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Behavioural Models of Motor Control and Short-Term Memory

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Abstract

We examined in this review article the behavioural and conceptual models of motor control and short-term memory which have intensively been investigated since the 1970s. First, we reviewed both the dual-storage model of short-term memory in which movement information is stored and a typical model of motor control which emphasizes the importance of efferent factors. We then examined two models of preselection effects: a cognitive model and a cognitive/efferent model. Following this we reviewed specific models of the control of movement end-location (the mass-spring model) and of movement distance (the coding strategy explanations). Finally, we discussed the contribution of both kinesthetic signals and abstract code to the storage of location and distance information for controlling limb movements.

INTRODUCTION

Motor processes have historically been the focus of examinations by researchers from a number of different disciplinary areas. Researchers from areas such as neurophysiology, neurology, neuropsychology and psychology have all, at one stage or another, attempted to understand the processes involved in the generation and control of skilled movement (see Prinz & Sanders, 1984).

In the area of neurophysiology, the interaction between afferent and efferent information and the effect of this interaction on movement and position sense has often been investigated. Specifically, the contribution of various sensory receptors to kinesthesis has been an area of controversy in the study of human performance. Until the early 1960s it was believed that the sense of

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position and movement of the joints depended solely on the joint receptors and that the receptors in musculature had no role in kinesthetic sensations (e.g., Rose & Mountcastle, 1959). However, it has recently been shown that the muscle spindle and the Golgi tendon organs are primarily responsible for kinesthetic sensations with cutaneous receptors having some secondary, subservient role in the sensing of joint movements. Joint receptors seem to only play a role in protecting hyper-extension or hyper-flexion of a joint with no primary role in kinesthesis (see Clark & Horch, 1986). Although these various joint, muscle and skin receptors appear to contribute differently to the perception of limb position and movement, the collective kinesthetic information derived from these receptors is undoubtedly of fundamental importance in the understanding of human motor control and learning (see Imanaka & Funase, 1992).

In neurology and neuropsychology the sensory and motor functions of various areas of the brain have been investigated (e.g., Evarts, 1979). A number of important findings on the sensory and motor functions of the brain have been revealed initially through studies on primates using electrophysiological techniques, and, more recently, through intensive examinations on humans. The motor cortex has been shown to receive various inputs from other cortical areas, such as the somatosensory and prefrontal cortex, and subcortical areas, such as the cerebellum and basal ganglia, and is now conceived of as the final relay station for output of motor commands to the spinal pathways. In addition, a long series of studies initiated by Sperry and Gazzaniga (see Gazzaniga, 1983; Sperry, 1982, for reviews) on split-brain patients has revealed a great amount of evidence for cerebral hemispheric differences in human performance (see Imanaka, Nishizawa, & Yamauchi, 1991). Collectively, the findings from these studies on both primates and humans suggest that human motor behaviour involves a complex interplay between both sensory and motor processes in the brain. Nevertheless a large number of questions remain unanswered regarding the precise function of the brain in human motor performance.

In psychology, researchers have long been interested in the relationship between perception and action, between cognition and motor acts, and between motor control and learning. Since the 1960s, the information-processing approach has dominated cognitive and experimental psychology (see Imanaka, Yamauchi, Funase, & Nishihira, 1993). This approach is based on the notion that humans behave like a sophisticated information-processing system, processing input information about both the external conditions of the environment and the internal conditions of the performer through a series of processing stages in order to control and learn skilled movement. Although researchers in this area have not been primarily interested in the functioning of the central nervous system or the peripheral organs per se, they have frequently referred to relevant findings about the anatomy and physiology of the central and peripheral nervous systems. In examining peripheral and central sources of information for movement control some psychologists have stressed peripheral feedback factors (e.g., Adams, 1971), some have placed great emphasis upon central control aspects, such as the nature of the efferent commands (e.g., Kelso, 1977b) and cognitive strategies (e.g., Roy & Diewert, 1975), while others (e.g., Schmidt, 1975) have focussed upon how both central and peripheral factors might be integrated for effective motor control and learning. The relative importance of peripheral and central factors appears to depend on the specific environmental situation (e.g., the environmental predictability) and the desired characteristics of the movement itself (e.g., the movement's duration). Most movements are probably controlled in terms of information from both central and peripheral factors with the relative balance of these factors being very movement-specific.

In this review article, we examined various conceptualization and behavioural models of motor control and short-term memory which have intensively been investigated since the 1970s. First, we reviewed both the dual storage model of motor short-term memory (Laabs, 1973) and a typical efferent model of motor control proposed by Jones (1972, 1974a, 1974b), who argued the importance of efferent factors and the central monitoring of efferent command. We then examined two models of preselection effects: a cognitive model and a cognitive/efferent model. Finally, we discussed the models of the control of movement end-location (i.e., the mass-spring model), the coding strategy explanations for distance information, and the contribution of both kinesthetic signals and abstract code to the storage of location and distance information for controlling limb movements.

THE DUAL-STORAGE MODEL: LOCATION VERSUS DISTANCE

Irrespective of positions emphasising either central or peripheral control factors, accurate motor control also requires access to information stored in a memory system. Such stored information is clearly necessary if the performer is to be able to generate a desired movement or correct an ongoing movement. A store of kinesthetic information must be available in order to meaningfully interpret current afferent information provided by the sensory receptors. Thus, the stored information or memory code is essential both for movement perception and movement control and learning. A major interest of psychomotor research has therefore been in understanding the internal memory code used for the short-term retention of information about limb movement. Most research effort has been directed at determining the role of different movement cues, particularly end-location and distance, in motor short-term memory.

