Human Movement Science 28 (2009) 566–577

Contents lists available at ScienceDirect

Human Movement Science

journal homepage: www.elsevier.com/locate/humov

Current status of the motor program: Revisited

Jeffery J. Summers [a,*], J. Greg Anson [b]

[a] Human Motor Control Laboratory, School of Psychology, University of Tasmania, Private Bag 30, Hobart, Tasmania 7001, Australia
[b] Department of Physical Education, University of Otago, Dunedin, New Zealand

ARTICLE INFO

Article history:
Available online 23 February 2009

PsycINFO classification:
2330

Keywords:
Motor program
Pre-programming
Internal representation
Hierarchical organization
Neural mechanisms
Motor engram

ABSTRACT

The motor program is a concept that has had a major influence on theorizing in the field of motor control. However, there has been a lack of consensus as to what exactly is a motor program and its role in movement organization and execution. In 1994 Morris, Summers, Matyas, and Iansek concluded from a review of the application of the motor program concept in the field of physical therapy that continued use of the term may impede progress in the field. In this paper we examine what has happened to the motor program concept in the thirteen years since the previous evaluation. The review indicates that although the term is still being used in different ways, the theoretical existence of a motor program appears to be generally accepted by researchers in experimental psychology, movement science, and neurophysiology. The recent development of powerful brain imaging techniques may allow determination of whether the motor program should be regarded as a metaphorical or literal concept.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

The explanatory construct "motor program" is one of the most durable and robust phenomena in the motor control literature. From a behavioral perspective it coexists with concepts like memory, learning, serial order, pre-cueing, and feedback. In biological perspectives "motor program" coexists with durable ideas like cell assemblies, neural models, and central pattern generators. If we ask the general question as to *why we need motor programs*, most people would probably answer that motor programs are good for us because they allow for fast and accurate execution of motor activities with minimal involvement of attention: the burden of control being delegated to automatic processes. In

* Corresponding author. Tel.: +61 3 6226 2884; fax: +61 3 6226 2883.
E-mail address: Jeff.Summers@utas.edu.au (J.J. Summers).

0167-9457/$ - see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.humov.2009.01.002

this view motor programs are associated with skill, practice, and efficient adaptation. Successful fast and accurate performance appears unexplainable unless it has emerged from anticipation, anticipation that is dependent on knowing what to do and how to do it *before* a temporally dependent signal indicates it is imperative to start the movement. This notion of knowing what and how to move before the movement is initiated has been one of the most compelling arguments for the existence of some form of internal representation or "motor program" of a skill.

The notion of a motor program, however, has been controversial and opposing views surrounding the concept became the center of the intense debate between advocates of so-called "dynamic" and "cognitive" approaches to motor behavior. In fact, in 1994 one of us (JS) co-authored a paper entitled "The current status of the motor program", published in the journal *Physical Therapy*. The particular focus of this paper was to evaluate the use of motor programming theory as a framework for clinical practice in physical therapy. In that paper concern was expressed that the motor program was being defined in a variety of ways by researchers within and across disciplines and concluded that "continued use of the term may impede progress in the field". Coincidentally GA was co-author on a paper entitled "Cortical cell assemblies: A possible mechanism for motor programs" published in the *Journal of Motor Behavior* in the same year (1994). The primary aim of this paper, therefore, is to evaluate what has happened to the motor program concept in the ensuing thirteen years. To do this effectively we need first to review the history of the motor program concept highlighting the iterations of the concept over the years leading up to 1994.

2. Origins of the motor program

Observations requisite to a motor program notion can be identified in anecdotes and legends dating back at least to the 15th century. For example, the legend of Klaus Störtebeker (c. 1360–1401) a German pirate who was sentenced to be executed by beheading relates that he asked to be allowed to walk, after having his head removed, along the line of his confederates and that as many as he passed before falling should be allowed to go free. Reports (Wikipedia and Erwin-Rosenthal, 2008) are inconsistent as to how many men Störtebeker's body passed before it fell or was tripped but apparently between 5 and 12, none of whom were spared the executioner's axe. That Störtebeker's body walked at all is an example of the influence a stored representation of neural signals, perhaps in the form of a central pattern generator or a primitive motor program that enabled the distribution of temporally correct impulses to the locomotor muscles that allowed walking to occur.

Beyond legend there is a fascinating history of research about the search for explanations to account for the mental processes and biological mechanisms underlying motor control and the human sensory-motor system. The derivation can be traced along at least two seemingly parallel and independent paths back to 18th century astronomers attempting to precisely measure the transit of stars. According to the German medical physiologist turned psychologist Wilhelm Wundt (1912), the historical record of the Greenwich Observatory in 1795 indicates "The astronomer . . . dismissed his assistant as unreliable because he acquired the habit of seeing all stellar transits half a second too late" (p. 268). Apparently the astronomer failed to appreciate that he had the advantage of anticipation and motor preparation facilitating his response while the assistant was always required to "react" to the astronomer's command. While Wundt's discussion emphasized issues of timing per se, it raised questions about the roles of attention, sensory modality, and precision of measurement in what was essentially a simple voluntary movement, requiring a fast and accurate response. Although he wrote about the physiological and psychological contributions to the time required to respond, Wundt (1912) also proposed that the two dimensions could not be separated and that it was impossible to: "ascertain with even conjectural probability the time-value of the mental component" (p. 275). A few years before Wundt's career began Frans Cornelis Donders (1818–1889) (Donders, 1868), who lived just over the border in Holland, and who was also medically trained, sought to unravel the mechanisms of mental processes from their underlying biology. Although the careers of Donders and Wundt overlapped chronologically it appears that these eminent scholars, pursuing answers to the same questions, never met and were unaware of the others existence. Even more remarkably they shared the mentorship of another eminent scholar, Hermann von Helmholtz who according to Woodworth (1938) invented the reaction time experiment (which was later to become an important instrument in tests of the motor program hypothesis) in 1850, yet neither Wundt (who worked for Helmholtz) nor Donders (a friend and colleague of Helmholtz) appears to have referenced Helmholtz in their writings. Donders, 14 years older than Wundt (1832–1920), published his now classic article "On the speed of mental processes" in Dutch in 1869, at least 10 years before Wundt set up "the first psychological laboratory in the world" at the University of Leipzig and importantly, before doctoral students like Cattell (who later became Woodworth's doctoral supervisor) had begun studying with him. It is clear that unlike Wundt, Donders considered the discovery of mechanisms underlying mental process to be very much associated with the physiological and metabolic processes of the brain and amenable to investigation: "... physiology tries to locate the various mental faculties as much as possible by experimentation, and especially to trace the nature of the action accompanying the mental phenomena." (Donders, 1969; translated from the original, 1869).

