

MOTOR CONTROL

Issues and Trends

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The Structure of Motor Programs

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I. Introduction

A good many motor tasks involve a complex series of movements. The skilled performer often differs from the unskilled performer in such tasks not necessarily in the quickness or precision of individual reactions and movements but in the coordination of the successive movements into a smooth and orderly sequence. When people are unskilled, they make a movement, evaluate the results, make another movement, reevaluate, and so on, and their performance is therefore quite irregular. As they acquire skill, the sequence of movements becomes structured so that it no longer is under direct visual control (Pew, 1966, offers good evidence for such a change). The movements anticipate or coincide

with the events in the environment that they are intended to deal with, and they appear coordinated with each other. In other words, the sequence of movements becomes stored in the memory system so that it can be executed without constant correction by reference to the environment. Understanding the mechanism of sequencing clearly is an important element in understanding skilled performance.

This chapter is concerned primarily with the nature of the memory structure that underlies skill. Some evidence will be described that led to a particular theory of sequence representation, namely, motor program theory. Essentially motor program theory posits that the sequencing of a skill is represented centrally and does not require peripheral feedback from prior movements to elicit succeeding movements. This is not to deny, however, the critical role of feedback in skilled performance; consequently, some consideration is also given to its role. After considering some practical applications of the program-feedback model to skill training, a more detailed analysis of the memorial structure will be given. Granted the sequence representation is a motor program, is the movement series stored as event associations, as position associations, as a higher order structure, or perhaps in more than one code? Is timing an integral part of the sequence representation, or is the ordering of events and timing of events separately represented? Questions of this sort will be discussed in the last section of the chapter.

II. The Motor Program Concept

A commonly held, early theory of sequence representation is S-R chaining; it is illustrated in Figure 1 based on Greenwald (1970). Early in practice, as shown in panel A, successive responses are elicited by successive cues in the environment. As a movement is issued a pattern of kinesthetic stimulation unique to the movement flows from the various joint, cutaneous, and stretch receptors in the moving limb. Because the kinesthetic stimulation from one movement occurs just prior to a succeeding movement, the feedback from one movement becomes conditioned to the next (panel B). A basic tenet of classical conditioning is that any stimulation that systematically precedes a response will eventually come to elicit that response. Eventually, therefore, the entire skill can be executed in response to a starting stimulus and in the absence of other external stimuli, because each succeeding response is elicited by the pattern of internal stimuli from the preceding response.

One long-standing argument against S-R chaining as a general theory of movement control is that feedback processing is too slow to account for very rapid sequences of movements such as finger movements in playing the piano

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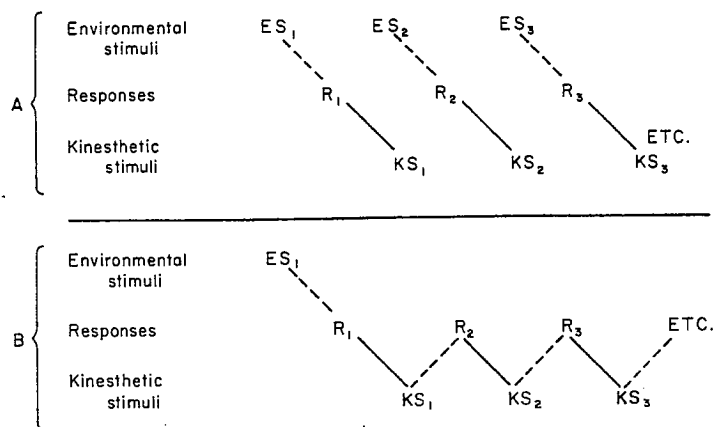


Figure 1 During initial learning of a skill, successive responses are controlled by environmental stimuli (panel A). According to S-R chaining theory, as learning progresses responses become conditioned to the kinesthetic feedback from the preceding response (panel B).

(Glencross, 1975; Lashley, 1951).¹ Many skills involve successive movements at intervals less than 100 msec, and yet the time to react to kinesthetic stimulation was reported to be 100 msec or greater (Glencross, 1975; Keele, 1968). Recently, however, Evarts and Tanji (1974), recording the electrical discharge from the muscles, a procedure more sensitive than those previously used, reported that monkeys can make use of kinesthetic feedback in about 40 or 50 msec. Such a rapid influence of feedback is not simply due to a built-in reflex, and instead involves flexible coupling of feedback to response as would be required for feedback to be useful in skill learning. The monkeys are able to respond by either pushing or pulling in response to the same kinesthetic signal, depending on prior instructions. Built-in reflexes should not be amenable by instruction. Thus, the argument that S-R chaining is impossible because of the time constraints of kinesthetic processing is less persuasive than previously thought.

More convincing evidence contrary to S-R chaining theory comes from studies that surgically eliminated kinesthetic feedback in animals. If the skill can proceed without kinesthesia, then S-R chaining, in which the stimuli are kinesthetic, cannot explain the sequencing. Many studies have in fact shown that movement sequences can be maintained when feedback is removed [Bossom (1974) and Hinde (1969) review several such studies]. Some examples are shown

¹ Some people have taken this argument of Lashley's as a general criticism of any associative chaining theory, but it properly applies only to a peripheral to central chaining theory and not one in which associations involve only central representations.

here of the wide range of skills, species, and methods over which movement persists following feedback removal.

Wilson (1961) in a now classic study severed the nerves that return feedback from wingbeats in the locust. Although the rate of beating slowed, the beat pattern was largely maintained, suggesting central rather than peripheral control. The vocal system of birds is innervated bilaterally by the hypoglossal nerve. When one side of the nerve or the other is severed, paralyzing the muscles on the denervated side, portions of the bird's song drop out (Nottebohm, 1970). The remaining elements of the song occur in the proper time slots, however, demonstrating that neither the missing kinesthetic feedback nor the missing auditory feedback from the eliminated segments is needed for triggering the remaining segments. Again S-R chaining theory appears ruled out, since the proper sequence of movements is maintained in the absence of some portions of the feedback. Related phenomena have been demonstrated in mammals as well. During grooming a normal mouse brings its forepaws in front of its face, and as the paws move toward the mouth, the tongue licks out and makes contact with the paws. In another sequence one forelimb crosses over the eye, and the eye closes just before contact. Fentress (1973a) amputated the forelimbs of mice at 1 day of age. Grooming behaviors were observed up to 30 days of age even though they no longer could serve a grooming function. The remaining portions of the limbs in the amputated mice went through the same grooming motions shown by normal mice and the tongue licked or the eye closed at the appropriate time even though no forepaw contact with the face was possible and all sources of feedback from that missing segment was lost. Apparently the movement sequence is inborn, since amputation occurred at one day, and its proper execution does not depend on the tactual, kinesthetic, or other feedback from the missing limb.

The control of movement by locusts, birds and mice may be far different from the skills of humans, however. For that reason, the experiments with perhaps the greatest impact on our thinking about human skills involved rhesus monkeys. Taub and Berman (1968) repeated a historic experiment by Mott and Sherrington (1895). Kinesthetic feedback was surgically eliminated from one of the monkey's front legs by severing the dorsal roots of the nerve bundles entering the spinal cord, eliminating the afferent feedback but not influencing the efferent input to the muscles.

As observed by Mott and Sherrington, monkeys avoided using the single deafferented limb. Historically, observations of this sort led to S-R chaining theory. Taub and Berman further observed, however, that restraining the normal forelimb encouraged the animal to use the deafferented one. Moreover, when both forelimbs were deafferented, "... the animals were able to use the limbs rhythmically and in excellent coordination with the hind limbs during slow and even moderately fast ambulation [p. 177]." The monkeys could also climb wire

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cages, and walking and climbing persisted with blindfolding in addition to deafferentation. More recently, Taub *et al.* (1973) demonstrated that infant monkeys both deafferented and visually blocked shortly after birth learn to walk, suggesting that the sequence of movements underlying walking does not depend on normal, detailed feedback for the development of the skill.

Criticisms of the Taub and Berman study have been raised on at least three points. The first two suggest that some kinesthetic feedback may have remained. One argument is that all afferents in the dorsal roots may not have been severed during the surgical procedure. As one guard against this possibility, Taub and Berman stimulated the nerve ends in the deafferented limb and observed no evoked cortical responses. Evoked potentials might be expected if some kinesthetic sense remained. Bossom and Ommaya (1968) also confirmed that monkeys could both walk and grasp objects when deafferentation was done with more precise microscopic surgery, making it more likely that all the desired dorsal afferents were cut. Second, a small proportion of the kinesthetic afferents may enter the spinal cord through the ventral roots rather than the severed dorsal roots (Bossom, 1974). The fact that Taub and Berman did not observe cortical evoked potentials to nerve stimulation and that Bossom and Ommaya found no reflex responses to pin pricks or pinching is some evidence, though not conclusive, that no functional kinesthetic sense remains after dorsal root deafferentation. Nevertheless, some reservation must be maintained about the Taub and Berman study if some afferents do enter the ventral roots. At the same time, however, the procedures of the Nottebohm and Fentress studies are not susceptible to the same criticisms, since some segments of the movement series were eliminated entirely. Although those studies do deal with lower animals, they lead to the same conclusion.