Kinesthetic Code for Distance and Central Code for Location

Laabs (1973) examined the retention characteristics of location and distance cues on constrained angular movements made in the horizontal plane by manipulating both starting position and movement length. Different retention interval conditions were also employed: immediate reproduction, 12-sec rest (i.e., an unfilled interval), and 12-sec delay filled with a backward-counting task or with a spatial task. Variable error (VE) and constant error (CE) were used to evaluate retention consistency and bias, respectively. Results showed that location and distance cues were reproduced with similar accuracy under the immediate reproduction condition. However, during the 12-sec unfilled interval, distance information spontaneously decayed but location information did not. When the retention interval was filled with an interpolated activity, response variability for location reproduction but not for distance became remarkably larger than during the unfilled interval.

Based on both his findings and the earlier findings of Keele and Ells (1972) and Marteniuk and Roy (1972), Laabs (1973) proposed a model of motor short-term memory in which location and distance cues were conceived to have different storage modes and different retention characteristics. Laabs' model postulated two modes of storage in motor short-term memory instead of the single mode proposed in the Pepper and Herman (1970) model. One mode was proposed to use a kinesthetic memory code that spontaneously decays, and the other a central memory code that is subject to forgetting by interference when the retention interval is filled with an interpolated activity. The kinesthetic code is thought to be responsible for the storage and retention characteristics of distance information, and the central code, for location information.

Assimilation between the Memory Traces of Actual and "Average" Movements

Laabs (1973) has also proposed that VE is an appropriate index of the decay and interference effects, whereas CE indicates response biasing effects. He explained response biasing effects in terms of the interaction between memory traces of an actual and an "average" movement, whereas Pepper and

Herman (1970) considered response bias in terms of the level of proprioceptive stimulation interacting with the memory trace for the given motor task. Laabs postulated that a reproduction movement is made in reference to both the memory trace of an actual movement and an "average" or "central" movement that is made up from the many similar movements experienced within the experimental trials. Thus, either the decay in the kinesthetic storage mode or interference in the central storage mode may cause a change in the strength of the referent movement trace for the "average" movement. This referent trace interacts with the memory trace of a given movement, resulting in the shift of CE toward the referent movement trace. Such interaction also produces increased VE.

Codability of Location and Distance Information

According to the Laabs' (1973) model, location cues provide a stable internal code whereas distance is not centrally coded. As a consequence movement location is reproduced more accurately than distance (Frekany, 1978; Keele & Ells, 1972; Marteniuk & Roy, 1972; Posner, 1967; Stelmach & Kelso, 1973). However, many studies have also reported contradictory evidence that distance information is centrally coded (Diewert & Roy, 1978; Kelso, 1977b; Roy & Williams, 1979; Walsh & Russell, 1979). Stelmach and Kelso (1973) stated that "the superior codability of location over distance appears to be a matter of degree" (p.406). For preselected movements, there have been reports that distance information can be coded and retained without decay (Colley & Colley, 1981; Jones, 1974b; Marteniuk, 1973; Roy, 1978; Roy & Diewert, 1975, 1978; Stelmach, Kelso, & Wallace, 1975; Walsh & Russell, 1980; Walsh, Russell, & Crassini, 1981; Walsh, Russell, Imanaka, & James, 1979; Walsh, Russell, & Imanaka, 1980) and even for constrained movements some studies have shown that distance information is centrally coded (Kelso, 1977b; Walsh & Russell, 1979; Walsh et al., 1979) and can be retained for at least 30 sec (Diewert, 1975; Walsh et al., 1981).

The Effect of Movement Size

The equivocal findings concerning superiority of location or distance cues for movement reproduction may well be the result of confounding effects due to movement size and movement length. Stelmach (1970) reported that subjects could not use location cues for short movements, relying rather upon distance cues. Keele and Ells (1972) also reported that reproduction movements showed greater consistency for short movements when distance cues were available. Gundry (1975) examined the spontaneous use of either distance or location cues for three different amplitudes of angular constrained movements

(20, 40, & 60°movements, which were 17.4, 34.9, & 52.3 cm, respectively). Gundry found that subjects tended to use distance cues to reproduce short movements and location cues to reproduce long movements and suggested that the previous findings indicating that location cues were more accurately reproduced than distance cues might have been the consequence of the use of tasks involving large movement amplitudes. Stelmach et al. (1975) reported that preselected distance information was more accurately and consistently reproduced in short movements (up to 23.9 cm), and less useful for long movements, than location information. These researchers also suggested that the preselection of movement extent is more important for short movements. Likewise, Roy and Kelso (1977) have argued that both location and distance cues may be reliable for short movements (about 10-20 cm), while for long movements (about 30-40 cm) location cues may be most useful. More recently, Walsh (1981) has also provided evidence arguing that distance is the preeminent cue for the recall of short movements ranging in distance from 8 to 16 cm. In addition to these studies, a number of other studies (e.g., Colley & Kitchen, 1983; Duffy, Montague, Laabs, & Hillix, 1975; Frekany, 1978; Roy, 1977) have also shown that distance cues are reproduced more accurately in short movements than longer movements. Collectively the weight of research evidence clearly indicates that distance information is most useful for short movements up to about 20 cm in length while location information is more useful for the reproduction of longer movements.

THE OUTFLOW MODEL: CENTRAL MONITORING OF EFFERENT COMMANDS

Two Hypotheses: CME and PFB

Contrary to theorists who had emphasised the importance of proprioceptive feedback (PFB) in motor short-term memory, Jones (1972) has argued for the importance of central monitoring of efferent commands (CME) in his "outflow" model of motor control. Jones examined the accuracy of voluntary duplication of rapid arm movements under three different conditions of standard movement presentation, that is, constrained active movements, unconstrained (i.e., preselected) active movements, and passive movements. Preselected active movements were reproduced more accurately than constrained and passive movements, while the constrained and passive conditions showed similar accuracy to each other. Jones proposed two possible hypotheses to explain these results. The first was that the reproduction of the standard movement was based on outflow (efferent) information plus inflow (afferent) information with proprioceptive signals being compared to the centrally monitored efference copy (Holst, 1954). The second was that proprioceptive feedback signals (PFB) may provide nothing more than registration of muscular effort and may not provide specific information about the direction or extent of movement. This latter interpretation was based on the observation that constrained movements were less accurately reproduced than preselected movements, although in both conditions proprioceptive signals were available during movement.