From our perspective, history indicates that despite Donders' conviction that mental processing was underpinned by brain activity, it was Wundt's legacy of introspection and behavioral measurement handed down to Cattell and through Cattell to Woodworth (Woodworth, 1899) that shaped much of the thinking about motor preparation and eventually the motor program hypothesis. Even Henry and Rogers (1960) "memory drum theory of neuromotor reaction" focused on the behavioral effects of memory demands on motor preparation. On the broader stage of psychology in general however, the nature of neural mechanisms underlying mental processes was addressed in detail with the publication in 1949 of Donald Hebb's "*The organization of behavior*" (Hebb, 1949). Hebb proposed a cortical cell assembly model and suggested that assemblies formed when groups of neurons worked together resulting in both structural and functional change at the synaptic level. This spawned what has become a vast literature in long-term potentiation – the pre-eminent mechanism to explain learning and memory in the brain. Hebb's model was also the impetus for linking a biological mechanism to the behavioral processes exemplified in the motor programming hypothesis (Wickens, Hyland, & Anson, 1994).

Ideas linking brain and motor behavior were initially voiced by Harvard University neurophysiologist Karl Lashley (1951) in his treatise on "*The problem of serial order in behavior*", seen by many modern writings in motor control and coordination as the origin of the concept of a motor program. At the time of writing the dominant view of sequence representation was S-R chaining in which successive responses are triggered by kinaesthetic feedback from the proceeding response. To Lashley, the "occurrence of pre-determined, orderly sequences" in language indicated that the integrated character of behavior cannot be explained by simple S-R chaining mechanisms. The problem, as he saw it, is that the constituents of such sequences have no intrinsic order of association and serial order cannot, therefore, be based on associative connections between elements. Importantly, Lashley argued that not only speech, but all skilled acts seem to involve the same problem of serial ordering even down to the temporal coordination of muscular contractions in such movements as reaching and grasping. The solution to the problem of serial order he proposed was to assume the existence of units of action that can be pre-set or pre-activated and that receive trigger commands specifying the order in which they are to occur when activated. Although Lashley never used the term 'motor program', the notions of the pre-selection of the constituents of a sequence of acts and the advance temporal organization of their unfolding, were the essential ingredients for the development of a particular theory of sequence representation, namely, motor program theory.

While the importance of identifying the problem of serial order as spanning across widely differing levels of behavioral organization cannot be denied, it may also be seen as the root of some of the present day difficulties in the appropriate use of the programming notion[1]. That is, positing similar mechanisms of order and organization irrespective of the nature of the units (muscles, movements, speech sounds, words sentences etc.) has allowed considerable license in the use of programming notions and blurred qualitative differences that exist between different levels of organization. The temporal organization of speech sounds, for example, covaries with meaning, whereas the temporal organization of

[1] For many of the arguments presented in this article I (JS) am indebted to many intense discussions of the motor program concept with my esteemed colleague and friend the late Andras Semjen.

muscle contractions covaries with dynamics. Thus, the former domain involves a degree of arbitrariness that cannot be expected to occur in the latter. The difficulty of implementing Lashley's intuitions on serial behavior across levels of organization has lead to a bifurcation giving rise to conceptions of the motor program that are primarily concerned with movements and muscle commands (movement control) and theories focusing on the cognitive representation of the expected unfolding of motor events (movement planning).

3. Keele (1968) – the motor program

The influence of Lashley's notion that sequences of behavior must be organized centrally before their initiation can be seen in, perhaps, the most widely quoted definition of a motor program "as a set of muscle commands that are structured before a movement sequence begins and that allows the entire sequence to be carried out uninfluenced by peripheral feedback" (Keele, 1968, p. 387). Contained within this definition were two important components: prior planning and movement execution without reliance on feedback control. For Keele, the notion that with practice a sequence of movements becomes stored in the memory system so that it can be executed without constant correction by reference to the environment provided a solution to the central issue in the study of skilled movements, "how the laborious, conscious movements of the novice come to be performed with the minimal involvement of attention." (Posner & Keele, 1973, p. 806).