A third, more serious issue has been raised by Bossom (1974). Whereas Taub and Berman emphasize the high degree of coordination in walking that monkeys retain following deafferentation, Bossom emphasizes the loss of elegance of movement control. Much recovery occurs following extensive postsurgical practice. The monkeys can, for example, extend their arms, bend their wrists, and curl their fingers around a food object, even when the arm is hidden from view. Apparently, however, the thumb is not used in such movements, and movements generally appear clumsy. It is possible that the more gross rhythmic movements involved in skills like walking can be sequenced without feedback, but that finer manipulative skills or more distal skills are dependent on feedback. If such is the case, it does not necessarily mean that feedback is a required stimulus for succeeding movements as in S-R chaining theory. Instead, the feedback may be necessary for either finer or more frequent corrections in the skill the finer the task required. Alternatively, the skills for which the motor program concept best apply may have a strong innate component. Manipulative skills may be primarily learned, and the mode of representation may be different.

As a whole these studies suggest that the sequence of movements in at least some skills is centrally represented as a motor program. An appropriate sequence of neural commands can be sent to the muscles, resulting in the desired movement, even though no feedback unique to individual movements returns from the periphery to stimulate successive movements. The motor program concept does not imply that feedback is not an extremely important element of skilled performance. It is. Furthermore, the existence of motor programs does not imply that S-R chaining is not also possible. Both mechanisms may coexist or apply to different skills. As mentioned, the skills on which the motor program concept are based have a strong innate component. Many human skills, on the other hand, are learned skills, and for that type of skill virtually no evidence exists on the form of representation. S-R chaining theory essentially is a learning theory, not a theory of innate representation, and it may therefore fare better for learned skills.

Evidence for motor programs in humans is less adequate than for animals because of the difficulty of manipulating kinesthetic sensations without permanent neural damage. One promising technique, explored by Lazlo (1966, 1967), uses a pressure cuff on the upper arm to block blood flow to the lower arm. Lazlo claimed that following cuff application, people lost their kinesthetic sensation prior to deficits in motor functions. Despite kinesthetic loss, people were able to tap their fingers, though at a reduced rate, even with blindfolds and auditory masking noise. Although some studies found greater deficits on more complex skills (for a review, see Glencross, 1975), Docherty (1973) demonstrated that a finger sequencing task could be performed fairly well under kinesthetic block.

Unfortunately, conclusions from studies using pressure blocks face severe interpretive problems. Glencross (1975) reported that people are able to perceive elbow and wrist movement when finger sensation is lost. Remaining sensory information perhaps could be used for performing the sequential task, especially since many of the muscles that operate the fingers are in the forearm where sensory cutoff appears less complete. On the other hand, Kelso *et al.* (1974) applied supramaximal electric shocks to the skin overlaying the median and ulnar nerves and above the point of application of the pressure cuff. Since the stimulation is supramaximal, any changes in evoked muscle responses cannot be ascribed to inadequate stimulation. Both the latency and amplitude of evoked muscle responses below the cuff exhibited considerable decrement before sensory perception disappeared completely. Thus, when decrements occur on tasks following cuff application, it may reflect motor impairment, not sensory loss. At this point, therefore, the kinesthetic block technique appears unanalytic.

Another approach for studying kinesthetic loss in humans is to observe people who have had dorsal roots cut to control pain or relieve spasticity. Although the operation has been done many times, there appear to be few studies of the

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motor consequences. Foerster (reported in Phillips, 1969) in the early 1900s found that patients with deafferentation of arms and hands could move them as directed, even without vision. As with monkeys, however, much fine control of the fingers was lost, and patients had difficulty moving individual fingers without moving others at the same time. Perhaps motor programs are involved to a greater extent in gross limb movements than in fine movements or finger movements or in sequential skills instead of isolated finger movements, but critical tests have not been conducted. One might ask, for example, whether highly practiced sequential skills such as typing can be executed with the fingers following deafferentation. Tasks involving isolated movements such as an animal plucking an object between thumb and forefinger or a person moving a particular finger may be difficult following deafferentation because such tasks do not involve highly predictable and sequential skills. By their nature they may be dependent on feedback, but other sequential finger skills might be more free.

In general, therefore, observations following deafferentation in humans are consistent with those of animals but not as conclusive. At least some simple movements appear to be made without kinesthetic feedback, ruling out S-R chaining theory as a necessary component. Again, however, evidence is lacking on the form of representation for more complex learned skills. The relative lack of evidence of the form of representation for learned skills requires caution. Nevertheless, it is useful to pursue the possible implications that motor program theory has for human learning, and this will be done later.

A. Follow-Up Servo Theory and Alpha-Gamma Coactivation Theories

Two predominant theories have been proposed regarding how a central representation is translated into the appropriate muscular movement. Both theories involve the gamma-efferent kinesthetic system.² Follow-up servo theory, discussed by Matthews (1964) and Phillips (1969), imparts a critical role to the gamma system in actually causing muscular movement. Alpha-gamma coactivation theory postulates parallel programming of both the gamma efferents and the main muscle system; the gamma system senses errors but is not critical in actually implementing movement.

The gamma system, often called the fusimotor system, has a unique property of adjustable sensitivity. Embedded within the main muscles are stretch receptors called muscle spindle receptors. If a main muscle is passively stretched, a spindle receptor embedded in the muscle is likewise stretched and the neural output from that receptor increases. The spindle receptor is also connected to its

² A more detailed description of the gamma system and other kinesthetic senses is given in many sources on neurophysiology. Two good sources are Howard and Templeton (1966) and Matthews (1964). In the present context only very general features of the gamma efferent system are described.

own unique muscle fiber, called an intrafusal fiber, and that fiber can be programmed independently of the main muscle by the gamma efferents. Alpha efferents innervate the extrafusal fibers of the main muscles. The intrafusal fibers, when activated by gamma efferents, are unable to move limbs, but they do control the degree of stretch in the spindle independently of the passive stretch caused by coupling to the main muscle. Furthermore, some of the afferent neurons that return feedback from the stretch receptor also make synaptic connections in the spinal cord with the alpha motoneurons that activate the main muscles. The fusimotor system, therefore, is one that can be directly programmed itself, but it is also passively influenced by the muscles to which it is coupled.

- ① In follow-up servo theory, the central nervous system programs the gamma neurons rather than the alpha motoneurons. Activation of gamma neurons contracts the spindles. Spindle receptors are therefore stretched, resulting in increased neural discharge, and that discharge feeds back on the alpha motoneurons. The alpha motoneurons in turn activate the main muscle, and the limb moves. As the main muscle contracts, stretch on the muscle spindle declines until the receptor output returns to baseline. At that point the output from the muscle spindle no longer facilitates the alpha neurons, so the main muscle stops contracting. Thus, the spindle system is programmed by the gamma efferents, and the main muscle reflexively follows until it nulls out the programmed stretch of the muscle spindles.

The follow-up servo notion appears at first unduly complicated, since the central nervous system presumably could directly program the alpha motoneurons going to the main muscles and hence eliminate the servo loop, but some reflection reveals attractive features of a follow-up servo. One perplexing observation about motor skills is that the same task is seldom if ever performed twice in exactly the same way. How can motor program theory explain such a result? If the system programs spindle settings, then the main muscles would be driven by the reflex loop to the desired position in space even though the starting position varies from trial to trial. Furthermore, spindle settings often may be changed before the servo loop has completed its operation. Thus, at the level of programming there could be a great deal of stereotypy in the sense of spindle settings, but the actual movement could exhibit much variability on different occasions.

A very similar point has been made by MacNeilage (1970) and Sussman (1972) regarding speech production. The same phoneme is acoustically different in the context of different surrounding phonemes. Moreover, the required movement for the tongue to reach a position desired for the production of a particular phoneme depends on the tongue's preceding position, which is, of course, different for different preceding phonemes. Must the brain store a motor program for every combination of phonemes? MacNeilage and Sussman propose

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instead that muscle spindles, not movements, are programmed and the movement is reflexively driven by the spindle system. Thus, the programming is context free even though the output varies with context. A servo system would, therefore, offer some economy in the flexibility of programming.