Experiments Comparing the Role of CME with PFB

Jones (1974b) conducted a further series of experiments to compare the potential motor control role of central monitoring of efferent signals (CME) with that which could be provided by proprioceptive feedback from joints and/or muscles (PFB). In the first experiment, he tested the hypothesis that the preselection of a movement results in a central record of efferent discharge, or efference copy, which may be regarded as a motor memory (or storage) system without the requirement of monitoring and storing proprioceptive feedback. Three types of movements (voluntary or preselected, constrained, and passive) were examined under three retention interval conditions (no delay, 15-sec rest, and 15-sec filled interval with a counting task). Under the no delay condition, preselected movements were reproduced with significantly less variability (in terms of VE) than constrained or passive movements, while the VE of constrained and passive movement did not differ. These results were consistent with the previous findings (Jones, 1972). In both the constrained and the passive conditions, forgetting occurred during the 15-sec retention intervals regardless of whether the interval was filled or unfilled, whereas in the preselected condition significant forgetting arose only for the filled interval. Since there was no forgetting of preselected movements with time but only when an attention-demanding interpolated task was added during the retention interval, Jones (1974b) concluded that the reproduction of preselected movement may depend on central processing, and that CME rather than PFB is necessary for motor rehearsal.

A second experiment by Jones (1974b) tested the possibility that subjects in the preselected condition might rely on the end-location rather than efference associated with the movement itself in reproducing the distance of preselected movement from either a fixed or a variable starting position. The same three retention interval conditions were used as in the first experiment. Results showed that although reproduction differences between the 0-sec delay and 15-sec filled delay were significant for both the fixed and variable start conditions, these two start conditions were not significantly different in reproduction performance for each retention interval condition. Such findings suggested that the results of the first experiment were not due to the subjects' use of location cues.

The Importance of CME

Jones (1974b) conducted a third experiment to test the further hypothesis that CME is not only a necessary, but also a sufficient, condition for rehearsal processes in motor short-term memory. In this experiment subjects were asked to move a slide against varying degrees of tension produced by adding attached weights of 0, 0.5, 1.0, and 1.5 kg to the slide. By changing the tension opposing movement Jones was able to manipulate the degree of PFB available to the subjects. Movements were made voluntarily (i.e., preselected) with variable starts and the same three retention intervals as used in the previous experiments were again utilised. Only the main effect of retention intervals was significant in this experiment with neither the effect of differential weighting nor the interaction of retention interval by weighting causing significant changes in reproduction accuracy. The results indicated that increasing PFB does not influence the consistency of the reproduction of preselected movement, suggesting that such peripheral information may not be utilised in the rehearsal of information in motor short-term memory. Jones proposed that less accuracy in the reproduction of constrained movements compared to preselected movements is due to the absence of CME during constrained movements. This is because there is no reason to assume that efferent commands to the muscles and feedback information from joints and/or muscles are different between constrained and preselected movements (Jones, 1974a). Based on these findings, Jones (1974a, 1974b) has concluded that CME is a necessary and sufficient condition for the rehearsal of information in motor short-term memory.

Less Importance of PFB

Jones and Hulme (1976) have subsequently examined the role of PFB information available during the criterion movement in movement reproduction. Subjects were asked to voluntarily reproduce the extent of a criterion movement made either voluntarily or passively, and also to do a signal detection task with visual stimuli during the execution of the criterion movement. Under such conditions it was found that the concurrent signal detection task significantly affected the accuracy of the reproduction of passive movement whereas it did not affect the reproduction accuracy of preselected movements. This finding therefore corroborated those of the previous studies (Jones, 1972, 1974a, 1974b) in suggesting that the reproduction of voluntary movement may be based on some pre-set instruction and may not require proprioceptive information. If this is indeed the case, efferent commands and CME should provide a reliable cue for the reproduction of distance moved because efferent commands for a preselected movement should be the same during both criterion and reproduction movements irrespective of the starting position. Jones' CME model therefore predicts that preselected distance cues should be reproduced quite accurately regardless of any changes in the starting position of reproduction movements.

A COGNITIVE MODEL OF THE PRESELECTION EFFECT

The Role of Prior Information for Distance

Roy and Diewert (1975, 1978) have investigated the role of prior information and cognitive strategies in an attempt to understand the superior retention of distance information in preselected movements compared to constrained movements. In their original study Roy and Diewert (1975) compared the codability of distance cues for movements made to experimenter-determined and subject-determined standards. Subjects moved a slide on a linear track a distance of 60 cm (total distance) and back to the start, and then were required to move the slide a distance equal to one-half the total distance of the standard movement. It was this distance that subjects were ultimately required to reproduce. One group of subjects determined their own standard (active condition), but the other group made movements to a stop located at the standard distance (constrained condition). Thus, all subjects had prior information of the distance of a standard movement that would be half of the total distance. Results showed that both groups reproduced the distance of standard movements to a similar degree of accuracy. This suggests that prior information about a to-be-remembered movement is important for the codability of distance information regardless of whether the experimenter or the subject determines the movement standard.

