cat or a crayfish standing on a stationary treadmill will normally begin to walk when the belt begins to move, provided that the internal excitation is high enough. This "drive" is an essential part. It may vary with time or developmental stage or from one species to another. For example, in one crayfish species adults could easily be induced to walk on a motor-driven treadmill. In contrast, young animals of the species or adults of another species could not be stimulated to walk on the same treadmill although they were quite active walkers under other conditions (Cruse & Müller, unpublished observation). Stick insects walk on a motor-driven wheel very reluctantly and only with additional tactile stimulation. Similarly, a decerebrated cat needs electrical or chemical stimulation to begin walking (Grillner, 1981).

In humans it may be hard to relate the initiation of movement to specific drives. Rather, one can speak about intentions. Intention can be conceptualized as tuning the CNS to process certain sensory information in particular ways. The state of the nervous system corresponding to an intention bears some similarity to a motor control structure. The main difference is that its function is not to control the execution of a movement but rather its initiation. The intentional state embodies rules for the assignment of particular input patterns to the establishment or the activation of pre-established motor control structures, similar to conditional GOTO statements in a computer program (Heuer & Prinz, 1987). In man, this assignment can be selected in a rather arbitrary way (for example, as a result of instruction or learning), but some assignments allow for faster and more accurate initiation of movement patterns than do other assignments.

Use of sensory information for parameter adjustment in advance of movement can be clearly seen in knowledge of results (KR) experiments, one of the traditional paradigms of motor learning. In a typical KR experiment subjects have to repeatedly perform a specified movement. After each performance or at longer intervals, they are given information about the accuracy of their movements. This information about the error on an previous movement can then be used to adjust parameters for the next performance. Thus, KR plays two roles. First, KR informs subjects about the target movement and thus is a prerequisite for the development of learning (i.e., creating a relatively permanent internal representations of the desired movement). Second, and this has only recently been recognized (Salmoni, Schmidt, & Walter, 1984), KR provides "external guidance" - external information which can be used for temporary parameter adjustment and may not be used to

form a part of the relatively permanent (i.e., learned) representation of the action. Subjects seem to rely partly on this external information for parameter adjustment, so that a performance decrement is observed when it is withdrawn.

Conclusion

To summarize, we have described various ways in which sensory information is used for motor control. Before the actual start of the movement, sensory information (type 3) is used for selecting and activating an appropriate motor control structure and specifying the initial parameter values for the autonomous control signal. During movement, sensory information (type 2) can be used for triggering successive units and for intermittent updating of parameters. These actions may depend either on the current state of the control structure, on the state of the monitored signals, or on a combination of both. Finally, sensory information (type 1) can be used continuously either as feedback, as a reference signal, or as a kind of time base for a motor program. In the latter instance, it defines the "time axis" on which the motor program operates. Sensory information used as feedback can be processed in parallel with the autonomous control signal. It serves to reduce or correct any errors due to changes in the peripheral transformation or to inaccurate parameter specification in the direct control path.

The diverse functions of sensory signals appear to make any simple answer to the question of how the motor system works unrealistic. Instead, one may have to be content with a set of specific answers to specific questions. The specificity enters with the requirements posed by each task and with the role of chance in the evolution of biological solutions. Each task appears to favour some control mechanisms over others in the development of motor control structures for performing the required action. This is particularly true with respect to the use of sensory information. The motor control structure itself determines, to a large extent, how and when sensory signals are processed. In this sense it is not only a "motor system" but rather a "sensorimotor system."

So far we have taken our examples from various species based on the implicit assumption that the basic ways of processing sensory information for motor control are invariant. Species, however, do vary. In particular, the variety of motor control structures seems to increase in higher species.

In the frog, for example, it seems to be possible to compile a rather complete list of the motor control problems this animal faces. More importantly, it is possible to identify anatomical structures that subserve these control problems - neural centers which process sensory information in a particular way for a particular movement patterns (see Ingle, 1982). These structures represent the higher-level anatomical substrates in the associated motor control structures. Thus, motor control structures in the frog seem to be "hard-wired." They process in a pre-established way: once they are established little or no plasticity remains. For example, lower animals do not adapt their motor actions to changed visual input

such as occurs when the eyes are surgically rotated in their sockets (see Taub, 1968).

The situation is radically different in humans. Humans adapt readily to even severe changes of visual input (see, for example, Welch, 1978), the assignment of output motor patterns to input signals is nearly arbitrary, and it appears impossible to compile an even modestly complete list of the motor control problems. Motor control structures in humans appear to be "soft-wired": they can be readily adjusted to meet changed environmental demands. Hence, attempts to find general rules for processing sensory information or for the parameterization of motor programs appear doomed to failure. The best that can be done is to find rules for particular tasks, that is, rules that hold for a particular motor control structure.

This sounds like a rather pessimistic view, but there is some consolation. Even if there are innumerable motor control structures, there are some that are particularly relevant and deserve study in their own right, such as locomotion. Also, there should be some general rules defining what is possible for motor control structures. Although these rules will probably not suffice to predict how motor control will actually work in particular situation, they may allow a range of possibilities to be specified. Finally, there may be some features that are shared by many motor control structures. For example, the parallel use of autonomous command signals and closed-loop control seems to be such a feature.

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