At this point the question may be raised whether follow-up servo theory is not the same as S-R chaining theory and whether it has not already been discounted by deafferentation studies. The two theories are, in fact, quite different. In S-R chaining theory, one movement is stimulated by the feedback from a preceding movement. If feedback from the preceding movement is eliminated or the preceding movement is eliminated altogether, the chain is broken. The studies of Fentress on mouse grooming and Nottebohm on birdsong discount S-R chaining theory because the remainder of a sequence is not broken when parts of a sequence are lost. With follow-up servo theory, however, the movement is centrally programmed and does not require feedback from a prior movement; it only requires feedback from the muscle spindles associated with the current movement.

The deafferentation studies of Taub and Berman and of Foerster pose greater problems for follow-up servo theory. If there are no spindle connections from an intact limb into the spinal cord and onto the alpha motoneurons (i.e., if the dorsal roots are cut), then no coordinated movement should occur. Coordinated movement does occur, however, seemingly rejecting servo theory. It is worthwhile to recall, though, that deafferentation has more serious consequences for fine movements than gross ones. Perhaps servo mechanisms are more important the finer the degree of movement control such as by hand or tongue. This issue will be returned to shortly.

Alpha-gamma coactivation theory bears some similarity to follow-up servo theory, but in principle it accommodates movement following deafferentation. In this theory, the two efferent systems are programmed in parallel. The motor program sends commands via the alpha route to activate the main muscles in the desired sequence and via the gamma system to activate the muscle spindles. Matthews (1964) and Phillips (1969) propose that this parallel system allows rapid error corrections but at the same time avoids extra starting time for movements entailed by follow-up servo theories.

Suppose, to simplify the argument, the motor program stimulates the muscle spindle via the gamma system to exactly compensate for movement of the main muscle. As the extrafusal fibers of the main muscle contract and shorten, they tend to release tension on the stretch receptor, but simultaneously the gamma system activates the intrafusal fiber counteracting the influence of the main muscle. When the two systems exactly counterbalance, no change will occur in receptor stretch and consequently the receptor discharge will remain constant. If, however, the moving limb encounters an unexpected force, the extrafusal fiber will not contract as much as it should, because extrafusal fibers are

connected to the bones and if the bones are prevented from moving, the extrafusal fibers are prevented from contracting. The intrafusal fiber, not being connected to the impeded bone structure, will continue contracting as programmed. The balance of forces on the stretch receptor will be lost and it will stretch, increasing in discharge and signaling that an unexpected impediment occurred. Because feedback returns to the alpha system it can act reflexively at either the spinal level or higher brain levels to boost input to the alpha motoneurons and overcome the unexpected impediment. Marsden *et al.* (1972) found corrective responses, presumably dependent on stretch receptors, to occur in human thumb movement about 50 msec following an unexpected force. At the same time Evarts and Tanji (1974) have shown that the reflex is capable of presetting so that an unexpected force can be countered with either a push or a pull, depending on prior instruction. This suggests that corrective action occurs at brain levels or brain functions can preset spinal reflexes by descending control.

Thus, alpha-gamma coactivation preserves some of the advantage of follow-up servo theory. It has a mechanism for fast compensation to unexpected forces, driving the limb by a servo mechanism to the desired position. But because alpha motoneurons are independently programmed, sequencing of movements can still occur following deafferentation, though the error correction capability would be lost.

B. Evidence Discriminating between the Two Theories

Both follow-up servo theory and alpha-gamma coactivation theory posit active programming of the spindle system predicting that spindle output should either increase or at least remain constant during active movement. If, on the other hand, the spindle receptor only responds passively to stretch of the main muscles, and is not itself programmed, the spindle output should decrease as the main muscles contract and reduce the stretch. One suitable preparation for studying whether spindle output increases, stays constant, or decreases during active movement is the intercostal muscles involved in breathing. The intercostal muscles are useful because a regular movement pattern is maintained even when the animal is anesthetized and immobilized. Von Euler (1965) found in cats that as the intercostal muscles contract, forcing air out of the lungs, firing rate from the muscle spindles increases, as predicted by active programming of the muscle spindles. Moreover, if during the course of breathing an unexpected load is placed on the intercostal muscles by temporarily occluding the windpipe and creating a partial vacuum to retard further muscle contraction, the spindle output is increased even further. This increased output to unexpected loads is exactly the sort of error correction expected by either theory.

A very similar phenomenon was observed by Taylor and Cody (1974) for

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movements of the jaw in licking and eating by cats. Whereas spindle output varied as a function of main muscle stretch during passive jaw movements, spindle output remained practically constant during self-generated licking, indicating active programming of the muscle spindle. The fact that output remained constant supports alpha-gamma coactivation.

A necessary implication of follow-up servo theory is that the gamma system must become active before the alpha system and the main muscles, since the alpha system is activated by the feedback from the gamma loop. Historically, studies indicated that the gamma system leads the alpha system but those studies involved animals under deep anesthesia. Apparently anesthesia can alter the time relationships of alpha and gamma. Phillips (1969) with his colleagues Koeze and Sheridan studied muscle responses from the hand of the baboon under light anesthesia that more closely approximates the normal state. They elicited the muscle responses by electrical pulses to the cortex and observed the onset times of the electromyographic response from the muscle and the discharge from muscle spindles recorded at the dorsal roots. Under some conditions they found spindle discharge to increase during muscle contraction. As with Euler's study of breathing movements and Taylor and Cody's study of jaw movements, this finding indicates active programming of the muscle spindles, since muscle contraction by itself would lead to a decrease in spindle output. In addition, the spindle discharge in some circumstances occurred at the same time as or followed the muscle response, indicating that the gamma system is not activated early enough for its discharge to feedback on and start the main muscles. This study therefore rules out follow-up servo theory and supports the theory of alpha-gamma coactivation.

Even more convincing evidence comes from a study by Vallbo (1971) of voluntary muscle contractions by people. He inserted an electrode into the median nerve of the arm and located responses from a single afferent fiber from a muscle spindle. Subjects in the experiment were then asked either to flex a finger for 2 or more seconds or twitch the finger. In either case a large proportion of spindle responses followed, rather than preceded, activation of the muscle underlying finger movement. Again this supports alpha-gamma coactivation theory.

The studies of the activation and timing of the spindle system are, therefore, consistent with deafferentation studies. Some movements are programmable directly through the alpha system to the main muscles without feedback from the spindle system. Some cautions are worth holding in mind, however. Neither Phillips' study of the baboon hand nor Vallbo's study of finger movement, the two studies most critical for differentiating the two theories, involved sequential movement skills. All they demonstrated is that movements can start without a follow-up servo mechanism, but they have little to say about whether terminal movement points are also programmed through the alpha system. There is some

provocative evidence that the gamma system or other feedback sources are more directly involved in finely controlled movements after they have started.

Smith *et al.* (1972) attempted to selectively anesthetize gamma fibers by injecting Xylocaine in the radial nerve. The gamma fibers are small in diameter compared to alpha fibers. Under the right dosage, the small fibers appear blocked, since hot and cold stimulation which also involves small fibers is not perceived. At the same time, strength and tactile sensations subserved by large fibers are normal. This suggests that alpha fibers are also intact. In one task following selective blocking of small fibers, subjects were asked to rapidly touch their noses. Normally one observes a slight pause just before touching the nose, but people with gamma blocking failed to stop their fingers on the first couple of tries and instead forcefully hit their cheeks or mouths, as though the feedback was needed for stopping the movement. Although they were soon able to overcome this failure to stop, the results raise the possibility that the gamma system is normally involved in terminating movements. Other interpretations, such as some motor impairment, are possible, however.

Evidence of a similar sort comes from Bizzi's studies (1974) of eye and head movements in monkeys. Normally when a spot of light comes on in the periphery of the visual field, the eyes make a saccadic jump to fixate on the spot. Very soon after the eyes begin moving, the head also begins to turn toward the source; as the head rotates, the eyes make a compensatory back turn in the sockets. Eventually the head is pointing at the spot, and the eyes are again pointing straight ahead in their sockets. When vestibular feedback was surgically interrupted, eye and head movements were both initiated but compensatory eye movement failed to occur; apparently that final phase of compensatory movement was reflex controlled. With several weeks of training, compensatory movement did recover, perhaps then under complete central control. Like Smith *et al.*, Bizzi appears to have uncovered a movement sequence that is initiated by program, but the termination normally is partly under feedback control, in this case vestibular feedback.