Two aspects of the initial definition, however, unintentionally caused animated debate and problems for the motor program that still plague the concept today. The first was the inference that the sequencing of a skill is represented centrally as a "set of muscle commands" and the second was the inference that entire sequences of actions can be executed "...uninfluenced by peripheral feedback" (p. 387). Although it became clear in his later writings (Keele, 1981; Keele & Summers, 1976) that Keele did not intend for the term "muscle commands" to be taken literally and that he saw a critical role for feedback in skilled performance in terms of performance monitoring and in updating or changing programs if needed, this initial definition provoked numerous criticisms. The primary concern was one of storage. That is, it is not clear how the CNS could store all the motor programs required to specify every muscle in the human body for the variety of movements a person can make. In retrospect, it is interesting to note that in the Keele and Summers (1976) book chapter "The structure of motor programs", the authors presented a more qualified view suggesting that the sequence of movements in at least some skills is represented centrally as a motor program. It was also acknowledged that the skills on which the motor program concept is based have a strong innate component, whereas many human skills are learned and evidence on the form of representation for such skills is lacking. It was even suggested that S-R chaining theory may provide a better explanation for learned skills.

In an attempt to address some of the limitations of the strict view of a motor program, Schmidt (1975) in his seminal *Psychological Review* article, "A schema theory of discrete motor skill learning", proposed the notion of a *generalized motor program (GMP)* as an abstract memory structure that provides the basis for generating responses within a movement class. The GMP, therefore, contains a set of invariant features that are shared by movements within a class with specific movement parameters being assigned prior to initiation by a recall schema. The impact of Schmidt's application of schema theory to the motor domain is undeniable with the paper receiving 862 citations as of the end of 2007 (see Newell, 2003; Schmidt, 2003; Shea & Wulf, 2005; Sherwood & Lee, 2003, for recent critical reviews of schema theory). Keele (1981) also clarified his position with regard to the motor program concept along similar lines arguing that it should be viewed as a multi-level of hierarchic system starting with abstract descriptions of the skill and ending with a specific sequence of muscular action. In his view the motor program, in its most general sense, can be defined as "a central representation of a sequence of motor actions" (p. 1400) that involves a number of brain areas in interaction. Given the prominence of "muscle commands" in the 1968 definition, it is interesting to note that the abstract representations do not include effectors or muscle groups. These features are now selected prior to execution, thereby allowing the same motor program to be executed with different effectors (e.g., signing one's names with left and right hands).

These re-definitions of the motor program concept provoked a flurry of research in two directions. The first concerned identifying the invariant properties that are contained in the abstract representation of a movement class and those mutable parameters that are specified prior to execution to tailor a movement to a specific situation (e.g., Summers, 1975). Not surprisingly because of the nature of the skill, handwriting was seen as an archetypical task for the application of motor program theory (Plamondon, Stelmach, & Teasdale, 1990; Stelmach, Mullins, & Teulings, 1984; Teulings, Thomassen, & van Galen, 1986). Although the subject of much debate, sequencing, relative timing, and relative force have been identified as invariant features of movements controlled by the motor program with overall duration, overall force, and effectors being mutable movement parameters (see Summers, 1981 for review).

The second line of research concerned the processes involved in the selection and parameterization of the motor program, that is, the planning of movement. Keele (1981) emphasized that:

> ...even for well-practiced programs, considerable planning for a movement occurs in the interim between a signal to respond and the beginning of the movement itself. (p. 1412).

As the pre-programming of responses was seen as a cognitive process, this aspect of the motor program concept became the focus of researchers in experimental psychology (e.g., Klapp, Abbott, Coffman, Snider, & Young, 1979; Rosenbaum, Inhoff, & Gordon, 1984; Sternberg, Monsell, Knoll, & Wright, 1978). Typically, the pre-programming process has been investigated in experiments which measure the time to initiate (reaction time) a movement sequence as a function of the nature of the sequence to be produced. The reaction time approach, however, has been plagued by methodological issues and debates over whether simple or choice reaction time is the most effective design to investigate pre-programming processes (see Klapp, 1996 for a review) and the extent to which online programming can occur (e.g., Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979). In general, the results from these studies have been interpreted within the information processing framework with its strong analogy between the workings of the brain and a computer (e.g., Anson (1982, 1989)). That is, the motor program being stored in memory had to be read out into a temporary buffer and assembled in the correct order before execution. In line with the computer metaphor, the results tended to show that the longer and/or more complex the movement sequence to be performed the longer the reaction time. Of particular importance in the research examining the programming process was the development of the movement pre-cueing technique which allowed the examination of the organization of the processes involved in the selection of response parameters (e.g., effector, direction, and extent) prior to movement initiation. By comparing the effects on reaction time of providing various forms and amounts of advance information about the dimensions of the required response, the temporal organization of the planning, and preparation processes can be determined (see Rosenbaum, 1983, for review). Despite numerous studies of the pre-programming process and the development of some sophisticated models of sequence generation, such as the hierarchical editor model (Rosenbaum et al., 1984) and tree-traversal model (Rosenbaum, Kenny, & Derr, 1983), the planning process is still not fully understood. Part of the problem, alluded to earlier, stems back to Lashley's assumption that all skilled acts involve the same problem of serial ordering. This view has lead, perhaps inappropriately, to the application of models developed in other areas of cognitive psychology, such as memory search paradigms (Sternberg et al., 1978), to the issue of the selection and parameterization of central representations of sequences of movements.

Thus the motor program concept underwent considerable metamorphosis in the 10 years following Keele's (1968) initial definition. In particular, the concept evolved more towards the planning aspect of the definition (process) than the internal representation of a sequence of movements components (product or entity). Keele, Cohen, and Ivry (1990), for example, defined the motor program as "...the representation of the orders of actions rather than their elementary movements... a plan" (p. 78). However, as indicated by Rosenbaum (1984) the terms programs and plans are not usually regarded as synonymous as: (1) programmed spans of activities are typically shorter than planned spans of activity; (2) programs, in contrast to plans, lead directly to motor activity; and (3) plans have a conscious component, whereas programs occur outside of consciousness. Furthermore, it appeared that many researchers chose to adhere to the original strict view of the concept. For example, Chez (1985) in the *Principles of neural science* stated that:

> Before we reach out for an object, our nervous system must first select a motor program that specifies (1) the sequence of muscles needed to bring the hand to the desired point in space and (2) how much each muscle must contract (p. 494).

