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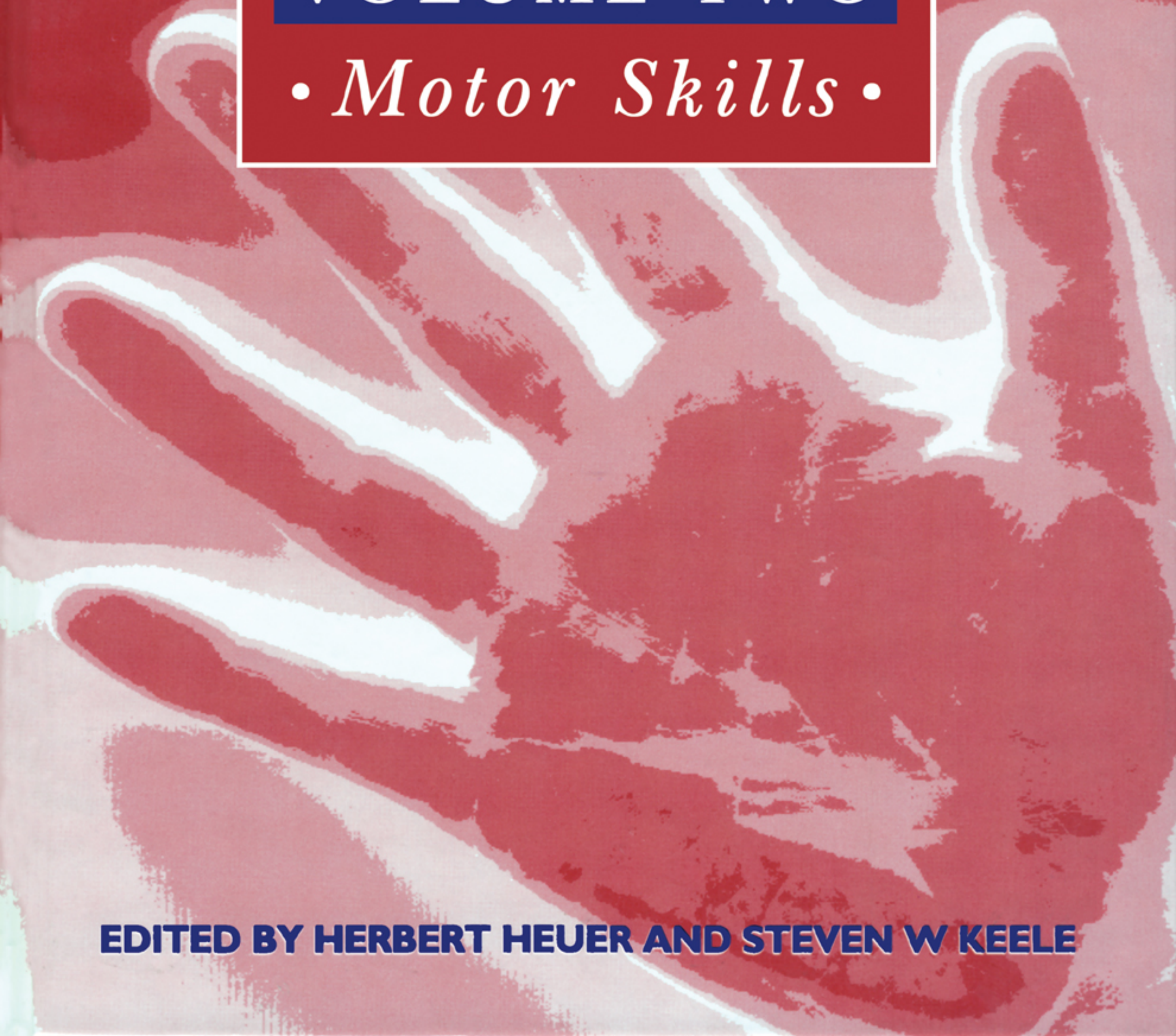
HANDBOOK OF PERCEPTION AND ACTION

VOLUME TWO

• *Motor Skills* •



EDITED BY HERBERT HEUER AND STEVEN W KEELE

Handbook of Perception and Action

Volume 2: Motor skills

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Preface

This book is part of a three-volume set on perception and action. The other two volumes deal with perception (edited by W. Prinz and B. Bridgeman) and attention (edited by O. Neumann and A. F. Sanders).