A final behavioral study is of interest in this context. Stelmach *et al.* (1975) required people to rapidly move a slider to a position along a track, remove their arm momentarily, and then recall the same ending location by moving from a different starting position. In one condition the first movement of the pair was determined by the subject himself. Since the movement was rapid, the subject presumably selected the stopping location prior to beginning the movement. In two other conditions, the subject's hand was either passively moved to a location matched to positions in the preselection case or the subject actively moved until hitting a stop at the location. In neither of the latter cases did the subject know in advance where he would stop. At the final stopping position, subjects in all conditions held position for 2 sec. Despite this end pause, preselection subjects were more accurate in reproducing the location. Why?

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There are perhaps several possibilities, but an intriguing one is that only the preselection condition allows advance programming of the movement. But programming of movement distance is not possible in this situation since the subjects reproduce location. Perhaps it is the muscle spindles that are set for a final location and are remembered during reproduction. If so, then the finding would constitute evidence that spindles are intimately involved in precise movement termination.

Although the bulk of evidence supports a motor programming theory involving alpha-gamma coactivation, these latter studies, while far from conclusive, raise the possibility that a hybrid between the coactivation and follow-up servo mechanisms might be involved. Perhaps the alpha system conveys programs for the initiation of movements and even their rough termination. Parallel with the initiation of movements through the alpha route, spindles may be coactivated. While they may not be necessary for starting the movement, they may come into play, as supposed by follow-up servo theory, in finely graded movement termination. Again, the fusimotor system may not be absolutely necessary for ending movements, but it may aid such termination and make it more precise. Coactivation theory, in contrast, gives the gamma system a role only in correcting errors and not in the normal stopping of movement. Such a hybrid system would include all the advantages of the follow-up servo theory, including partial explanation of context dependent variations in movement, but also would be consistent with rapid starting of movements, the persistence of movements following deafferentation, and coactivation of alpha and gamma. Such a hybrid model is similar to a servo-assisted model proposed by Merton (1972) but is only speculative at this time as evidence is suggestive but definitely not conclusive.

The main conclusion to draw at this point is that at least some skills appear under motor program control. Some skills are directly programmed through the alpha route, but subsidiary programming may also occur through the gamma route resulting in more precise movement termination. Yet other skills may not be under program control. Thus, we do not know whether finer skills or skills performed by distal elements such as the fingers are programmed, since they are disrupted more by loss of feedback; they could be programmed, but feedback is needed for more frequent correction, or feedback may actually be needed for initiating movements as supposed by S-R chaining or closed-loop conceptions of skill.

C. General Functions of Feedback

At this point it is useful to broaden the discussion to other feedback sources to gain a fuller perspective on the interaction between program and feedback in skill development and maintenance. A very instructive skill for this perspective is birdsong. Bird species that have been most useful in studying skill development

are ones exhibiting some flexibility in song development such as the Oregon Junco, White-crowned Sparrow, and European Chaffinch. In normal development young birds are exposed to adult singing in about the first 4 months of life and begin to sing themselves at about 10 months of age. Nottebohm (1970) and others report that the young nestling can be exposed to adult song either in nature or in the laboratory in those first 4 months, and even when isolated for the remaining months, it will learn the proper dialect. In contrast, birds that are not exposed at all to the adult song learn only a rudimentary version. The young birds must, therefore, store in memory a template of the auditory sound pattern in order to subsequently learn the song.

Building on preliminary observations of this type, Konishi (1965) exposed young birds to adult song so that a template was stored. Some birds were then deafened prior to learning to sing themselves. Their subsequent song development was even more impaired than for birds never exposed to an adult song, but at least able to hear themselves. On the other hand, if deafening was delayed until the song was firmly established, the song remained remarkably stable. Konishi found the song of one White-crowned Sparrow to persist very well for at least 18 months after deafening.

The model of skill learning and maintenance that emerges both from the studies of birdsong and the numerous studies underlying the motor program concept is illustrated in Figure 2. One component of the skill is a template or

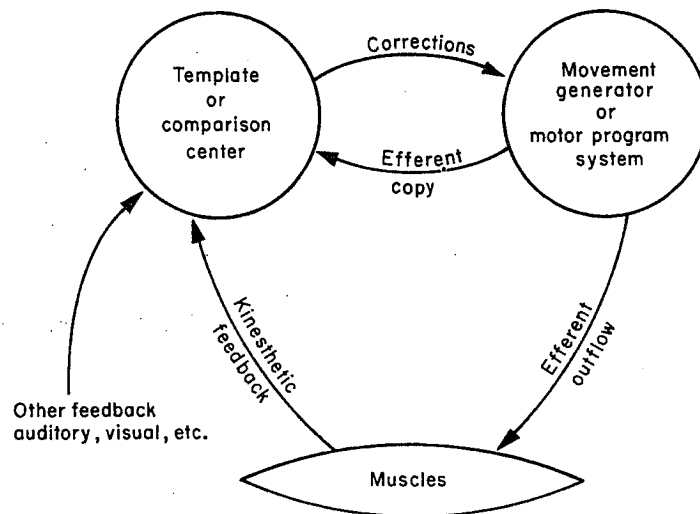


Figure 2 A model of skill learning and a mechanism for the detection and correction of errors.

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model of how the feedback should appear if the skill is properly performed. In birdsong an auditory template is emphasized, but conceptually in other cases a template could as well include visual and kinesthetic components.³ A motor program center generates a series of movements via efferent outflow to the muscles. The movements generate kinesthetic feedback from the limbs and the movements have a variety of other sensory consequences—auditory, visual, and vestibular—depending on the skill. The feedback is then matched to the template, and any resultant error leads to correction of the motor program. Eventually the program will emit an appropriate series of movements, and the program with further practice becomes stabilized.

This model of skill learning is similar in many respects to a theory of Adams (1971). In Adams' theory, feedback is also compared to a template of ideal feedback established during training, and deviations of current feedback from the template are the basis for corrections.

If the environment in which a skill is performed is very stable or predictable, the feedback loop can be cut and the skill can be maintained by the program. With birds, once the song is well learned the auditory feedback can be eliminated (Konishi, 1965) and at least parts of the kinesthetic feedback can be eliminated (Nottebohm, 1970) with little or no song impairment. If the skill is robust it may still be fairly well maintained with greatly impoverished feedback even in a varying environment. Monkeys, for example, walk on four legs, a relatively stable stance, so that the skill persists rather well following deafferentation and blindfolding.

For many human skills, however, the environment is less than perfectly predictable and the skill itself may be imperfectly executed so that error constantly arises. Feedback cannot then be eliminated; it is continually needed for monitoring the movement to ensure that performance is progressing as planned and for updating or changing programs as needed (Pew, 1974). But in the absence of a need for correction, the feedback does not stimulate the succeeding movement as posited by S-R chaining theory. The model in Figure 2 thus presents a combination of closed-loop and open-loop capability.

Many people have noted a tremendous difference between the highly stereotyped skills of birdsong and walking by monkeys and the great degree of flexibility of human skill. Human skills seldom are executed in exactly the same way twice. The movement can be large or small—one's handwriting on the blackboard is similar to handwriting with paper and pencil despite enormous differences in the muscles involved—there are differences in speed, exact sequencing, orientation, and so on. Although these observations pose as yet unsolved

³ There may be important properties of an auditory template, however, and that is an idea well worth exploring in skill learning. Auditory patterns coupled with movement patterns permits real time feedback, and audition may be better than vision for displaying temporal patterns.

problems for understanding skills, they are not necessarily inconsistent with motor program theory; the theory as specified just does not go far enough for a complete understanding of these problems. The problems posed for S-R chaining are more serious. When the actual muscles involved dramatically change from one performance of a skill to another, the feedback is also changed. Previously unexperienced feedback patterns should result in skill breakdown, since that feedback would not be conditioned to the next response. Motor program theory stripped to its essentials, in contrast, merely proposes that the sequencing of movements is centrally generated and does not directly depend on prior feedback for its execution. Exactly how the sequencing is determined is unspecified.

Some conceptual advances in understanding the knotty problem of skill variation have been made by Pew (1974) and Schmidt (1975). Both have suggested that motor programs do not directly specify either a series of specific muscle movements or expectations for particular feedback. Rather they are best viewed as a schema of possible movements and expected feedback. In the context of a particular situation, parameters such as speed, size, orientation, and so on are applied to the schema to generate a particular sequence of movement. At the same time the schema generates a set of expected feedback consequences (the template) that should arise if the skill is performed as specified. Schmidt (1975) has fleshed out many details of a schema conception of motor programs. For the present chapter, however, it is sufficient to view a motor program as a central representation of a motor sequence that can in the absence of error be initiated and carried out without subsequent stimulation from kinesthetic feedback. At this simplistic level, the model portrayed in Figure 2 has implications for skill learning, and it raises various psychological issues regarding the nature of representation.