In the 1994 review of the physical therapy literature (Morris, Summers, Matyas, & Iansek, 1994), it was also noted that, although there has been great interest in motor program theory as a basis for physical intervention, in most instances the original definition of the motor program as a set of muscle commands was being used.

In the early 1990s a number of researchers in the motor control field expressed concern at the almost universal usage of a term that had such an extremely loose definition (e.g., Alexander, DeLong, & Crutcher, 1992; Shaffer, 1992; Summers, 1992). For example Shaffer (1992) stated that: "The term motor programming is nowadays used so loosely that it is at danger of losing its meaning." (p. 181) and even more forthright was Alexander et al.'s (1992) appraisal of the concept:

> In its most general form, the concept of the motor program is relatively unassailable ... At best, "motor program" is a convenient but misleading label that serves mainly to obscure our ignorance of the brain's actual approach to motor processing. We suspect that widespread, uncritical usage of this poorly defined term may in fact have impeded progress in understanding the neural substrates of motor control. (p. 658).

However, by far the greatest challenge to the motor program concept has come from proponents of the emerging (no pun intended) ecological/dynamical systems approach to human behavior (Kugler, Kelso, & Turvey, 1982).

4. The dynamical systems approach

In their seminal paper Turvey, Fitch, and Tuller (1982) argued that the understanding of the control and coordination of movement will be directly correlated with "...the degree to which we can trim down the homunculus concept" (p. 243) from explanations of skilled behavior. They set up a strawman debate typifying current models of motor behavior as requiring a homunculus-type entity to select a motor program from a library of programs stored in memory and then orchestrating the execution of the movement sequence on the cortical and spinal level keyboards (Summers, 1998). The ecological approach challenged the prescriptive nature of the motor program concept and its failure to exploit the intrinsic dynamics of structural and functional constraints that shape movement output. In place of the motor program dynamical theorists proposed coordinative structures that are considered as intentional, soft-assembled, autonomous multi-level entities governed by dynamical principles of self-organization. That is, coordinative structures are assembled to achieve a particular goal and, being soft-assembled, they exist only until the goal or intention is achieved. Furthermore, as they function autonomously there is no need for online central/attentional control. In many respects the above characteristics are also attributes of traditional motor programs. The critical difference between the two concepts appears to be the notion of self-organization which allows the "trimming down of the homunculus" in movement control and coordination. Enunciating the dynamical principles of self-organization is beyond the scope of the present paper and the reader is referred to Kelso (1995) and Thelen and Smith (1994).

In 1992 Abernethy and Sparrow presented an analysis of publications in the *Journal of Motor Behavior* for the period 1975–1989 linked theoretically to either motor program or dynamical systems perspectives. It was concluded that the motor learning and control field was in the midst of a Kuhnian-type paradigm crisis that was unlikely to be resolved through reconciliation of the two views. The authors suggested that the field was destined to enter a period of paradigmatic debate and division but were unable to predict the view that would emerge as dominant.

The above describes the background against which the 1994 *Current status of the motor program* review was written. At that time it was argued that the lack of consensus as to what exactly is a motor program or whether it is a metaphoric or literal term made its continued use questionable. In the remainder of this paper we will examine what has happened to the motor program concept since the 1994 review.

5. Motor programs vs. coordinative structure

Despite Abernethy and Sparrow's negative prognosis, a few motor program proponents have argued for reconciliation between the two theoretical perspectives (Semjen, 1996; Shaffer, 1992; Summers, 1989, 1992). For example, Summers (1989) suggested a general model of bimanual coordination in which the timing of two-handed movements may be a secondary consequence of the entrainment between low-level oscillatory mechanisms or it may reflect some higher level control process. The interaction between oscillator mechanisms is responsible for the preferred/intrinsic tendencies (i.e., synchrony/in-phase and alternation/anti-phase) observed between the limbs in voluntary activity. Higher order processes that can influence the coupling between the oscillatory systems produce the adaptability and flexibility characteristic of skilled performance. The particular level at which timing is controlled by factors such as the task demands and stage of learning.

Other more formal integrated models have also assumed that skilled actions are arranged on two levels in the brain, a *motor program level* on which the goal structure of action is represented, and a *motor system level* which can autonomously compute a coordinated movement to a goal. Thus in this view, motor programming is seen as generating a transient and continuously renewed representation of motor goals/targets that can be used by a self-organizing motor system to realize these goals (Semjen, 1992; Shaffer, 1992). These two-level 'hybrid' models have been proposed predominantly by cognitive theorists and still seem to provide the most compelling models of skills that involve the production of complex sequences of movements, as in language, handwriting, typing, and piano playing (see also Oliveira & Ivry, 2008). Interestingly, there has been a recent proposal by a dynamical theorist that a potentially profitable future direction may be "...to consider dynamics as the background for tasks – particularly natural, rhythmic movements – on which are superimposed cognitive constraints" (Amazeen, 2002, p. 249).