There are moments in the process of editing a book that are rather pleasant. These come from the pleasures of reading excellent chapters and from the dialogs on substantive issues between editor, author and reviewers. For these moments we wish to thank first and foremost the contributors to this volume. Second we wish to thank those who have commented on drafts of the chapters. We solicited help from some individuals in editing chapters, and we would like to acknowledge the assistance of H. Forssberg, D. Lee, D. G. MacKay, D. A. Rosenbaum and R. A. Schmidt.

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Introduction

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Humans are spectacular, compared with other animals, in matters of mental capability. They memorize new materials, employing systematic processes of rehearsal and organization to do so. Once stored in declarative memory, the contents can be expressed in arbitrary ways – by speech, by writing, by demonstration. Humans have an enormous capacity to reason. They solve problems. They create. Humans have capacities of language nowhere approached by other animals. No wonder psychology has expended so much effort in understanding cognition in all its manifestations.

Still, it has often been remarked that cognitive psychology, the study of these various capacities, leaves an organism stranded in thought, unable to engage in action (Guthrie, 1935). This criticism makes clear that the study of action – the study of movement and skill and the internal processes that lead to them – is a legitimate area of psychological investigation. Indeed, in modern psychology the study of action, or what is commonly called the study of motor control, is a vigorous field of investigation.

At first glance one might suppose the study of motor control is the study of only peripheral processes, such as how neurons control muscles, and how muscles are activated. Were this so, motor control would be in the domain of physiology and biomechanics with little to be gained from psychology. It is unlikely, however, that an organism so highly developed in cognition would have evolved a system in which action is independent of cognition itself. Indeed, human intelligence manifests itself not only in cognition but in the action products of cognition. Not only do humans express language, but they also have amazing flexibility in the motor systems for such expression – speech, typing, handwriting, even the singing telegram and sign language. Only humans knit sweaters, build cabinets, play the trombone. Only humans dance, play soccer, and engage in gymnastics. The variety of human skills is practically endless, and new skills are invented every day.

Such competence in skill led a pioneer in the study of motor control, Karl Lashley (1951), to comment that human ability to produce sequential action is as much a mark of their intelligence as any other human endeavor. Human motoric capabilities are no less impressive than those of memory, of reasoning, of language. Indeed, some have suggested and even argued (e.g. Bruner, 1968) that human cognition has grown out of some of the same evolutionary developments in the human brain that led to extraordinary motor skill.

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Rozin (1976) argued that what has made humans intelligent in so many domains is a kind of brain organization in which computations that may have evolved for particular purposes have become accessible for a variety of tasks. Thus, brain systems that code phonetics and are useful for speech, according to Rozin, also are accessible to visual inputs in the course of reading. Such shareability of computational systems among different task domains also extends to computations involved in motor control. Greenfield (1991) has argued that brain systems that support hierarchical organization in language, one of the key features of human language, also support the hierarchical control of action. Ivry (1993) has argued that cerebellar systems involved in motor timing also are employed in a wide variety of perceptual timing. Such modular organization, in which computations supplied by a brain system are accessible both for motor control and for other acts of cognition, may help to explain why it is that human intelligence manifests itself in the motor domain as well as in cognition.

The great diversity of human skills poses a problem regarding how to research them. It would make little sense in a handbook to describe each skill separately: how to play cricket, how to bowl, how to dance the tango. Such an endeavor would be of interest only to practitioners of each activity. On the other hand, sometimes lessons can be extracted only from particular and highly practiced skills. This may be because some aspects of skill only emerge once the performer becomes unusually proficient. Moreover, some principles of skill may be particular to certain activities. Beyond this, some skills are considered to be particularly important or characteristic for humans, and on that basis deserve full investigation. Such considerations argue that the study of skill is best approached in two ways.

One approach is to search for general principles that apply to a large class of skills. Approximately half of this handbook analyzes skill from this perspective. The second approach examines particular skills, and the other half of this handbook analyzes skill from that perspective.

There are five chapters that deal with general processes. Although these often make reference to particular skills, their focus is on principles that should be manifest in many domains. One chapter, by Rosenbaum and Krist, is concerned with the planning of action. Clearly, one feature that distinguishes human motor control and makes it such an integral part of cognition is that human action involves planning. However, planning is not sufficient for being able to actually produce what has been planned. The human body is a biomechanical system that operates in a physical environment and, for example, to move a finger in a certain way requires deriving the input signals that are needed to achieve the desired output. This is the problem of control as discussed by Jordan. Moreover, the human body consists of several limbs. For several skills the limbs have to cooperate, and such cooperation faces constraints. Heuer's chapter on coordination deals with such constraints on multilimb movements.