D. Implications for Skill Learning

Loop films and video feedback have both been heavily investigated as aids to skill learning. With loop films, the technique of a highly skilled performer is shown many times to a learner. The learner then tries to copy the performance of the model. Video feedback involves the use of movies or video tape recordings to play back the learner's own performance so that he can observe the errors he has made and presumably correct them. It appears fair to say that neither technique has proved highly useful in skill training. Brumbach (1969) reviewed 31 studies that used one or the other technique as a teaching aid. Of those only 10 indicated that films were helpful, but as Brumbach pointed out, 5 of those 10 studies had serious problems such as no data shown, no statistical tests, etc. Three of the remaining five had mixed results favoring the use of films.

One possible reason for such a dismal failure is that most studies used only loop films and a few used only video feedback. Only 4 of the 31 studies used

both techniques. The advantage of film for learning shows up in learning. One when the skill feedback generated by the film provides

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both techniques together and 3 of those 4 were among the studies showing an advantage of film techniques over control training procedures. The model of skill learning shown in Figure 2 indicates two general components involved in skill learning. One is the template, i.e., memory for what the feedback should be like when the skill is properly performed. The other component is the actual feedback generated from execution of the motor program. Learning with a loop film provides a template but inadequate feedback to complete the learning loop. Since people have a difficult time visualizing the movements of their body, the situation is not unlike a bird with an auditory template but deaf so that it is unable to compare its own performance to the template. Learning with only video feedback presents the opposite problem; there is an inadequate model for comparison with the feedback. Figure 2 suggests that the most effective skill learning requires a careful match of the feedback provided to the template stored. Usually no emphasis is given to the quality of the match between two sources of information, and this principle might be useful in investigating training procedures.

Although feedback is an essential component of skill learning, sometimes portions of the feedback can be dropped once they have served the role of establishing the proper movement sequence. In birdsong auditory feedback is critical during learning but not essential once the movement pattern is well established. This implication is quite different than would be expected from strictly closed-loop theories of skill such as S-R chaining.

In cases where natural sources of feedback are impoverished, therefore, it may prove useful to temporarily provide artificial feedback merely for purposes of learning. For example, movements in some skills could be coupled to sound transducers to provide an auditory sound pattern that varies with the movement and that can be compared with sound patterns produced by experts. Once the skill is learned, the auditory feedback can be dropped. A possible advantage of this technique is that auditory feedback can be provided in real time whereas video feedback often can be provided only after the skill is performed. The auditory feedback may also provide the learner with a greater appreciation of the temporal aspects of the skill.

Two research programs on speech production attempted to exploit the possible benefit of feedback substitution in cases where natural feedback is inadequate. One involved learning a foreign language and the other, still in progress, involves speech training in the deaf.

A prevalent problem in learning a second language is that some important sound distinctions in the new language are difficult to perceive, and this handicap impairs pronunciation learning. To help overcome the problem, Kalikow and Rollins (1973) and Kalikow (1974) extracted various acoustic features and throat vibrations from spoken words and visually displayed transformations of them on an oscilloscope screen. In Mandarin Chinese, the tone

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quality arising from variations in the fundamental voice frequency is a determinant of meaning. Contours of the fundamental frequency as it changes within a syllabic or multisyllabic utterance can be displayed on the scope. By presenting transformations of a teacher's utterance and a student's utterance next to each other, the student receives cues on how to improve pronunciation. Kalikow found in comparison to control groups without the aids that the visual system modestly improved pronunciation of both Mandarin Chinese by native English speakers and English by Spanish speakers. Unfortunately, with the current development of the system it is not yet clear that the modest improvement is worthwhile from either economic or student-time viewpoints.

Nearly the same system is being explored by Nickerson and Stevens (1973) to train the deaf to speak. Again, visual displays present transformations of the learner's speech to be compared with a model. As yet, results from this project are not available. Nonetheless, in view of the modest success with second language learning, better achievement might be expected with the deaf, since their natural feedback from speaking is even more impoverished.

An implication of S-R theory is that the skill must be executed for learning to occur, for only in that way will kinesthetic feedback be available for conditioning to succeeding movements. Figure 2 suggests instead that important components of the skill may be learned without actual movement production. One component is an accurate template of desired feedback. As with birdsong, sometimes the template may be established prior to learning movements. This may be the procedure underlying the outstanding success of the Suzuki method of violin teaching (Pronko, 1969). In the Suzuki method very young children are exposed to selected pieces of music, sometimes for months or years, prior to actually handling an instrument. Perhaps the detailed music templates that the children store in memory allow them to subsequently recognize errors in their own sound production and later the sequencing of movements that lead to the sound.

✓ Besides storing a template without actual movement, it also may be possible to store part of the motor program itself. Mental practice is known to improve performance on many skills (e.g., Lawther, 1968). What is the explanation? A central element of motor program theory, is that it represents sequences of successive movements. Any skill in which sequencing is a major component might be helped by mentally rehearsing the sequence of environmental events or required movements until the sequence is firmly stored in the memory system. Summers (1973) tested this idea in a study consisting primarily of responding as rapidly as possible to events that tend to occur in sequential order. Rehearsal of the event order was effective even when movements were not used until later in the task.

Motor program theory suggests several ways, therefore, in which skill training might be improved. It suggests that the quality of the match between feedback

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and model is critical. It suggests that temporary provision of artificial feedback may be useful, particularly when it can be matched with a comparable model. In some instances the establishment of feedback templates prior to actual movement practice may be beneficial. In other circumstances, mental rehearsal of the sequence of events may be useful.

III. Memory Structures of Motor Programs

Granted that movement sequences in skills often are centrally represented, how do we conceptualize the memory structure? Is the program a chain of associations between central representations of the movements or are successive movements associated not one with the other but with positions in a more abstract structure? For movement sequences exhibiting a high order of regularity, are the movements stored in the form of generative rules? We would also like to know how the timing of motor skills is meshed with the sequence representation. These are the issues addressed in this final section.

A. Simple Movement Structures

One approach to the problem of representation was investigated by Keele (1975). To capture in abstract form the sequential property of many skills, a task was developed in which sequencing was the primary component. There were eight lights in a horizontal line and beneath the lights was a row of response keys, one key for each light. When a light appeared, the subject pressed the corresponding key, extinguishing the light. Another light requiring a response then came on, and so on. During the initial training the lights appeared in a recurring order. If the lights are designated 1 through 8 from left to right, the order of occurrence for all subjects was 18347562 after which it cycled back to 1 with no break. This task is much like playing a piano or typing with the exceptions that it is simpler, very easy to learn, and cycles repetitively through the sequence much as does walking. Within a half-hour subjects can execute the series at rapid speeds.

Once the skill is well imprinted in memory, how is it represented? Two possibilities were compared by examining response times when the proper order of events was momentarily disrupted and then restarted. One possible representation, event-to-event associations, posits that successive movements are associated with each other. The other hypothesis, event-to-position associations, posits that movements are not associated one with the other but with positions in the sequence.

To obtain a better idea what these hypotheses mean, consider the experimental situation. Suppose a subject is presented sequentially with lights 3475,

1 8 3 4 7 5 6 2 . . .	Normal sequence
1 8 3 4 7 5 <u>8</u> . . .	The last event 8 is out of order
1 8 3 4 7 5 8 <u>3</u> . . .	Event association (3 normally follows 8)
1 8 3 4 7 5 8 <u>2</u> . . .	Position association (2 is in its normal position)

Figure 3 Examples of restarting a sequence of events following an out-of-order event for subjects assigned to the Event Association group and for subjects assigned to the Position Association group.

which are in correct order, and the next light is out of order and is light 8 (recall that the complete correct sequence is 18347562; see Figure 3). Because light 8 is unexpected, people are slow in responding to it. Now there are at least two interesting ways for the sequence to restart following an unexpected event. In the one case the very next light is 3, the one that normally follows light 8. The hypothetical sequence then is 3475834 . . . and so on till the next out of order event. In the second case, light 2 follows 8, so the hypothetical sequence would be 3475821 . . . until the next light out of order. The unexpected event 8 replaces the expected event 6 but subsequent events occur in their proper positions. Light 2 is normally the second light after 5 regardless of which light intervened. In the first case, therefore, an event is predictable by the preceding event, even though the preceding event itself may be out of order. In the second case, an event is predictable by the position in sequence regardless of what the preceding event was.