6. Neural mechanisms for motor programs

Although Keele (1968) used the term motor program metaphorically, its continued use has led many researchers to regard the concept as a literal entity. This view has been bolstered by papers suggesting possible physiological mechanisms for motor programs. Wickens et al. (1994) argued that a motor program may be conceptualized as a cell assembly (Hebb, 1949), which is represented in the motor areas of the cerebral cortex in the form of strengthened synaptic connections between cortical pyramidal neurons. The basal ganglia are given the role of selecting and activating the stored cell assemblies. In this account the motor programming process involves bringing the cell assembly close to ignition point so that only a small amount of additional input is required to push the activity above some threshold to produce initiation of the movements controlled by the motor program.

This proposed neural corollary of the motor program concept has been invoked to explain the finding that when an acoustic startle stimulus (124 dB) is presented in a simple reaction task, the prepared movement is involuntarily initiated much earlier in comparison to voluntary initiation (Valls-Solé, Rothwell, Goulart, Cossu, & Munoz, 1999). Since startle elicited RTs appear to be too short to have involved cortical loops, it has been suggested that the motor program responsible for the response had been prepared and stored subcortically and its initiation triggered by the startling stimulus (Carlsen, Chua, Inglis, Sanderson, & Franks, 2004; Carlsen, Dakin, Chua, & Franks, 2007; Valls-Solé et al., 1999). Furthermore, in line with the hypothesis that cell assemblies are the neural mechanism for motor programs, it has been proposed that under certain circumstances (e.g., simple RT tasks) a motor program may be stored subcortically in the reticular formation either as strengthened synaptic connections or a reduced threshold between reticular neurons (Carlsen et al., 2004).

It also appears that the opposite effect to that of a startle stimulus can be induced in a simple RT task by the delivery of a single stimulus (electrical or magnetic) to the brain in the interval between the imperative stimulus and the onset of the voluntary response. That is, a single brain stimulus can delay (or facilitate depending on the timing and intensity of the stimulus) the execution of the movement by up to 150 ms without affecting the agonist and antagonist EMG pattern once the movement is initiated (Day et al., 1989). The authors suggest that the brain stimulus delayed movement initiation by inhibiting a group of strategically placed neurons in the motor cortex making them unresponsive for a brief period to command signals indicating initiation of the motor program. The selective facilitation or inhibition of a response evident in startle and interruption paradigms are, therefore, consistent with the original notion of a motor program as consisting of a sequence of agonist/antagonist muscle commands stored in memory that can be loaded into a motor buffer either cortically or subcortical in preparation for movement initiation.

Given that Keele's (1968) definition of a motor program was greatly influenced by studies on the development of birdsong, it is perhaps not surprising that the strict view of a motor program as a structure specifying all the details of movement has played a dominant role in many neural models of animal behavior. In these models, as in that of Wickens et al. (1994), the basal ganglia play a prominent role as the group of nuclei that influence the selection and activation of motor programs. In this literature there is a direct link drawn between the motor program concept and the concept of central pattern generators (CPGs), neuronal networks located in the spinal cord that appear to underlie locomotion, and other basic movement patterns in animals and perhaps humans. Grillner and colleagues, for example, argue that the nervous system contains a toolbox of motor programs (innately determined neuronal networks) in the brain and spinal cord that are designed to produce the basic motor repertoire needed for survival. Sophisticated neuronal models of the selection and activation of these motor programs have been developed involving the interaction between pallidal and striatal basal ganglia neurons with higher level input from the cerebral cortex and thalamus (see Grillner, Hellgren, Menard, Saitoh, & Wikstrom, 2005 for a review). Clearly, the concept of the motor program in this literature is closer to the original 1968 definition than the later revisions. For example, in a review paper entitled "Motor control programs and walking" (Ivanenko, Poppele, & Lacquaniti, 2006) the authors argue that "...motor programs may be considered as a characteristic timing of muscle activations linked to specific kinematic events" (p. 339) and for the control of arm movements in the octopus it is suggested that the motor program is embedded within the neural circuitry of the arm itself (Sumbre, Gutfreund, Fiorito, Flash, & Hochner, 2001). Interestingly, typing the term 'motor program' into GOOGLE produced the following definition:

> A motor program or action pattern is a distinctive stereotyped pattern of movement carried out by most healthy members of a species. They are shaped by the animals genetic heritage, "wired in" to the nervous system.

7. Current status of the motor program

Over the 40 years since the Keele (1968) paper the theoretical existence of the motor program has become accepted by researchers in the fields of experimental psychology, movement science, and neurophysiology. Despite this general acceptance there is still no objective measure of what a program is, what it contains, and how and where it is created. The concept has also survived the onslaught from the dynamical systems approach that has offered a radically different model of motor learning and control. For as Newell (2003) observed, the protagonists seem to have tired of the debate and agreed to disagree. The field appeared to have settled into, in Kuhnian terms, a period of normal science with researchers pursuing the theoretical framework to which they have become aligned. Perhaps as Keele (1998) has argued:

> The gulf between those who think about motor control in terms of "motor programs" and those who think about motor control in terms of dynamical systems is due less to competing conceptualizations for the same phenomena than to the kinds of phenomena with which different groups of investigators are concerned. Investigators of a dynamical systems persuasion very often are

> concerned with movement processes per se and most often with movements that repeat periodically. The focus in many of the studies taking a programming or process decomposition view comes instead – at least for me – from a concern with a rather different class of skills that exhibit quite different phenomena. These skills include such things as keyboard skills, phoneme sequencing in speech, and the assembly of a set of actions as in woodworking. ....Skills of this sort typically are learned and are not developed from a special evolutionary base. (pp. 403–404).