Movements evolve in time. This is a trivial statement. However, there are many skills for which timing is not a secondary aspect but is specified by task requirements instead. Musical skills belong most obviously to this class, and precise timing in such tasks is not at all trivial. Vorberg and Wing develop a variety of theoretical issues with respect to explicitly controlled timing of motor action. It is trivial also to say that motor skills can be improved through practice. Again, understanding how this happens is another and less easy matter. Much effort has been invested in determining how practice can be optimized. Ivry in his chapter takes a different approach, one less focused on training procedures *per se*, but rather on what is learned during the course of learning. Understanding the latter perhaps will have deeper implications for training procedures than a direct attack on procedures themselves. Moreover, emphasis on the structure of what is learned should lead to a better understanding of why some procedures are better than others.

The second half of this handbook is composed of five chapters dealing with individual skills. Given the extensive variety of skills of which people are capable, how should one choose which ones are most worthy of discussion? One possibility is to consider skills that are universal, or nearly so, such as speaking or writing. A second possibility is to study subskills that are components of several other more complex skills. Both possibilities are exercised in the five chapters of the second half of the handbook.

The most basic as well as probably most important subskill that plays a large role in many other skills is posture and locomotion. Woollacott and Jensen examine these activities from different theoretical perspectives. Almost of the same generality is reaching and grasping – that is, transporting the hand to a spatial location and adjusting the fingers to the shape of the object in that location so that it can be grasped. Jeannerod's chapter discusses both of these components as well as their relationships. Although catching does not have the same generality as posture and locomotion or reaching and grasping, it is a critical component of a large number of other skills. Moreover, it is a sufficiently general subskill that it may have an innate basis, being found in rudimentary form in the youngest of infants. A variety of issues, including how catching is adjusted to precise spatiotemporal parameters of the environment, are discussed in the chapter by Savelsbergh and Whiting.

The final two chapters deal with rather universal skills of language production. Fowler reviews what is known about speaking, while Teulings deals with handwriting and includes some discussion of typing. While speech may in some sense be special in that parts of the brain may have evolved in large part to support it, it is quite unlikely that the brain has evolved specifically for handwriting. There is enough difference between these two language production skills to justify separate treatments, although similarities may be discovered at the higher levels of control.

The organization of the material covered by this volume into two sections – one on general concepts and the other on particular skills – represents two different perspectives on related issues. Thus the reader should expect to see some overlap between the main sections. Such repetition is beneficial. Repetition in different contexts, as we have learned from the concept of 'elaboration' in memory research, helps to build the web of ideas that represents knowledge. It is the hope of the editors of this volume that the knowledge assembled herein will find its way from one material substrate – paper – to another one: 'mind stuff'.

REFERENCES

Bruner, J. S. (1968). *Processes of Cognitive Growth: Infancy*. Worcester, MA: Clark University Press.

Greenfield, P. M. (1991). Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. *Behavioral and Brain Sciences*, **14**, 531–595.

Guthrie, E. R. (1935). *The Psychology of Learning*. New York: Harper.

Ivry, R. (1993). Cerebellar involvement in the explicit representation of temporal information. In P. Tallal, A. Galaburda, R. R. Llinas and C. von Euler (Eds), *Temporal Information Processing in the Nervous System: Special Reference to Dyslexia and Dysphasia*. Annals of the New York Academy of Sciences, vol. 682, 214–230.

Lashley, K. S. (1951). The problem of serial order in behavior. In L. A. Jeffress (Ed.), *Cerebral Mechanisms in Behavior* (pp. 112–136). New York: John Wiley.

Rozin, P. (1976). The evolution of intelligence and access to the cognitive unconscious. In J. M. Sprague and A. N. Epstein (Eds), *Progress in Psychobiology and Physiological Psychology*, vol. 6. New York: Academic Press.

Part I

General Concepts

Chapter 1

Antecedents of Action

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1 INTRODUCTION

In seeking to understand the control of motor behavior, it is natural to inquire into the antecedents of action – the events that precede and allow for the execution of voluntary movements. In this chapter, we consider the *representations* formed before movements are carried out and which are vital for the successful realization of the actor's intentions. Such representations have been called *plans* or *motor programs.* The term 'motor program' connotes a representation of forthcoming activity that codes details about movements. The term 'plan' connotes a higher-level representation. Regardless of which term is used – here we will generally use 'motor program' or simply 'program' – two main questions have generally occupied the attention of those concerned with the representations presaging movement: (1) What aspects of movements are represented in advance? (2) What is the time course of the programming process?