Roy and Diewert (1978) later confirmed this finding by conducting an additional series of experiments involving three different movement conditions, namely, preselected movements, constrained movements with prior information, and constrained movements without prior information. The condition of constrained movement without prior information produced significantly poorer reproduction accuracy than the other conditions, while equivalent reproduction accuracy was found for the preselected movements and the constrained movements with prior information. Furthermore, Roy and Diewert examined the role of active movement in the retention of the preselected distance information by making a comparison between active and passive preselected movements. This experiment involved four movement conditions, namely, preselected active, preselected passive, non-preselected active, and non-preselected passive. (The preselected conditions in this experiment were the same as the constrained condition with prior information in the first experiment). Reproduction accuracy in the two preselected conditions was superior to that in the non-preselected conditions in this experiment, corroborating the findings of Jones (1972, 1974b), Kelso (1977b), and Stelmach et al. (1975). Comparisons between the active and passive preselected conditions however showed no differences in reproduction accuracy. This finding suggested, contrary to Jones (1974a, 1974b), that efferent information during the presentation of criterion movement may not be responsible for the superior retention of preselected movements. These findings of Roy and Diewert (1978) were also replicated by Roy (1978) and Runnings and Diewert (1982). Thus, it may be concluded that an important aspect of preselected movements is the availability of prior information or strategies about the termination of the standard movement. Moreover it appears that active movement, involving efference, during the presentation of the standard may be of little importance in the storage of information for the reproduction of preselected movements.

As noted earlier, Jones (1972, 1974a, 1974b) proposed that the central monitoring of efferent commands (CME) to the muscles alone is responsible for the superiority of the reproduction of preselected movements over constrained movements. Stelmach et al. (1975) examined the CME hypothesis, as it pertains to the preselection effect, by comparing the reproduction of location and distance cues for preselected movements. According to the CME hypothesis, the reproduction of distance cues should be performed more accurately than the reproduction of location cues when the starting position is altered. This is because the efferent commands for the reproduction of a preselected distance should be available from the criterion movement whereas, for the reproduction of location, a new set of efferent commands will be necessary. Stelmach et al., however, showed superior reproduction of movement location rather than distance, indicating that the availability of efferent command information from the criterion movement is not primarily responsible for the preselection effect.

The Role of Prior Information for Location

Stelmach et al. (1975) also conducted further experiments to compare the reproduction accuracy of the end-location of preselected, constrained, and passive movements under 0-sec, unfilled 15-sec, and filled 15-sec retention intervals. Results showed that the reproduction accuracy of preselected location was superior to that of constrained and passive location conditions, and that these conditions were not differentially affected by the addition of an interpolated task. These findings suggested that prior information rather than afferent information about the end-location of a criterion movement may facilitate retention, and that preselection may facilitate retention without requiring additional central processing capacity. Stelmach et al. also noted that preselection facilitates the encoding of proprioceptive information, since preselection could provide a corollary discharge (Sperry, 1950) in which internal information flows from the motor area to the sensory area, preparing it to receive peripheral feedback from the execution of the forthcoming movement. In summary, Stelmach et al. (1975) have emphasised the role of internal efferent information in the preselection effect, rather than invoking an explanation based on an encoding strategy that requires central processing capacity.

COMBINING COGNITIVE AND EFFERENT EXPLANATIONS OF THE PRESELECTION EFFECT

Movement Plan and Efferent Information

Kelso (1977b) investigated the relative contribution of cognition (in the form of a movement plan) and efferent commands in explaining the superior reproduction of preselected movements over constrained movements. Groups of subjects experienced either an active or passive criterion movement under either preselected or constrained conditions and were then required to actively reproduce the movement (Experiment 1). Such a design allowed the availability of either efference or a movement plan to be manipulated. Kelso found that active preselected movements were reproduced with smaller errors than any of the other movement combinations, suggesting that access to planning processes alone may be insufficient to facilitate movement encoding. Kelso also found that the active movement group was superior to the passive group in terms of both accuracy and consistency while the passive group with active reproduction was also superior in consistency to the passive group with passive reproduction (Experiment 2). Based on these results, Kelso argued that both movement plan and efferent information were responsible for the superior reproduction of preselected movements. Summers, Levey, and Wrigley (1981) have also suggested that both strategy and efferent information are responsible for the superior reproduction of preselected distance information, while also suggesting that strategy alone is responsible for the superior reproduction of preselected location information.

Evidence from Nerve-Block Experiments

Kelso (1977a) further investigated the relative contribution of efferent and afferent sources of information in the encoding of preselected movements. He employed an afferent nerve block technique (Laszlo, 1966; Laszlo & Bairstow, 1971a, 1971b) with a wrist-cuff to eliminate proprioceptive feedback from joint and cutaneous sources. Subjects were asked to reproduce a finger positioning movement under normal and wrist-cuff conditions. When both starting positions of the criterion and reproduction movements were the same (Experiment 1), no significant differences in reproduction accuracy were found between the normal and wrist-cuff conditions. This suggested that proprioceptive feedback is not crucial in the reproduction of preselected movements when both location and distance information are available. When the starting position differed between the criterion and reproduction movements however (Experiment 2), the reproduction of preselected location was unaffected by the cuff manipulation whereas the reproduction of preselected distance deteriorated in comparison to the normal condition. In addition, the reproduction of location was superior to distance under the cuff condition, although no differences were found in reproducing the two cues under the normal condition. Furthermore, response bias in the reproduction of location cues was relatively unaffected by changes in starting position whereas the reproduction of distance revealed a strong positive response bias. This bias was more pronounced under the cuff condition.

Kelso (1977a) proposed that the observed superiority in reproducing preselected location compared to preselected distance, was due to the subject's use of a "tension programming" that predetermines the appropriate relationship between relevant agonist and antagonist muscles, allowing terminal location to be reproduced independently of the changes in starting position. Kelso also suggested that location information from preselected movements may be coded independently of proprioceptive feedback while distance information may be dependent on proprioception. Consequently, the Kelso (1977a, 1977b) findings reject Jones' (1974b) CME hypothesis, which emphasises only the central monitoring of efferent commands, on the grounds that it fails to recognise both the cognitive aspect and the afferent component of preselected movement reproduction (Kelso & Wallace, 1978).