The issue, of course, is how well people can respond to the first event back in sequence. If the return to sequence is predicted by events, then people should respond rapidly to the first event back in sequence only if the memory structure consists of event-to-event associations. On the other hand, if the return is predicted by position, people should do well only if the memory structure consists of event-to-position associations.

People in the experiment received training on the cyclical sequence until they could respond rapidly and the skill presumably was well set in memory. On the next day the task remained about the same, but people were told that 20% of the lights would be out of the expected order, and following such an intrusion the sequence would restart. For half the people the event succeeding an out of order one was predicted by the identity of the out of order event. For the other half, the event succeeding the out of order one was predicted by the position in the sequence. An additional variable was the interval between one response and the next light. With a relatively long interval (1500 msec RSI), allowing ample time for anticipation of the following light, it was expected that people could effectively use either type of sequence return. But at short response-stimulus intervals (50 msec RSI) people might experience difficulty in using one type or the other of sequence return.

Reaction times are shown in Figure 4 for unexpected lights, designated the 0 position in the sequence, and for the first, second, third, and fourth lights back in sequence. Although people in the position condition respond slightly faster on the average when a long RSI allows ample time for preparation, they are slower than event condition subjects at the short RSI. In other words, when the subjects are pressed for time, they are unable to effectively use position information, but use of event information suffers little. The improvement in reaction time from the unexpected event to the first back in sequence is a measure of preparation for the succeeding event. At the long RSI both conditions show an improvement on the order of 160 msec. However, at the short RSI, when spare time is not available, people in the event condition again show a large improvement but people in the position condition show very little improvement. The modest improvement that does occur in the latter case is probably in part an artifact: If two successive unexpected events occur, the second one is usually responded to faster than the first as though the unexpected is no longer surprising. When time is short, an event predictable by position is little or no better, therefore, than another unpredictable event.

Our results suggest that in some skills a sequence of events and their corresponding movements are stored in a chain of event-to-event associations. This conclusion is very much in line with the theoretical position of Wickelgren (1969), though he was primarily concerned with the phonetic representation of words. A classic paper by Lashley (1951) suggested in contrast that the memory structure of serial order is independent of the actual events that fit into the

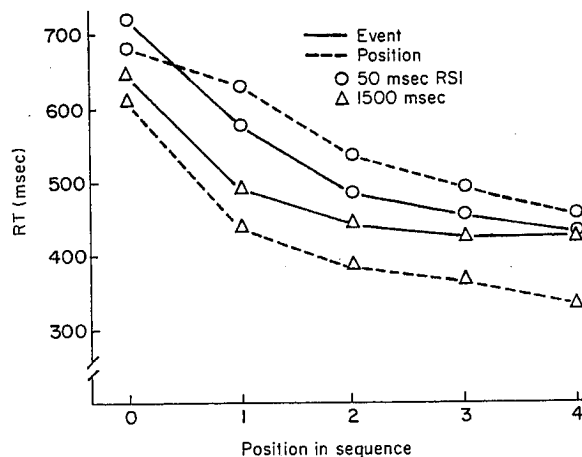


Figure 4 Mean reaction time to correct responses for out-of-sequence events (○) and the first, second, third, and fourth events back in sequence. The interval between a response and the next stimulus is short (50 msec) or long (1000 msec).

structure. A position structure of the sort investigated in this study would be an example of a structure other than event associations but by no means the only possible one. According to the position conception, the skill is represented as a number of slots, one for each movement. As the skill progresses, one slot after the other is examined for content, and the event or movement contained in the slot is prepared for. Preparation for a movement depends not on the preceding event but only on the current position. A position stepping structure is not supported by this experiment, but in other skills with structural regularities, a representation that is neither event associations or purely position associations may be indicated. This point will be returned to later.

The preceding experiment does not support the position hypothesis as outlined, but with other assumptions the position theory might be accommodated to the data. For example, when an unexpected event occurs, a position marker might skip forward in the sequence until the position of the unexpected event is found. According to this view a position hypothesis would make the same prediction as the event association hypothesis for the preceding data. The next experiment dealing with repeated elements was therefore designed as a further test between the two theories.

A conceptual problem faced by the event-to-event hypothesis concerns repeated elements. If the identical movement occurs at more than one place in a movement sequence, and each time it is followed by a different movement, then how are simple one-to-one associations able to determine what movement should follow the repeated one? In typing, if the letter H follows the letter T in one position and E follows T in another position, how does the typist know whether to type H or E following a T if only event associations are used. Associational hypotheses might be elaborated in several ways to handle this problem. Wickelgren (1969), for example, proposed that seemingly identical elements in different portions of a sequence in fact are not identical and differ slightly depending on their surrounding movements.⁴ Nevertheless, repeated elements, even though partially differentiated by context, should be more similar to each other than to other elements. While repeated elements in a sequence do not destroy the sequencing, they should constitute weak links in the associational chain. In structural models such as Lashley's, however, there should be no particular problem deciding which movement should follow the repeated one, for there are no event-to-event associations.

Wickelgren (1966) investigated the issue of repetition in short-term memory for lists of nine letters. In some lists, a letter was repeated twice and followed by a different letter in each case. During recall when an error was made on an item

⁴It may be noted that this explanation partially answers the problem mentioned earlier that the same movement varies with context. According to Wickelgren, movements that are conceptually the same may actually be represented differently if they occur in different contexts.

1 4 3 6 4 5 4 2 . . .	Normal sequence
1 4 3 6 4 5 4 <u>3</u> . . .	Out-of-order associated event
1 4 3 6 4 5 4 <u>6</u> . . .	Out-of-order unassociated event
1 4 3 6 4 5 <u>3</u> . . .	Out-of-order control (doesn't follow repeated event)

Figure 5 Examples of different types of out-of-order events in the repeated event experiment.

following a repeated item that error was often an intrusion of the item that followed the repeated one at the other place in the list. Such associative intrusions were more common than in control lists without repeated elements. These results are consistent with an event-to-event associative model.

Short-term memory may be rather different than well learned skills, however, so we explored the repeated elements problem in our skills paradigm.⁵ Six lights and six response keys were used instead of eight as in the earlier experiment. In this case, however, one of the lights occurred three places in a sequence, each time followed by a different light, so the total event sequence was eight in length. As before, the sequence recycled after the last item. The order of lights was different for each of 12 subjects, but all sequences obeyed the same structure. An example of one sequence is 14364542. . . Each subject practiced on the fixed sequence over 400 cycles in one session. During the second session, when all subjects were quite proficient on the task, 30% of the lights were out of order and the remaining lights occurred as expected in the learned sequence.

Of particular interest are the reaction times and errors to the out of sequence lights, and they were classified into three types as illustrated in Figure 5. On some occasions the repeated light occurred in its proper order but was followed by an out-of-order light. If the out-of-order light normally followed the repeated event at another place in the sequence it was called an associated light. Thus, for the illustrative sequence, if 14364 is followed by 3 or by 2, then 3 and 2 are associated events. If a repeated light is followed by one that normally does not follow the repetition in any position (lights 1 and 6 in the illustration sequence), it was called an unassociated event. Finally, any out-of-order light following a nonrepeated light is a control. If Wickelgren's (1969) associative hypothesis is correct, out-of-order but associated lights should result in faster reaction times and fewer errors than either unassociated or control lights, since occurrence of the repeated light should elicit all of its associates.

The reaction times and proportion of errors to the three types of out-of-order events are shown in Table I. The results conform to expectations, but statistically not all of them are significant. The associated events were faster than

⁵ This experiment is not published elsewhere.

Table I
Mean Reaction Times (msec) and Proportion of
Errors for Out-of-Order Events

	Associated	Unassociated	Control
RT	506	516	532
Error	0.095	0.112	0.144

control events for all 12 subjects ($p < .01$) and more accurate for 9 subjects, with 2 ties and 1 reversal ($p < .05$). Although 8 of 12 subjects show faster reaction times and greater accuracy for associated than for unassociated events, these two comparisons are not significant. Examination of the table shows, however, that unassociated events are faster and less error prone than control events. Why would that be since both are controls in the sense that neither is associated with a repeated event? One possibility is that events following the repeated one are relatively ambiguous and hence are not strongly prepared for. In the absence of a strong expectation, any out-of-sequence event following a repeated light tends to be responded to faster than out-of-sequence events following nonrepeated lights, although associated events are responded to fastest of all. This tentative explanation is consistent with the Wickelgren hypothesis that repeated elements produce weak links in the associative chain.