A third question is logically related to the two questions raised above: (3) When is it possible to *avoid* postulation of representations for forthcoming motor acts? We introduce the latter question not out of antipathy for mentalistic accounts of behavior, nor because we believe that the nervous system should be viewed as a 'black box'. On the contrary, progress in cognitive and neural science indicates that such aversions have little place in modern research. The reason for avoiding the assumption of representations when possible is that we respect a major new focus in the study of motor control, namely, a focus on *physical* constraints. This focus originated with Bernstein (1967), who argued that what the body can do is largely shaped by its physical characteristics and by its physical interactions with the external environment. Bernstein's ideas about action are similar to Gibson's (1979) ideas about perception. Gibson argued that one may be mistaken in assuming that the perceiver engages in problem-solving or unconscious inference (Helmholtz, 1866/1962) to pick up useful perceptual information. He argued that the structure of optic arrays directly reveals properties of the environment. Hence, in the same way that structured properties of optic

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arrays may obviate perceptual representations, physical properties of the actor–environment system may obviate motoric representations. If the physical characteristics of the actor–environment system can 'take care' of details of forthcoming movements, it may be unnecessary to specify them in motor programs.

Accepting this perspective implies that a careful analysis of the physical properties of the actor–environment system can suggest opportunities for relieving the burden on the motor programming system. On the other hand – and this is how our approach differs from those who endorse the Gibsonian perspective (Turvey, 1990) – when a careful analysis of the actor – environment system provides little indication of how physical parameters alone can give rise to behavior, one may be ill-advised to eschew representations altogether.

Bernstein (1967) made another point that influences our thinking: although physical constraints often limit what can be done, many physically acceptable options are usually available for carrying out a task. Bernstein called this the *degrees of freedom* problem. He used this term when referring to the fact that the degrees of freedom of the motor system, expressed in mechanical, muscular, or neural terms, usually exceed the degrees of freedom inherent in the description of a task to be performed. A well-known example is the task of touching a point in three-dimensional space. Such a point, by definition, has just three degrees of freedom. Yet the body has many more degrees of freedom. Hence, to select a reaching movement, a decision must be made about which of the infinite number of movements that *can* be used to reach the point should be performed. The problem is mathematically ill-posed. Nevertheless, under normal circumstances it is solved instantly, effortlessly and without conscious awareness. Understanding how it is solved constitutes the degrees of freedom problem. The relevance of the problem for the study of the antecedents of action is that, as long as one assumes that a movement pattern has been selected, the solution to the degrees of freedom problem can be assumed to have been represented before the pattern was carried out.

Considering the degrees of freedom problem naturally suggests a metric of complexity. In general, the more complex an action, the larger the number of degrees of freedom it has. Because it is convenient to consider actions of varying complexity, this chapter is organized with respect to a complexity metric, from actions that are ostensibly simplest to those that are ostensibly most complex. It is sensible to organize the discussion this way because, as has been argued by many authors, behavior can be broken into constituents. A trip to the supermarket, for example, can be broken into a set of behavioral episodes: going to the store, selecting and purchasing the items that are needed, bringing them home, putting them away, and so forth. Each of these episodes can be broken into smaller episodes, each of these can be subdivided still further, and so forth. The smallest behavioral acts that might be considered while remaining within the realm of behavioral science are discrete movements involving one mechanical degree of freedom. We begin our review with such acts. Next we turn to discrete movements involving more than one mechanical degree of freedom. In the final section we consider entire series of motor acts involving many degrees of freedom.

Before turning to these topics, we turn to matters of evidence. We consider those factors that can be taken to suggest antecedent representations and which, just as strongly, seem not to admit of purely physical determinations of action selection or control.

2 FACTORS SUGGESTING ANTECEDENT REPRESENTATIONS

How can one tell that a motor program has been established for an observed action? We have already suggested one answer: when an action is carried out, although other actions are possible, some decision must have been made to favor the action that occurred. Logically, all the factors distinguishing the action that occurred from those that did not are candidates for the factors contained in the motor program. The number of such factors is potentially limitless; they correspond to all possible ways in which an action can be characterized. What is more likely is that the only factors that are represented are those that are necessary and sufficient to specify the action that will be performed at a given time. A major aim of research on motor programming is to determine just what those factors are. A number of measures, criteria and inferential methods have been devised for this purpose.