THE MASS-SPRING MODEL OF LIMB POSITION CONTROL

The Equilibrium-Point Hypothesis

Kelso's (1977a) "tension programming" explanation mentioned above is referred to as the "mass-spring" model or equilibrium-point hypothesis. This model was originally developed by Asatryan and Fel'dman (1965; Fel'dman, 1966a, 1966b) and then later presented as a control system for the reproduction of limb positions (Adamovich & Fel'dman, 1984; Berkinblit & Fel'dman, 1988; Berkinblit, Fel'dman, & Fukson, 1986; Fel'dman, 1974a, 1974b, 1976, 1980a, 1980b, 1981, 1986; Fel'dman & Latash, 1982a, 1982b). The basic concept underlying the equilibrium-point hypothesis is that any limb position can be determined as an equilibrium-point where the external load imposed on the limb and the muscle tension of the limb are equal and opposite (or alternatively where the tension of opposing agonist and antagonist muscles are in balance with each other). In determining an equilibrium-point, relevant muscles are believed to act like a somewhat complex mass-spring system, with the tension within the muscles varying in direct proportion to the degree of stretch imposed on the muscle just as would be expected from the length-tension relationship of an ordinary spring.

Invariant Length-Tension Functions

The presence of spring-like length-tension relationships within muscle was demonstrated in a series of experiments by Asatryan and Fel'dman (1965; Fel'dman, 1966a, 1966b) and by Davis and Kelso (1982), in both of which an unloading method was used. In both series of experiments by Asatryan and Fel'dman and by Davis and Kelso subjects were required to maintain the elbow joint angle against an external load and not to intervene voluntarily when deflections of the elbow were elicited by systematic reductions in the external load, made by the experimenter. The relationship between the elbow joint angle and its torque was examined for various initial joint angles. The observed torque-angle functions for each initial joint angle were parallel and non-intersecting, just as would be expected for different stiffness of ordinary springs. Asatryan and Fel'dman called these individual torque-angle (or length-tension) functions "invariant characteristics" and interpreted the final joint angle (or muscle length) observed when the muscle was completely freed of external loads as the threshold angle (or threshold muscle length) for the simple stretch reflex.

Feldman's Explanation

Asatryan and Fel'dman (1965; Fel'dman, 1966a, 1966b, 1986) have hypothesised that an equilibrium-point is determined by both the threshold muscle length and the invariant (stiffness) characteristic of each muscle. The threshold length is assumed to be controlled by central commands descending to alpha and gamma motoneurons, while the invariant characteristic is a result of specific length-tension functions based on the stretch reflex. When the threshold length remains constant, the muscle acts like an ordinary spring on the basis of its invariant characteristic, namely, the static muscle force is simply in proportion to the difference between the current muscle length and its threshold length. A shift in the threshold length provides a transfer from one invariant characteristic (i.e., a length-tension function) to another and results in the establishment of a new equilibrium-point. This results in a change in both muscle length and force, with the limb being moved to the equilibrium-point. It is accordingly assumed that the timing and amplitudes of the EMG bursts accompanying movement are not centrally controlled (or programmed). Fel'dman (1986) argues that independent central change in the threshold length underlies voluntary control of limb positions and, as a consequence, this control mechanism elicits complex EMG patterns.

Bizzi's Version

The equilibrium-point hypothesis or mass-spring model of motor control has been corroborated in investigations conducted on both monkeys and human subjects. Bizzi and his coworkers (Bizzi, Polit, & Morasso, 1976; Bizzi, Dev, Morasso, & Polit, 1978) investigated the control mechanisms for the termination of a centrally initiated head movement at a visual target, using both intact and deafferented monkeys trained to move their head to the target. In these experiments either inertia or unexpected torque disturbances were applied during the head movements. Under inertia disturbance conditions the head movements elicited in response to the visual stimulus initially overshot the target position but then moved back to the target. When a constant opposing torque was applied during the movements, an undershooting was observed but this head position was corrected, moving the head to the target position, as soon as the torque was removed. Bizzi et al. concluded that the central commands establishing final head position are preprogrammed and not affected by afferent inputs, suggesting that final head position is specified as an equilibrium-point between agonist and antagonist muscles. These findings were also corroborated by Polit and Bizzi (1978, 1979), who demonstrated, in both intact and deafferented monkeys, consistent final limb positions regardless of shifts in initial limb position.

Different Implications: Feldman versus Bizzi

Bizzi's version of the equilibrium-point hypothesis is slightly different from the original model of Fel'dman, particularly with respect to the explanation given to account for the controllable variables of spring-like muscle activity. Bizzi (1980) has emphasised that central commands descending to alpha motoneurons are essential to change the tension of the opposing agonist and antagonist muscle groups, and hence to shift the equilibrium-point. In other words Bizzi proposes that EMG activity causes a shift in equilibrium-point as EMG bursts and their parameters are believed to be an expression of a central program. In contrast, Fel'dman (1986; Berkinblit & Fel'dman, 1988; Berkinblit et al., 1986) argues that in voluntary motor control the central nervous system uses the stretch reflex, with its threshold muscle length being modified by central commands descending to both alpha and gamma motoneurons, as the means of inducing a shift in equilibrium-point. This shift in equilibrium-point is assumed to cause EMG bursts which in turn bring about a change in limb position. Thus, the cause and effect relationship between the shift in equilibrium-point and EMG burst activity is inversely interpreted by Bizzi and Fel'dman.