To check the explanation, the data were analyzed from the first session in which the subjects responded as rapidly as they could to lights that always occurred in their proper order. If the linkage between a repeated event and ensuing events is rather weak, because of associative ambiguity, those events should be responded to rather slowly or with high errors. The relevant data are shown in Table II. Although reaction times do not differ among event types, errors do differ. As predicted, 9 of 12 subjects exhibited higher error rates for events following repeated events than for controls ($p < .05$). When these data are put together with the earlier data there is sufficient consistency to conclude that a repeated event elicits associations of all the events that follow it in different positions.

This second experiment using a somewhat different method supports the conclusion of the first experiment that some skills are represented in memory as associations between successive movements or events. The particular skills studied in the two experiments are of a particular type, however. They have no inherent structure other than linear ordering of events. Thus, we have mainly shown that for unstructured sequences of eight or nine events a position representation is not adopted and instead event-to-event associations are formed. This outcome might have been expected from general memory theory and observations of absolute judgments (Keele, 1973; Miller, 1956). When the number of events exceed about half a dozen there are too many for strict position recall, since that involves only one level or one dimension of organiza-

Table II
Mean Reaction time (msec) and Average Number
of Errors per Subject to Different Event Types

	Next event following repeated event	Repeated events	Control events
RT	267	265	270
Errors	3.45	2.83	1.33

tion. Instead they are recalled in a highly structured manner. If the events are quite unrelated to one another, associations between successive events are likely to be used. But when some other basis exists for categorizing events, recall is structured around categories or in a hierarchical organization (e.g., Mandler, 1967; Nelson and Smith, 1972). The issue arises, therefore, whether movement sequences with a possible structural basis other than linear positions lead to storage modes other than event-to-event associations.

B. Higher Order Structures

The issue of higher order structure in skills was investigated by Restle and Burnside (1972) using a procedure very similar to our own. Six buttons were placed beneath a six-light display. Lights came on every 0.7 sec and subjects tried to execute the corresponding button responses coincident with light onsets. Responses preceding or following the light by 0.3 sec were defined as correct and others were errors. In this paradigm the data of major interest are errors, whereas in our experiments reaction time was of major interest. Points of transition from correct responses to errors should give hints about the structure in memory.

In one study by Restle and Burnside, sequences of 16 lights were used. An example is 1234666662323543. After the last light the sequence recycled with no break. This sequence is composed of a run (1234), a reverse run (543), repetitions (66666), and a trill (232). Subjects watched the pattern of lights until they felt they had learned it and then began responding. The issue, of course, is whether the structure influences performance.

High error rates were produced to the last 6 in the repetitions (the error was often 2, anticipation of the next subsequence), to the first 2 in the trill (the error was often 6, a repetition overrun), and to the 5 in the reverse run. Following the first run of 1234, a common error was to make response 5. Quite clearly, therefore, subjects used the organization inherent in the list for structuring their own performance. If the beginning part of the sequence is a run, subjects apparently apply the rule, "generate a run beginning with 1." When the

stopping point is forgotten, 5 is a likely error despite the fact that in the actual sequence it never follows 4 and hence should have no associative basis. Errors in general tend to occur at the beginning and end of units as though subjects had encoded a rule but forgot the termination point of one unit and the starting point of the next.

This first experiment by Restle and Burnside involved structured units but no higher level structure that relates units. In a second study they compared the sequence 123234345456654543432321 with the sequence 432456123654234321345543. The subunits of three elements are identical in the two cases but in the former case the units are also organized at a second level. Those people learning the more organized sequence made fewer errors in total, and they particularly made fewer errors at the transition between runs. As in studies of verbal memory, hierarchical structure appears to facilitate the learning process.

Lashley's conjecture that the representation of skills consists of structures into which events are placed appears, therefore, to be correct when movement sequences have permissible structures. When higher order rules or structures are present, they take precedence and override a mechanism based on sequential associations. In Restle's terminology a particular structure might be specified as: $M[T(R[T])]$ where M refers to mirror image, T refers to transposition, and R to repeat. Successive sets of parentheses denote successive levels in a hierarchy, i.e., at the lowest level transpositions occur; at the next higher level repeats occur; and so on. This particular structure stands apart from particular event assignments, as Lashley suggested. When the number of ordered events and the beginning elements are known, the rest of the events can be rule generated. Thus, if 6 lights are used, as in the Restle and Burnside study, and the first light is 1, then the rule application results in 1212232365655454. 1 is transposed to 2, the 2-element unit is repeated, the 4-element unit is transposed, and the 8-element unit is mirrored.

The conclusions regarding serial ordering of skills is very similar to conclusions regarding ordered memory for verbal materials. Serial lists of words apparently can consist in part of associations between successive events. Thus, some studies (e.g., Breckenridge and Dixon, 1970) found positive transfer from serial learning to paired associate learning when the pairs were constructed from successive words of the serial list. On the other hand, when more complex structures are available, people appear to use those rather than sequential association (Estes, 1972).

In everyday skills, event-to-event structures and higher order structures probably both exist. Many movement sequences have little or no repetition of elements and the elements are not spatially or otherwise related to each other except by direct association. The pattern of foot and hand movements in shifting an automobile may be such an example. On the other hand, musical skills almost certainly involve higher order rules. Even among lower animals,

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some skills may be rule governed rather than consisting solely of sequential associations. Fentress (1973b), in observing grooming patterns of mice, noted that the same component movement appeared in different grooming units. Nevertheless, the response to follow the repeated component was quite predictable by knowledge of the grooming unit in which the repetition was embedded. As seen earlier, an associative theory akin to Wickelgren's (1969) can handle the problem of repeated elements. Fentress noted in addition, however, that the unpredictability of a mouse's response was much greater near the beginning and end of units. This is reminiscent of Restle's observations, suggesting organization by units rather than strict sequential associations.

C. The Integration of Timing with Motor Programs

Almost all skills are finely timed as well as ordered. If a movement occurs in the correct order, but grossly out of time, the skill may completely fail. How is the timing integrated with the sequencing? The sequence representation and timing might be independent so that one program specifies sequencing and another attaches timing parameters as the sequence is unfolded. If so, then the same sequence could be readily executed with different time constraints. Alternatively, sequencing and timing might be integrated and inseparable.

Glencross (1973) observed handle cranking and noted that although different people cranked at different speeds, the relative time of different component movements remained rather constant. The duration of each component divided by the total cycle time was about the same for different people. Armstrong (1970) taught people patterns of lever movements. During reproduction from memory, relative timing of the different components of the pattern remained approximately constant although total time for the pattern varied. These results suggest that while overall speed is a parameter that can be attached to a motor program, the relative timing is part of the program itself. However, neither Glencross nor Armstrong instructed people to use different timing. Furthermore, the timing on those tasks may have been highly determined by mechanical constraints of the apparatus and limbs. A task is needed in which time constraints are arbitrarily imposed during training. Once the skill is well established, conditions are established in which the timing is no longer advantageous. In such a case does the learned timing persist?

Summers (1974) trained people to press the corresponding nine response keys to a repeating nine-light pattern. The sequence was different for each person, but an example is 591742683 and so on, repetitively. During a first session, subjects learned the sequence with no attempt to learn timing, but during the second session they were informed of the timing and attempted to learn it. For one group (551), the interval between one response and the next light was either 500 or 100 msec in the following rhythm: 500-500-100-500-500-100-

500-500-100 and so on.⁶ Thus, the 9-element event pattern is matched with a 9-element time pattern. Another group (511) had similar training except the time pattern involved a long pause and two shorts (500-100-100). There were also two control groups. One had a constant 300 msec interval between one response and the next signal. The other had randomly determined intervals of 100, 300, and 500 msec that changed on each run through the sequence.

By the end of the second session, subjects were able to both reproduce the event sequence and the time pattern even when the lights were turned off and the pattern had to be reproduced entirely from memory. The time patterns as produced from memory at the end of training are shown in Figure 6. Of interest later is that the short and long interresponse time, when reproduction is from memory, are in about a 2:1 ratio.

During the third session the instructions were changed. Subjects were told to respond as rapidly as possible while keeping errors to a minimum; timing was no longer important. The critical question is whether subjects can discard the slow portions of the timing pattern they were trained on in order to produce all elements of the sequence as rapidly as possible. The results are shown in Figure 7.

All groups do respond faster than previously, but the two groups trained with time patterns are still influenced by the pattern of training, particularly group 511. For that group the time structure remains slow-fast-fast, although the exact proportions are changed somewhat from training. The 551 group, though retaining some time structure, has departed from the slow-slow-fast structure of training to slow-medium-fast under speeded conditions. Moreover, when the data are analyzed separately for the first block and last block of 10 blocks of speed trials, the 511 group exhibits virtually no change in the time structure. The 551 group, however, changes from a clear time structure on the first block to a near flat function on the tenth block.