2.1 Anticipation

A major source of information about programs for forthcoming movements are changes in the way movements are performed depending on what movements will follow. Many examples of anticipation have been described in the literature on motor control. Domains in which anticipation has been studied include speaking, jumping, and reaching and grasping. Examples of anticipatory behavior from these domains are, respectively, anticipatory lip rounding (Bengueral and Cowan, 1974), bending down to facilitate forthcoming upward jumps (Alexander, 1984), and preshaping the hand in anticipation of forthcoming grasps (Jeannerod, 1981, and this volume).

These examples are interesting from different perspectives. Jeannerod's (1981, and this volume) observations concerning hand preshaping might be attributed to the perception of affordances (Gibson, 1979): the actor might be assumed to pick up information about the properties of objects to be grasped, and the action system might be assumed to be tuned to that information. Provided there is tight coupling between the perception of the object to be grasped and the corresponding grasping behavior, one might conclude that complex transformations do not exist between the percept and the act. This argument has been put forward by those favoring an ecological view of behavior.

While we do not deny the importance of the ecological view – indeed, we think it is an important methodological advance because it discourages postulation of cognitive events when physical or low-level sensory events might suffice to explain phenomena of interest – we wonder how informative the ecological account is in this context. We ask whether the ecological description begs more questions than it answers. What is the nature of the coupling that ensures proper hand grasps and the proper unfolding in time of the hand shape that is used? As anyone familiar with robotics knows, getting a robot to reach for and grasp a seen object is a nontrivial problem. The presence of perceptual information may indeed guide action, as Lee and Thomson (1982) and others have suggested, but this cannot be the whole story. Preshaping the hand is just one example of an anticipatory behavior that seems to demand postulation of *knowledge* of objects, *knowledge* of the hand's capabilities, and skillful mapping between the two.

Bending down to prepare upward jumps is another interesting example of anticipation. As in the case of manual preshaping, one might argue that the jump is tuned to the perceptual information of the object for which the actor is aiming. Still, the fact that downward motion is incompatible with the ultimate upward motion seems problematic for a simple ecological account. The reason for moving down before moving up is easy to understand in mechanical terms, and therefore in terms congenial to the ecological perspective: bending down stretches the tendons, which allows for the storage of elastic energy; when this stored elastic energy is released, it adds upward momentum (Alexander, 1984). The *decision* to move down is harder to explain, however. Limb tendons may store elastic energy, but deliberately moving down to store elastic energy cannot be explained without recourse to learning and memory. The point is that postulating motor programs need not imply willful ignorance of physics, as some critics of motor program theory have charged (Kelso, 1981). What is programmed is in most cases programmed with respect to the physical properties of the motor system as well as the perceptual environment in which performance occurs. It would be foolish to think otherwise, and no one pursuing a motor programming perspective has, as far as we know, ever suggested that cognition should replace rather than complement physics.

The last example of anticipation that we wish to mention at this point is anticipatory lip rounding, as in pursing the lips before saying the /t/ in 'tulip'. Anticipatory lip rounding demonstrates that information about the /u/ is available before production of /t/. This example of anticipatory behavior differs from the two examples discussed above in that it does not involve visual perception. Anticipatory lip rounding presumably does not depend on having seen others purse their lips in advance of /u/. There is, in fact, no obvious way to explain anticipatory lip rounding in terms of picking up perceptual information. A more straightforward explanation is that the speaker simply has a plan or program for the entire utterance, and that as the /t/ is being prepared, so too is the imminent /u/. Every detailed account of anticipation effects in speech production makes just such an assumption (Jordan, 1986). That anticipation effects in speech span only certain numbers and types of linguistic elements (Fromkin, 1980) provides support for the view that the effects are mainly governed by cognitive factors.

2.2 Errors

Not all overt anticipatory behaviors are adaptive. Some appear by accident and reveal underlying mechanisms for planning and control. One example is the exchange error in speech. Reversing initial phonemes, as in 'The queer old dean' instead of the 'The dear old queen', suggests that the initial phoneme of the later word ('queen') was available before the initial phoneme of the earlier word ('dear'). Exchange and other types of speech errors allow one to develop detailed models of the representations underlying forthcoming utterances (see, for example, Dell, 1986; Fowler, this volume; Fromkin, 1980). In general, errors in any performance domain, speech or otherwise, reveal hidden properties of the mechanisms underlying those domains, whether the mechanisms are motivational (Freud, 1901/1971) or computational (Norman, 1981). Analyses of errors have, in fact, permitted detailed accounts of programs for speech (Dell, 1986; MacKay, 1987), typewriting (Grudin, 1983; see Rosenbaum, 1991, for review), keyboard performance (Rosenbaum, Kenny and Derr, 1983) and handwriting (Ellis and Young, 1988). What these models share is the major assumption that there are distinct levels of representation, with levels activated earlier providing information about wide spans of behavior (e.g. the entire word, in typewriting), and levels activated later providing information about smaller constituents (e.g. individual keystrokes). That the errors being modeled correspond to errors made by patients with localized brain damage (Ellis and Young, 1988) suggests that the representations are rooted in physical (neurological) reality.