Further Evidence

Evidence for the equilibrium-point hypothesis is also available from experiments conducted on intact human subjects. Schmidt and associates (Schmidt & McGown, 1980; Schmidt, McGown, Quinn, & Hawkins, 1986) examined the effects on the accuracy of a rapid limb positioning movement in either the horizontal or vertical plane of altered limb loads (achieved by either adding or subtracting a mass). Positioning performances (in terms of CE and VE) in the horizontal plane were not affected by the change in the load on the limb. In the vertical plane, however, when a mass was unexpectedly added, there was a tendency for the movement endpoint to be shifted in the direction of undershooting, while when a mass was unexpectedly removed the movement endpoint tended to shift in the direction of overshooting. These observations were consistent with a prediction from the equilibrium-point hypothesis or mass-spring model. The added (or subtracted) mass under the horizontal movement conditions does not increase the external load on the limb and therefore should not produce any shifts in equilibrium-point, whereas increases in the external load in the vertical movement conditions should result in a shift in equilibrium-point. The observed shift in response bias (i.e., undershooting with mass added and overshooting with mass reduced) is precisely what would be expected in a strictly mechanical mass-spring system. Kelso and Holt (1980) have also reported evidence for the mass-spring model, in their case using functionally deafferented human subjects and a rapid finger positioning task.

Limited Implications of the Mass-Spring Model

On the basis of these findings it appears that the equilibrium-point hypothesis or mass-spring model may have an advantage over a feedback-based control models, such as traditional closed-loop models, in explaining the control of limb-positioning movements (and the reproduction of movement location). This is because, within the mass-spring model, a limb is hypothesised to be able to move to an equilibrium-point from any initial limb positions and under any perturbations. However, it has frequently been reported that a change in initial limb position affects the accuracy of achieving a final limb position (Larish, Volp, & Wallace, 1984; Wallace, Frankeny, & Larish, 1982) and systematically biases the end-location of reproduction movements (e.g., Kerr, 1978; Walsh et al., 1979). Since study of the mass-spring model has usually been restricted simply to rapid limb (or finger) movements (e.g., Kelso & Holt, 1980; Polit & Bizzi, 1978, 1979; Schmidt & McGown, 1980; Schmidt et al., 1986), it may be that the model is less able to explain the control of slow movements. The issues with respect to the possible differential control of slow and fast movements, in conjunction with short-term memory, have recently been investigated by a number of researchers (e.g., Imanaka & Abernethy, 1990).

CODING STRATEGY FOR DISTANCE INFORMATION

Two Types of Coding Strategies for Distance

Diewert and Roy (1978) conducted a series of experiments to examine the possible use by subjects of two distinct cognitive strategies for encoding movement distance information: a location strategy and a counting strategy. In the first experiment, subjects were asked to reproduce the distance of a criterion movement under one of six different experimental conditions. These conditions provided variations in the reliability of location cues by altering both the starting position and the direction of reproduction movements. This experiment revealed a monotonic increase in VE scores for the reproduction of distance as location information became less reliable. This trend held for variations in location reliability from the most reliable condition to the fourth most reliable one. However, further decreases in the reliability of location information beyond this point actually resulted in decreases in VE. Subjects' verbal reports about their own encoding strategies revealed that a number of subjects employed a counting strategy as the utility of location information decreased. This also suggests that, at least in some of the conditions, location information might have been used by some subjects in conjunction with an extrapolation procedure (based upon perceived changes in the starting position from the criterion to the reproduction movement) as a means of reproducing distance (Sullivan & Salmoni, 1975).

The Counting Strategy

The second and the third experiments by Diewert and Roy (1978) examined the precise nature of the counting strategy used by subjects, and found that this strategy may be most useful for encoding movement time and velocity. A fourth experiment directly compared the usefulness of the two cognitive strategies (location and counting) for encoding movement distance. Subjects in this experiment were specifically instructed to use either the location or the counting strategy. Results supported and extended the findings of the previous experiments in this series. Diewert and Roy concluded that both location strategy and counting strategy are useful for encoding movement distance. Moreover, memory for distance does not seem to involve the use of kinesthetic information, but may rather require subjects to use analytic processes, such as extrapolation from changes in the starting location or estimation from movement time and velocity, as the means of reproducing movement distance.

The finding that a counting strategy is useful in encoding distance is in agreement with a much earlier study (Leuba, 1909), which suggested that movement rate and time information may be used to encode movement distance. Roy and Williams (1979) and Summers et al. (1981) have also suggested that distance information may be primarily encoded in terms of movement velocity and/or movement time, and this is supported by evidence from Carlton (1978) that information about movement rates is rehearsable. Similarly, Laabs (1973) reported from his study that there were some subjects who tended to use a counting strategy to remember and reproduce the distance of criterion movements.

The Location-Based Strategy

Although Sullivan and Salmoni (1975), Roy (1977, 1978), Roy and Diewert (1978), and Diewert and Roy (1978) have indicated that distance information is based on the integration of location information, some studies have reported evidence that could refute the notion that location information subserves memory for movement distance. Stelmach, Wallace, and McCracken (1977) examined whether extending the length of time spent at the beginning and the endpoint of a criterion movement could strengthen the encoding of distance information, and found no facilitation. Russell (1978) also reported that the time spent at the endpoint of a criterion movement is not a confounding factor in studies of linear positioning. He suggested, however, that a duration of 2 sec at the movement's end-location may be the most suitable for tasks of this type. Doody (1977) investigated the possible use of a location-based strategy for encoding distance information by employing two different conditions for presenting the starting positions of reproduction movements. In one condition, the subject's hand was moved directly from the endpoint of the criterion movement to a new starting position for the next reproduction movement. In a second condition, the subject's hand was first moved back to the initial starting position and then on to the new starting position for the reproduction movement. Doody found no difference in absolute (AE), variable (VE), and constant (CE) errors between the two conditions, suggesting that explicit information about the change in the starting positions may not be essential for the encoding of distance information. Kelso and Holt (1980) also reported similar results indicating that information on changes in starting position has little influence upon reproduction accuracy.