In recent years, however, there has been a renewed interest in the cognitive aspects of motor performance, sparked in part by a controversial paper in 2001 in the journal *Nature* by Franz Mechsner and colleagues. In this paper Mechsner, Kerzel, Knoblich, and Prinz (2001) presented a series of cleverly designed experiments suggesting that the constraints on bimanual coordination may have a perceptual origin, rather than reflecting motor system constraints as had been argued by dynamical systems researchers. The strong claim "...that human voluntary control is purely and directly perceptual-cognitive, or psychological, in nature" (Mechsner, 2004, p. 368) has fuelled research into representational issues in movement planning and control (see Oliveira & Ivry, 2008; Rosenbaum, Cohen, Jax, Weiss, & van der Wel, 2007 for reviews of these issues). It has been suggested that this provocative claim has been put forward as a form of cognitivist's revenge for perceived downgrading of cognitive issues by proponents of the dynamical systems approach (Summers, 2004). Not surprisingly, it has re-ignited old passions and a spate of research from the two sides demonstrating the importance of either motoric or perceptual-cognitive constraints on bimanual coordination. As with similar past debates between extreme viewpoints, it seems likely that eventually it will be recognized that both cognitive and motoric constraints operate during bimanual coordination but at different levels of a hierarchically organized motor system. Interestingly, in this "cognitive vs. motoric" debate the term motor program is rarely used, with the proponents of the cognitive perspective arguing that the primary source of constraint in bimanual coordination is how the task goals are conceptualized rather than how the movements are programmed (Oliveira & Ivry, 2008).

8. The future of the motor program concept

A cursory review of the current literature in the fields of experimental psychology, human movement science, and neuroscience clearly indicates that the motor program concept is alive and well. In the vertebrate motor system, the link between the motor program concept and the stereotyped movements identified with central pattern generators seems well-established. Likewise, in the human neuroscience literature, motor programs have achieved the status of physiological entities often with a particular location in the brain and are seen as being involved in the production of many, if not all, skilled actions. For example, investigations of motor preparation in reaching and grasping tasks in humans have assumed that pre-specification of existing grasp motor programs is responsible for the observed delay prior to the initiation of the movement.

> We suggest that the parietal-premotor circuit may prepare and then maintain grasp motor programmes during the delay period, forwarding them to primary motor cortex only at the time they are finally needed for action (Prabhu et al., 2007, p. 199).

Similarly, in a recent fMRI study, chronic complete spinal cord-injured patients were able to differentiate behaviorally and neurally between attempted execution and motor imagery of foot movements, suggesting brain representations remained when execution was not possible – a form of phantom limb phenomena. The authors conclude that the central motor programs for the execution of foot movements are preserved in paraplegic patients (Hotz-Boendermaker et al., 2008).

A related development in the neuroscience field has been the revival by one group of researchers of the supposition that the neural pattern or motor engram (Bernstein, 1967; Lashley, 1950) of a motor skill is stored somewhere in the brain *in toto* so that, when activated, it unfolds as a skilled motor act. Monfils, Plautz, and Kleim (2005) present a neurophysiological account of motor skill learning in which the reorganization of movement representations or motor maps within the primary motor cortex is seen as a neural substrate for the learning process. In this approach, motor maps are capable of producing and acquiring skilled movements and as such can be regarded as motor engrams. While Lashley's search for the location of the "engram" in the brain was not fruitful, the linking of skill learning with changes in the pattern of connections within motor maps controlling task-related synergies may offer a profitable future direction.

In the field of experimental psychology, as previously indicated, there has been a resurrection of cognitive representational explanations of motor control phenomena after some 30 years of dominance by the non-representational dynamical system approaches (e.g., Ivry, Diedrichsen, Spencer, Hazeltine, & Semjen, 2004; Oliveira & Ivry, 2008). This has lead to a re-emphasis of Lashley's (1951) notion that sequences of behavior are controlled by hierarchically organized central plans. Rosenbaum et al. (2007), for example, reviewed a number of studies involving a variety of tasks including sequences of finger taps, hand positioning movements, human and simulated hand writing, and suggest that the plans for not only sequences of behavior but also single movements are organized hierarchically. It is also proposed that the assembly of motor plans involves gradually changing control parameters of existing plans to accommodate the requirements of an upcoming movement sequence. With regard to the motor program concept, Rosenbaum et al. astutely remark: "If one conceives of a plan or 'motor program' as a *memory for what is to come*, the concept of a plan or motor program need be no more contentious than the concept of *memory for what has happened.*" (p. 528).

At the beginning of this review we asked the question why do we need a motor program. This question, however, has another aspect which is "do we need motor programs for the execution of any action, regardless of skill level or involvement of attention"? Or more generally "do we need motor programs in a theory of motor control"? Clearly, proposing that motor programs are needed for theoretical reasons has much greater implications than the suggestion that motor programs are needed to account for well-learned, quasi-automatic motor sequences. The well-documented finding that the time prior to the initiation of a sequence of movements is sensitive to the number and nature of the elements in the forthcoming sequence provides strong support for a planning or preparatory process prior to movement onset. The activation of a completely prepared movement by a startle stimulus also suggests that the end product of the preparatory process can be stored subcortically.

What is clear from our review of the literature is that the prognosis of Abernethy and Sparrow (1992) that the paradigm crisis engulfing the field would only be resolved by the demise of either the motor program or dynamical systems approach has not eventuated (see Aune, Pedersen, & Ingvaldsen, 2008). Perhaps, as some have argued, there will be reconciliation between the two approaches. Ultimately, the future of the motor program concept may depend on the extent to which advances in neurophysiological and imaging techniques can provide data supporting the prediction that functional states of the brain reflect the critical features of motor preparation including memory, response initiation and inhibition, and precise timing of fast, accurate movements.