2.3 Reaction Time

Another indication of motor programs is the time taken for an action to begin. The time can be measured in different contexts: (1) when the actor is informed in advance about which action will be required but has to wait for an imperative signal (*simple* reaction time); (2) when the actor is informed in advance that one of a number of possible actions will be required but has to wait for a signal indicating which action should be performed (*choice* reaction time); and (3) when the actor is informed in advance that a given action will either be required or not and must wait for a signal indicating whether or not to perform the response (*go/no-go* reaction time). In all these conditions, one component of the reaction time corresponds to the time to process the signal (i.e. to detect or recognize it), another corresponds to the time to select the response (i.e. deciding *which* response to perform, *whether* to perform the response, and/or *when* to perform the response), and a third corresponds to the time physically to initiate the response.

Based on these assumptions, it is possible to draw inferences about motor programs from observed reaction times. For example, one can rely on the simple reaction time to begin a sequence of movements, where across conditions the sequence begins with the same movement but is completed with different movements. If the first movement is the same across the conditions but the simple reaction time depends on the number or identity of subsequent movements, the change in the initial reaction time can be taken to suggest that information about the entire sequence was represented in advance.

This logic has been pursued by a number of investigators (Henry and Rogers, 1960; Sternberg *et al.*, 1978). Henry and Rogers (1960) studied the performance of n successive manual responses, where the value of n varied. When n equalled 1, the task was to lift the hand as quickly as possible from a start button. When n equalled 2, the task was first to lift the hand from the start button (as in the $n = 1$ case) and then to grab a tennis ball. When n equalled 3, the first two tasks were the same as for $n = 2$, but a third task (striking an obstacle) was added. Henry and Rogers found that the time to lift the hand from the start button increased with n. Hence the same response took longer to initiate depending on the additional tasks to be performed. Because subjects were aware of what task was supposed to be performed and were highly motivated to perform rapidly and accurately, it is hard to interpret the result in terms unrelated to motor preparation (e.g. identifying a choice signal). Henry and Rogers argued, in fact, that instructions for the forthcoming movement sequence were loaded into a buffer after the imperative signal appeared. The loading time, by hypothesis, increased with the number of instructions, which in turn was assumed to increase with the number of movements to be performed.

Analogous sequence length effects were obtained by Sternberg *et al.* (1978) using other kinds of response sequences (speaking and typewriting). They explained their results in similar terms, although they favored a buffer *search* model rather than a buffer *loading* model. The important point for the present discussion is that the changes in simple reaction time observed by Sternberg *et al.* were not artifacts of the tasks they employed, such as changes in the musculature with task context, or variation in the amount of air held in the lungs prior to uttering long as opposed to short phrases (Sternberg *et al.*, 1980; but see Fowler, this volume). Instead, their simple reaction time effects reflected the internal state of the actor, which, judging from the data, varied systematically with properties of the sequence to be performed.

In considering the implications of reaction time effects for inferences about motor programs, it is important not to insist that, for programs to be implicated, reaction times must increase with response complexity. This requirement has been propounded by some. Consider the following quotation:

> 'Bernstein. . .showed that the sprinter reacts to the starter's gun with the same latency as it takes to lift a finger off a button. Yet, the sprinter has to perform a highly coordinated activity involving a larger number of muscles and body segments (plenty of "elements"!). One answer to the dilemma is that the skilled athlete has discovered ways to reduce the degrees of freedom of the motor system, so that the action is performed as a single, functional unit.' (Kelso, 1982, pp. 237–238)

As the above quotation indicates, a metric of response complexity may not always be apparent. Nonetheless, the *absence* of a complexity effect need not be attributed to the absence of motor programming, nor to bankruptcy of the motor program concept. The true measure of complexity might differ from the one the investigator assumes or surmises; in this connection it is a *virtue* of the reaction time method that it allows one to determine what factors do in fact define complexity. (Note that Kelso implicitly used this logic in the above argument.) For example, Sternberg *et al.* (1978, 1980) showed that the number of stressed syllables was the key determinant of the simple reaction time to begin saying a phrase. On the basis of this result, they concluded that the stress group is a fundamental unit of speech production. This conclusion differed from earlier hypotheses, such as the view that syllables (stressed *and* unstressed) comprise the basic units of speech (Klapp, 1974).