If subjects can use location cues as reliable basis for encoding distance information, then reproduction performance should not be affected by changes in starting position. However, effects of starting position manipulation upon the reproduction of distance have often been reported (Kerr, 1978; Marteniuk & Roy, 1972; Shibayama, 1983; Stelmach & Kelso, 1973; Walsh et al., 1979; Imanaka & Abernethy, 1992a). Thus, it is suggested that a location strategy may not effectively contribute to the encoding of distance information.

KINESTHETIC SIGNALS AND ABSTRACT CODE: THE SWITCHED-LIMB PARADIGM

The Target Hypothesis

Russell (1976) advocated the use of the target hypothesis as means of explaining the selective retention of location information in motor memory. The target hypothesis was originally developed by MacNeilage (1970) to explain a basic problem in speech production; the problem of how the oral articulators (i.e., the tongue and lips) are able to achieve a relatively invariant end location specific to a given phoneme despite having variable starting positions (brought about by differences in the requirements of the preceding phoneme). Explanations based on rule-governed rearrangements of a set of invariant motor commands to the oral articulators could not account for this basic problem in speech production (MacNeilage, 1970). The target hypothesis postulates an internal space coordinate system, within which target location of the oral articulators for a particular phoneme is coded as a specific point. The generation of the necessary movement patterns for speech production is assumed to be based on the spatial location information coded within the space coordinate system. Russell extended MacNeilage's target hypothesis to limb movements and proposed that the spatial location for limb movements is coded into memory as a specific point within the individual's space coordinate system. The actual kinesthetic signals derived from a limb movement were believed to be converted into a more abstract form and coded as a spatial location within the space coordinate system. Russell postulated that movement production and control is achieved by a response generator using spatial location information rather than relying upon stored neural commands or their sensory consequences.

Examinations of the Target Hypothesis

Supporting evidence. Wallace (1977) tested one particular prediction of the target hypothesis – the prediction that the reproduction of limb location is based on an abstract location code rather than upon the actual kinesthetic signals available from the criterion movement. To test this prediction Wallace developed the switched-limb paradigm, in which subjects were required to reproduce the end-location of the criterion movement with the opposite hand to the hand used for the criterion movement. This switched-limb paradigm is assumed to force the subject to rely more on abstract information than upon specific kinesthetic information available from the criterion movement. Wallace conducted three experiments in which subjects were required to reproduce the end-location of a criterion movement, using an experimental design in which both the hand used (same-limb or switched-limb) and the movement direction (same or opposite) were manipulated. When the direction was the same for both the criterion and reproduction movements, reproduction accuracy (in terms of AE and VE) of the switched-limb condition did not differ from the same-limb condition. This finding supports the target hypothesis. However, when the direction of movement was altered from criterion to reproduction, switched-limb reproduction became inaccurate while same-limb reproduction was not affected. Wallace concluded from these data that there is a limitation in the generality of the target hypothesis, and that the abstract location code can only be utilised only when movement direction is the same for both criterion and reproduction movements. He also suggested that under the same-limb condition, the specific kinesthetic signals may be the primary source of information about the end-location of the criterion movement. This was because the alteration of movement direction did not interfere with the same-limb reproduction.

Non-supporting evidence. Larish, Stelmach and McCracken (1979) examined the reproduction accuracy of both vertical and horizontal limb movements under matching, same-limb, and switched-limb conditions. Same-limb and switched-limb conditions required subjects to make a criterion movement, remove the limb from the end-location, and then reproduce the end-location with the same or opposite limb. The matching condition required subjects to move one limb to a criterion location, then, while maintaining this position, move the opposite limb to match the same end-location. Matching and same-limb reproduction were generally not different in accuracy (in terms of AE), while switched-limb reproduction was less accurate than both the matching and same-limb conditions. These results therefore did not corroborate Wallace's (1977) findings, implying rather that the abstract location code is retained less accurately than the kinesthetic afferent information. Larish and Stelmach (1982) conducted similar experiments using vertical and horizontal positioning movements, and reported that reproduction performances were not different between the same-limb and switched-limb conditions when the spatial targets could be coded in conjunction with body reference points. In contrast, when the spatial targets could not be easily linked to body reference points (such as when the targets were located outside egocentric space), the switched-limb reproduction was less accurate than the same-limb condition. Larish and Stelmach concluded that when a positioning movement is to be based on the spatial location code, body-based spatial reference points are necessary.

Concurrent Contributions of Kinesthetic Signals and Abstract Code

Empirical evidence. Summers, Sommer, Sharp, Levey, and Murray (1982) investigated the reproduction of movement distance under same-limb and switched-limb conditions. These researchers also manipulated movement direction to reduce the reliability of the specific kinesthetic information from the criterion movement under the same-limb conditions. When movement direction was the same for both criterion and reproduction movements, same-limb reproduction was more accurate (in terms of AE) than switched-limb reproduction. When movement direction was altered, reproduction accuracy was not different between the same-limb and switched-limb conditions. Based on these findings, Summers et al. concluded that when movement direction is invariant same-limb reproduction is primarily made on the basis of the sensory consequences of the criterion movement. However, when either movement direction or the limb used is altered between the criterion and reproduction movements, the kinesthetic information derived from the criterion movement is difficult to utilise for the reproduction of movement distance. Hence, under these conditions, the abstract information derived from the kinesthetic signals available during the criterion movement is used to guide the reproduction movement. Summers et al. suggest, therefore, that distance is coded on the basis of both kinesthetic and abstract information, with the balance between these two information sources varying according to the specific experimental conditions or movement context.