References

Abernethy, B., & Sparrow, W. A. (1992). The rise and fall of dominant paradigms in motor behaviour research. In J. J. Summers (Ed.), *Approaches to the study of motor control and learning*. Amsterdam: Elsevier Science Publishers BV.

Alexander, G. E., DeLong, M. R., & Crutcher, M. D. (1992). Do cortical and basal ganglionic motor areas use "motor programs" to control movement? *Behavioral and Brain Sciences, 15*, 656–665.

Amazeen, P. G. (2002). Is dynamics the content of a generalized motor program for rhythmic interlimb coordination? *Journal of Motor Behavior, 34*, 233–251.

Anson, J. G. (1982). Memory drum theory: Alternative tests and explanations for the complexity effects on simple reaction time. *Journal of Motor Behavior, 14*, 228–246.

Anson, J. G. (1989). Effects of moment of inertia on simple reaction time. *Journal of Motor Behavior, 21*, 60–71.

Aune, T. K., Pedersen, A. V., & Ingvaldsen, R. P. (2008). Dominant paradigms in motor behavior research: The motor-action controversy revisited. *Perceptual and Motor Skills, 106*, 573–578.

Bernstein, N. (1967). *The coordination and regulation of movements*. Oxford: Pergamon Press.

Carlsen, A. N., Chua, R., Inglis, J. T., Sanderson, D. J., & Franks, I. M. (2004). Prepared movements are elicited early by startle. *Journal of Motor Behavior, 36*, 253–264.

Carlsen, A. N., Dakin, C. J., Chua, R., & Franks, I. M. (2007). Startle produces early response latencies that are distinct from stimulus intensity effects. *Experimental Brain Research, 176*, 199–205.

Chez, C. (1985). Voluntary motor control. In E. R. Kandell & J. H. Schwartz (Eds.), *Principles of neural science*. New York: Elsevier.

Day, B. L., Rothwell, J. C., Thompson, P. D., de Noordhout, M. D., Nakashima, K., Shannon, K., et al. (1989). Delay in the execution of voluntary movement by electrical or magnetic brain stimulation in intact man: Evidence for the storage of motor programs in the brain. *Brain, 112*, 649–663.

Donders, F. C. (1868). On the speed of mental processes. *Acta Psychologica, 30*, 412–431 [Translated and reprinted in W. G. Koster (Ed.) 1969, *Attention and performance II*]. Amsterdam: North-Holland.

Grillner, S., Hellgren, J., Menard, A., Saitoh, K., & Wikstrom, M. A. (2005). Mechanisms for selection of basic motor programs–roles for the striatum and pallidum. *TRENDS in Neurosciences, 28*, 364–370.

Hebb, D. O. (1949). *Organization of behavior: A neuropsychological theory*. New York: Wiley.

Henry, F. M., & Rogers, D. E. (1960). Increased response latency for complicated movements and a "Memory Drum" theory of neuromotor reaction. *Research Quarterly for Exercise and Sport, 31*, 448–458.

Hotz-Boendermaker, S., Funk, M., Summers, P., Brugger, P., Hepp-Reymond, M.-C., Curt, A., et al. (2008). Preservation of motor programs in paraplegics as demonstrated by attempted and imagined foot movements. *NeuroImage, 39*, 383–394.

Ivanenko, Y. P., Poppele, R. E., & Lacquaniti, F. (2006). Motor control programs and walking. *The Neuroscientist, 12*, 339–348.

Ivry, R. B., Diedrichsen, J., Spencer, R. C. M., Hazeltine, E., & Semjen, A. (2004). A cognitive neuroscience perspective on bimanual coordination. In S. Swinnen & J. Duysens (Eds.), *Neuro-behavioral determinants of interlimb coordination* (pp. 259–295). Boston: Kluwer Academic Publishing.

Keele, S. W. (1968). Movement control in skilled motor performance. *Psychological Bulletin, 70*, 387–403.

Keele, S. W. (1981). Behavioral analysis of movement. In V. Brooks (Ed.), *Handbooks of physiology: Sec. 1: The nervous system: Vol. 2: Motor Control (Pt 2, pp. 1391–1414)*. Baltimore, MD: Williams & Wilkins.

Keele, S. W. (1998). Replies to J. J. Summers: Has ecological psychology delivered what it promised? Commentary 1: Programming or planning conceptions of motor control speak to different phenomena than dynamical systems conceptions. In J. P. Piek (Ed.), *Motor behavior and human skill* (pp. 403–408). Champaign, IL: Human Kinetics.

Keele, S. W., Cohen, A., & Ivry, R. (1990). Motor programs: Concepts and issues. In M. Jeannerod (Ed.). *Attention and performance* (Vol. 13, pp. 77–110). Hillsdale, NJ: Erlbaum.

Keele, S. W., & Summers, J. J. (1976). The structure of motor programs. In G. E. Stelmach (Ed.), *Motor control: Issues and trends* (pp. 109–142). New York: Academic Press.

Kelso, J. A. S. (1995). *Dynamic patterns: The self-organization of brain and behavior*. Cambridge, Mass: The MIT Press.

Klapp, S. T. (1996). Reaction time analysis of central motor control. In H. Zelaznik (Ed.), *Advances in motor learning and control* (pp. 13–35). Champaign, IL: Human Kinetics.

Klapp, S. T., Abbott, J., Coffman, K., Snider, R., & Young, F. (1979). Simple and choice reaction time methods in the study of motor programmimg. *Journal of Motor Behavior, 11*, 91–101.

Kugler, P. N., Kelso, J. A. S., & Turvey, M. T. (1982). On the control and coordination of naturally developing systems. In J. A. S. Kelso & J. E. Clark (Eds.), *The development of movement control and coordination*. New York: Wiley.