A second reaction to Kelso's (1982) complaint is that we are too ignorant of the inner workings of the motor programming system to insist that any one measure – particularly one as indirect as reaction time – should always be expected to vary with sequence complexity. After all, the biological system may have evolved to promote rapid initiation of complex but adaptive action patterns (e.g. sprinting toward prey). The fact that the time to initiate those patterns is no longer than the time to initiate simpler patterns for which rapid initiation has not been selected need not cast doubt on the role of preparation.

A third reaction to Kelso's (1982) challenge is that other sorts of reaction time measure can be used to great advantage to shed light on motor programs.

Consider choice reaction times. When a given response is paired with other possible responses, the choice reaction time for the common response changes depending on what other response is possible (Heuer, 1984; Kornblum, 1965). Such choice context effects provide fuel for the argument that actors' preparatory states shape their performance. Choice context effects are not merely due to peripheral interactions related, say, to muscle tension extending across effectors poised for action. They also appear when choices are made between alternative *sequences* of responses. When a given finger-tapping sequence is paired with various alternative sequences, for example, the choice reaction time for the common sequence decreases with the serial position of the first difference between the sequences (Figure 1.1). Thus, if the two sequences share all but the first response, the choice reaction time is longer than if the two sequences share all but a later response (Rosenbaum, Inhoff and Gordon, 1984). Because these choice context effects appear when the same response sequence is produced following the same stimulus and where the alternative stimulus is the same in all conditions, it is difficult to accept the idea that the effects result from factors other than the actor's internal state. Detailed modeling of choice reaction times in sequence-choice experiments has led to the idea that programs for forthcoming response

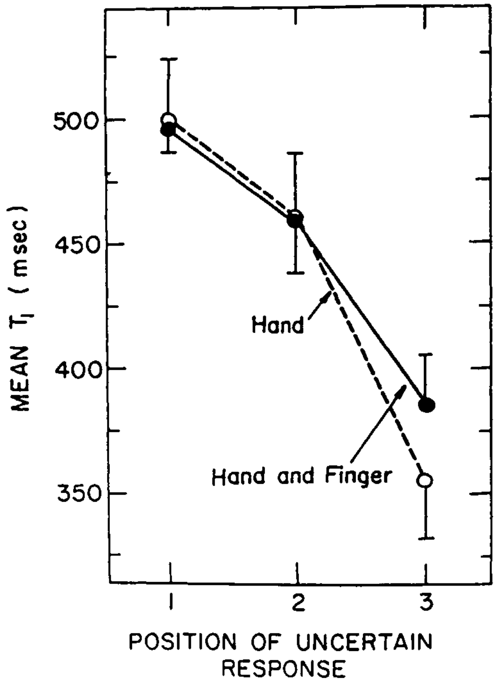

Figure 1.1. *Choice reaction time to initiate a finger-tapping sequence when the position of the uncertain response was at the first, second or third serial position (i.e. when the alternative sequences shared only the same second and third responses, only the first and third responses, or only the first and second responses). The uncertain response either differed with respect to hand or to finger and hand. The two possible sequences in each trial were revealed ahead of time and were highly practiced. [From Rosenbaum, Inhoff and Gordon, 1984.]*

sequences are organized hierarchically, and that information needed to differentiate the sequence to be performed from the sequence that was possible but not required is added to the program after the choice signal is identified, but before the early portions of the sequence are physically produced (Rosenbaum, 1987).

2.4 Perceptual–Motor Interactions

Another source of evidence for motor programming is the fact that registration of perceptual information, or response to it, depends on the preparatory state of the actor. Consider the fact that the subjective amplitude of the sounds of one's own speech or chewing is considerably lower than would be expected from the actual amplitudes of those sounds. Afferent signals generated during these oral activities are suppressed, in part via inhibitory efferent signals to the peripheral receptors and initial relay nuclei (Granit, 1955). Through these centrifugal effects, appreciation of one's self-generated speaking and chewing sounds is attenuated by central neural activity.