Retention characteristics. Fober and Reeve (1985) investigated the retention characteristics of the kinesthetic information and of the abstract spatial information. Subjects were required to reproduce the end-location of a criterion movement following either a 5-sec or 30-sec retention interval, using either the same limb or switched (opposite) limb. No differences were found between the two reproduction conditions at either of the retention intervals, although under both limb manipulations reproduction accuracy (in terms of AE and VE) decreased as the retention interval increased. This finding suggests that the retention characteristics are similar for abstract spatial information and specific kinesthetic information for retention intervals up to at least 30 sec.

The nature of movement representation in memory has also been examined through the use of a learning paradigm. Reeve and Cone (1980) examined the encoding and retention characteristics of location information acquired over a number of learning trials. Blindfolded subjects learned the criterion end-location of a linear movement with the right hand over 13 trials in which KR (knowledge of results) was given on each trial in terms of both the direction and amplitude of the subject's response to the criterion location. The learned location was then reproduced without KR under either same-limb or switched-limb conditions. No significant differences between the same-limb and the switched-limb reproduction conditions were found. This finding was consistent with the prediction from the target hypothesis (Russell, 1976), that kinesthetic information is converted into an abstract spatial code within a spatial coordinate system, and that reproduction is based on this abstract code. However, Lee and Magill (1985) have reported some evidence against the abstract representation of location information in memory. In one of their experiments (Experiment 2), blindfolded subjects learned the end-location of a constrained linear criterion movement, made to a metal stopper, over 16 trials of practice. The subjects were then required to reproduce the learned location, without the stopper, either with the same-limb or the switched-limb for a further 16 trials. Results showed reproduction of the same-limb condition to be superior to the switched-limb condition, both in terms of response accuracy

(AE) and consistency (VE), suggesting that movement representation is based on response-produced feedback information available during the acquisition trials.

Summary and Implications

Collectively then, a number of studies have presented some support for the target hypothesis (Russell, 1976), whereas evidence inconsistent with this viewpoint has also been reported (e.g., Imanaka & Abernethy, 1992b). For example, abstract location information may not be as accurately utilised as specific kinesthetic information for the reproduction of movement location when movement direction is altered between the criterion and reproduction movements (Wallace, 1977) or when body-based spatial reference points are not available (Larish & Stelmach, 1982). Kinesthetic information is utilised more accurately than abstract information for the reproduction of movement distance when movement direction is invariant but is difficult to use when movement direction is altered, even when the same-limb is used (Summers et al., 1982). In addition, no differences in the retention characteristics between the kinesthetic and abstract codes have been reported (Fober & Reeve, 1985). Collectively, these findings suggest that movement reproduction may be based, to some extent, on both specific kinesthetic information and abstract information (cf., Stein, 1983), with the balance of these two sources being dependent upon the specific movement situation.

This notion that movement reproduction may be based on both kinesthetic and abstract information is consistent with a recent neuropsychological view of spatial cognitions. Kritchevsky (1988) has argued that complex spatial tasks are dependent on both spatial and nonspatial functions in the brain, and that the spatial functions are independent of the sensory modality involved in spatial cognition. Kritchevsky suggests that regardless of the sensory modality employed, sensory information regarding the location of an object or body parts may become encoded as an abstract spatial quantity stored in a mental coordinate system. This notion of spatial cognitions is generally the same as the target hypothesis proposed by Russell (1976). Russell's target hypothesis, involving the notion of both spatial coordinate systems and abstract information, is based on data from long-term memory experiments. However, the Kritchevsky concept is not limited to long-term memory but relates to spatial perception, which necessarily also involves the short-term memory of spatial sensory stimuli. The notion of abstract information can therefore be extended into the motor short-term memory domain as well as the long-term memory domain. Accordingly, the respective roles of specific sensory information and more abstract information in motor tasks seems to be an important issue worthy of further investigation.

CONCLUSIONS

We examined the models of motor control and short-term memory which have intensively been investigated since the 1970s. In examining peripheral and central sources of movement information, some researchers have stressed either peripheral feedback factors or central control aspects, while others have focused on both factors to be integrated for effective motor control. We first reviewed both the dual-storage model of short-term memory in which information about movement location and distance is stored (Laabs, 1973) and a typical efferent model of motor control which emphasises the potential motor control role of central monitoring of efferent signals (the CME model proposed by Jones, 1972, 1974a, 1974b). In conjunction with the CME model, we then examined two models of preselection effects: a cognitive model (Roy & Diewert, 1975, 1978) and a cognitive/efferent model (Kelso, 1977a, 1977b). Following this we reviewed specific models of the control of movement end-location (both the Bizzi's and Feldman's versions of mass-spring model) and of movement distance (the coding strategy explanations proposed by Diewert & Roy, 1978, and other researchers). Finally, we discussed the contribution of both kinesthetic signals and abstract code to the storage of location and distance information for controlling limb movements.

Although these models and conceptualizations of motor control and short-term memory have been proposed since the 1970s, the underlying mechanisms of perceptual-motor control and motor short-term memory are still far from clear. The issues of perceptual-motor control, other than those of motor short-term memory (see Imanaka et al., 1993, for the reason of the cessation of this sort of investigations that arose in the early 1980s), have recently been examined, more intensively than in the 1970-80s, by a number of researchers (Colebatch & McCloskey, 1987; Gandevia, McCloskey, & Burke, 1992; McCloskey, 1993; McCloskey, Macefield, Gandevia, & Burke, 1987) from different disciplinary areas, such as neurophysiology, neuropsychology and psychology. In particular, some researchers (e.g., Biguer, Donaldson, Hein, & Jeannerod, 1988; Taylor & McCloskey, 1991; Rubens, 1985) suggest that both visual and kinesthetic afferent information may well concurrently (with an interaction between these two types of information) mediate the control of limb and/or whole body movements. This implies that such a multisensory contribution to motor control should be further investigated to fully understand the mechanisms underlying various human motor behaviours.

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