Apparently, in some instances, timing is an integral part of a motor program and cannot be entered independently of the sequencing. This is apparently true only for some time patterns, however; for other patterns the trained timing rapidly deteriorates.

D. Rhythm and Timing

Some insight into why the 511 group differed from the 551 group might be gathered from a consideration of rhythm. Earlier we concluded that unpatterned sequences of events are stored as event-to-event associations. However, when

⁶The response to stimulus intervals in Summer's study were 500 or 100 msec. When a normal reaction time to the stimuli is added to these response-stimulus intervals, the total response to response intervals are closer to 2:1 ratio than 5:1. This is important for a later discussion about rhythmicity.

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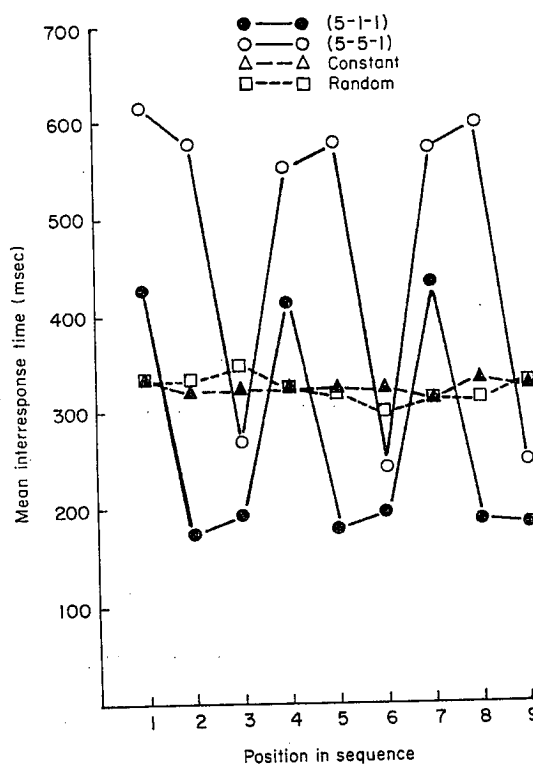


Figure 6 Mean interresponse times when the sequence and timing of responses are reproduced from memory.

events are organized into structures such as hierarchies, the sequence is much easier to learn and event-to-event associations are overridden. A similar issue arises for timing: Are some time patterns structurally simpler than others and hence easier to learn and more durable than others?

One structural basis for timing is rhythm. Martin (1972) suggests that rhythms are symmetrical, hierarchical structures of time patterns in which all the elements in the output occur at equal time intervals. Because it is hierarchical, the number of elements in a pattern must be a power of 2 if the hierarchical tree involves only binary branching. Martin only discusses binary branching, but rhythms could be based on more complex groupings such as powers of 3 (tertiary branching) or combinations with tertiary grouping at one level and binary branching at another. Groupings based on even larger elements such as 5 or 7 may be possible in principle but difficult for people to perceive or produce

in practice. The implication of this hierarchical notion is that if the number of events in a sequence is neither a power nor a multiple of 2 or 3, then blank elements must be inserted at appropriate points to make it appear rhythmic. For example, if there are 5 events in a repeating pattern, the sequence may not appear rhythmic unless 1, 3, or 4 blank time intervals are inserted to bring the number of elements including blanks to 6 (multiple of 3), to 8 (a power of 2), or 9 (a power of 3). Each element, including the blanks, would then occur at equal time intervals.

Now consider the 511 sequence used in Summers' experiment. Recall that when subjects produced the timing from memory, the ratio of slow to fast interresponse intervals was about 2:1. Furthermore, to be rhythmic each subelement of a sequence must fall at equal time intervals. The subsequence slow-fast-fast could then be viewed as a sequence of four elements: the slow interval is composed of two elements equal in length to each fast element. One subelement is identified with a sequence event and one is blank or a null event. For example, one portion of the sequence 591742683... in that experiment would become 5-blank-9-1, with each of the four resulting elements appearing at equal time intervals. Because the number of elements is 4, a power of 2, it is rhythmic.

The 551 timing in contrast is difficult to make rhythmic. If each slow element is composed of two subelements equal in length to the fast elements, producing,

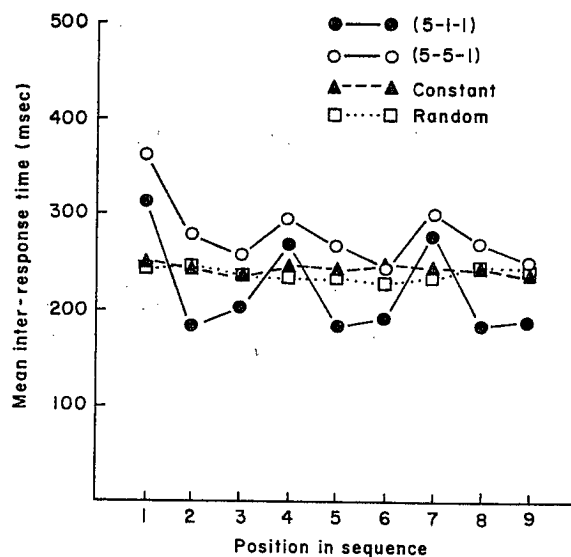


Figure 7 Mean interresponse time when people attempt to produce the sequence as rapidly as possible without regard to timing.

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for example, the subsequence 5-blank-9-blank-1, then there are a total of five elements which is neither a power nor a multiple of 2 or 3. If subjects attempt to make the slow elements three times as slow as the fast elements, producing 5-blank-blank-9-blank-blank-1, the result is still a poor rhythm.

Thus, the reason that the 551 timing may not persist as an integral part of the motor program is that structurally it is more awkward than the 511 timing.

This analysis of Summer's experiment is obviously *post hoc*. Unfortunately there appear to be few, if any, studies examining rhythm from a motor skills standpoint. A study that illustrates the role of rhythm in perception and immediate memory, however, was conducted by Sturges and Martin (1974). They presented either 7- or 8-item sequences of high and low tones at equal intervals per tone and at either 3.3/sec or 4.4/sec. Each sequence was either repeated, for a total of 14 or 16 equal interval tones, or a slightly different sequence was repeated, and subjects judged whether the sequences were the same or different. The 7-item sequences were constructed by deleting the last item from an 8-item sequence. From the earlier discussion it may be recalled that to be apparently rhythmic, a sequence must contain a number of elements that is a power or multiple of 2 or 3. Therefore, some of the 8-item sequences were rhythmic,⁷ but none of the 7-item sequences could be, at least by simple criteria of rhythmicity. The results demonstrated the rhythmic 8-item sequences to be judged more accurately than the shorter 7-item sequences. Furthermore, within 8-item sequences, rhythmic ones were judged more accurately than nonrhythmic ones.

Although the evidence is not as clear as it is for event structures, it appears that rhythmic time structures influence skills differently than arbitrary time patterns. When the timing is rhythmic, it may well be learned more easily, and it appears to become an integral part of the movement sequence and not easily divorced from the sequencing. Although the tempo can be altered, rhythm cannot. When the time structure is more arbitrary, on the other hand, it appears to have a more transient relationship with the sequencing, and it gradually becomes altered to a simpler structure such as constant time intervals.

IV. Summary

A major aspect of motor skills is the sequencing of movements, and this chapter is primarily concerned with the memorial representation of sequencing. An S-R chaining theory of sequence representation is inadequate to explain the

⁷In the Sturges and Martin study, the first and fifth items of rhythmic 8-item sequences were accented. In the nonrhythmic sequences, the accent fell on the first and fourth or first and sixth elements. Details of rhythm rules can be found in Martin (1972).

rich complexity of skilled performance. Some skills can be performed in the absence of kinesthetic feedback, suggesting a central representation. Even when feedback is intimately involved in movement, its role appears to be more of a monitor for detection and correction of errors than for stimulating subsequent movements. Many skills, therefore, appear represented in the central memory structure as a motor program, rather than as a peripheral-central S-R chain. This conception of skill, simple as it is, when combined with conceptions of the role of feedback, has potential implications for skill training.

The central representation (motor program) could be a chain of associations, though not involving peripheral feedback as stimuli. Although this representation appears to underlie movement sequences unstructured except for linear ordering of events, sequences with inherent structure appear to be stored as hierarchical structures or movement generating rules. The timing of events rather than being independent of sequencing appears to be an integral part of the motor program, particularly for rhythmic time structures.

Acknowledgments

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