Central gating of sensory input related to one's own behavior has been studied most intensively in connection with the *efferent copy* model of von Holst and Mittelstaedt (1950). In a classic study, these investigators asked why the housefly can move laterally with respect to a seen wall when the wall is stationary, but when the wall is moved laterally in a particular direction the fly moves with the wall, maintaining its alignment with it. The question von Holst and Mittelstaedt sought to answer was why the alignment behavior does not occur when the fly makes spontaneous movements in front of the nonmoving wall, for, in either case, the receptive surface of the eye receives the same visual stimulation – in one case induced by eye movement in a stationary environment, in the other by environmental movement projected onto a stationary eye. The answer put forth by von Holst and Mittelstaedt (1950) is that an efferent copy is used to cancel perceptual changes accompanying self-generated movement. According to their model, if the fly turns x° to the left, the perceptual system cancels visually registered motion corresponding to x° rightward movement. The stability of the seen environment is ensured by subtracting a signal corresponding to self-generated movement from a signal corresponding to the perceptual input.

Some who favor an ecological perspective have challenged the efferent copy model on the grounds that it may be unnecessary. They have argued that perceptual information accompanying self-generated motion may be sufficiently different from perceptual information accompanying self-generated stability that there is no ambiguity between these two situations. According to this view, the visual changes accompanying self-generated motion might be sufficiently different from the visual changes induced by external motion that an efferent copy system would be superfluous.

This argument may be valid in some circumstances. For example, given that proprioceptive feedback from the extraocular muscles is richer than was previously thought (Skavenski and Hansen, 1978), it may be unnecessary to invoke an efferent copy mechanism to explain the stability of the visual world accompanying eye movements. Thus, inflow from the eye muscles might help distinguish self-generated retinal motion from externally generated retinal motion. Another possibility is that retinally registered visual change may indicate whether the actor, environment, or both are moving. On the other hand, perceptual processing is affected by motor activity in such a wide range of contexts that it is difficult to dismiss the efferent copy idea entirely. In fact, several results seem to *demand* acceptance of the efferent copy model. Two are mentioned below.

One result is that responses of the cat's limb to mechanical disturbances depend on when during the step cycle the disturbance is applied (Forssberg, Grillner and Rossignol, 1975). If pressure is applied to the dorsum of the cat's paw during the *stance* phase (when the leg is extended and the paw is planted on the ground), the response is greater downward pressure, as if the cat were trying to get a firmer foothold. However, if pressure is applied to the dorsum of the cat's paw during the *swing* phase (when the leg is moving forward toward the next footfall), the response is greater upward motion, as if the cat were trying to avoid an obstacle. The change in the response to sensory input depending on the phase of the walking cycle demonstates that information about motor activity shapes perceptual or perceptual-motor processing, as assumed in the efferent copy model.

The second source of information for efferent copy is a recent report concerning the discharge properties of neurons in the monkey parietal lobe related to visual stimuli presented at varying times relative to saccadic eye movements (Duhamel, Colby and Goldberg, 1992). As shown in Figure 1.2, at first, when the monkey fixated a stimulus in one part of the visual field (the mountain), the receptive field

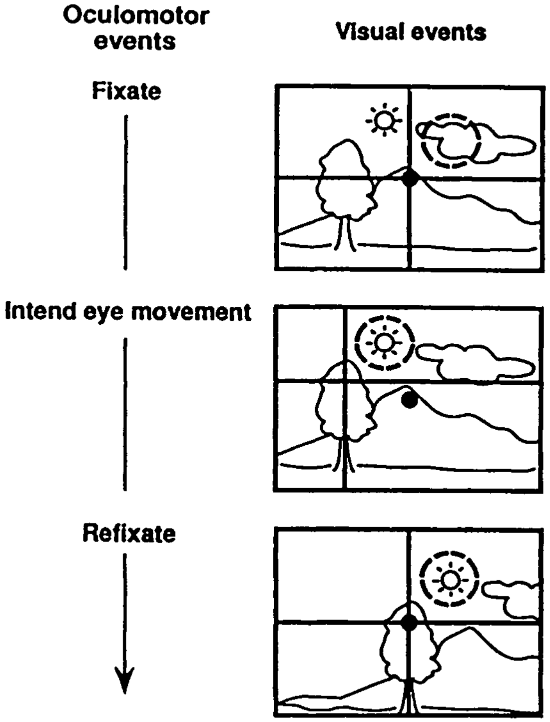

Figure 1.2. *Changes in the receptive field properties of a parietal cortex neuron in relation to current and forthcoming eye positions. See text for details. [From Duhamel, Colby and Goldberg, 1992.]*