Lashley, K. S. (1950). In search of the engram. *Symposia of the Society for Experimental Biology, 4*, 454–482.

Lashley, K. S. (1951). The problem of serial order in behavior. In L. A. Jeffress (Ed.), *Cerebral mechanisms in behavior* (pp. 112–131). New York: Wiley.

Mechsner, F. (2004). A psychological approach to human voluntary movements. *Journal of Motor Behavior, 36*, 355–370.

Mechsner, F., Kerzel, D., Knoblich, G., & Prinz, W. (2001). Perceptual basis of bimanual coordination. *Nature, 414*, 69–73.

Monfils, M.-H., Plautz, E. J., & Kleim, J. A. (2005). In search of the motor engram: Motor map plasticity as a mechanism for encoding motor experience. *The Neuroscientist, 11*, 471–483.

Morris, M. E., Summers, J. J., Matyas, T. A., & Iansek, R. (1994). Current status of the motor program. *Physical Therapy, 74*, 738–752.

Newell, K. M. (2003). Schema theory (1975): Retrospectives and prospectives. *Research Quarterly for Exercise and Sport, 74*, 383–388.

Oliveira, F. T. P., & Ivry, R. B. (2008). The representation of action. *Current Directions in Psychological Science, 17*, 130–135.

Plamondon, R., Stelmach, G. E., & Teasdale, N. (1990). Motor program coding representation from a handwriting generator model: The production of line responses. *Biological Cybernetics, 63*, 443–451.

Posner, M. I., & Keele, S. W. (1973). *Skill learning. Handbook of research on teaching*. Chicago: Rand-McNally.

Prabhu, G., Voss, M., Brochier, T., Cattaneo, L., Haggard, P., & Lemon, R. (2007). Excitability of human motor cortex inputs prior to grasp. *Journal of Physiology, 581*, 189–201.

Rosenbaum, D. A. (1983). The movement pre-cueing technique: Assumptions, applications, and extensions. In R. A. Magill (Ed.), *Memory and control of action* (pp. 231–274). Amsterdam: North-Holland.

Rosenbaum, D. A. (1984). Motor programming: A review and scheduling theory. In H. Heuer, U. Kleinbeck, & K.-M. Schmidt (Eds.), *Motor behavior: Programming, control and acquisition* (pp. 1–33). Berlin: Springer-Verlag.

Rosenbaum, D. A., Cohen, R. G., Jax, D. J., Weiss, D. J., & van der Wel, R. (2007). The problem of serial order in behaviour: Lashley's legacy. *Human Movement Science, 26*, 525–554.

Rosenbaum, D. A., Inhoff, A. W., & Gordon, A. M. (1984). Choosing between movement sequences: A hierarchical editor model. *Journal of Experimental Psychology: General, 113*, 372–393.

Rosenbaum, D. A., Kenny, S., & Derr, M. A. (1983). Hierarchical control of rapid movement sequences. *Journal of Experimental Psychology: Human Perception and Performance, 9*, 86–102.

Schmidt, R. A. (1975). A schema theory of discrete motor skill learning. *Psychological Review, 82*, 225–260.

Schmidt, R. A. (2003). Motor schema theory after 27 years: Reflections and implications for a new theory. *Research Quarterly for Exercise and Sport, 74*, 366–375.

Schmidt, R. A., Zelaznik, H. N., Hawkins, B., Frank, J. S., & Quinn J. T., Jr. (1979). Motor-output variability: A theory for the accuracy of rapid motor acts. *Psychological Review, 86*, 415–451.

Semjen, A. (1996). Emergent versus programmed temporal properties of movement sequences. In H. Helfrich (Ed.), *Time and mind* (pp. 23–43). Seattle: Hogrefe & Huber Publishers.

Shaffer, L. H. (1992). Motor programming and control. In G. E. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior II* (pp. 181–194). Amsterdam: North-Holland.

Shea, C. H., & Wulf, G. (2005). Schema theory: A critical appraisal and reevaluation. *Journal of Motor Behavior, 37*, 85–101.

Sherwood, D. E., & Lee, T. D. (2003). Cognitive effort and schema theory: Implications for a new theory of motor learning. *Research Quarterly for Exercise and Sport, 74*, 376–382.
Stelmach, G. E., Mullins, P. A., & Teulings, H.-L. (1984). Motor programming and temporal patterns in handwriting. *Annals of the New York Academy of Sciences, 143*, 144–156.
Sternberg, S., Monsell, S., Knoll, R. L., & Wright, C. E. (1978). The latency and duration of rapid movement sequences: Comparisons of speech and typewriting. In G. E. Stelmach (Ed.), *Information processing in motor control and learning* (pp. 117–152). New York: Academic Press.
Sumbre, G., Gutfreund, Y., Fiorito, G., Flash, T., & Hochner, B. (2001). Control of octopus arm extension by a peripheral motor program. *Science, 293*, 1845–1848.
Summers, J. J. (1975). The role of timing in motor program representation. *Journal of Motor Behavior, 7*, 229–241.
Summers, J. J. (1981). Motor programs. In D. H. Holding (Ed.), *Human skills*. New York: Wiley.
Summers, J. J. (1989). Temporal constraints in the performance of bimanual tasks. In D. Vickers & P. L. Smith (Eds.), *Human information processing: Measures, mechanisms, and models* (pp. 155–168). Amsterdam: North-Holland.
Summers, J. J. (1992). Movement behaviour: A field in crisis? In J. J. Summers (Ed.), *Approaches to the study of motor control and learning* (pp. 551–562). Amsterdam: North-Holland.
Summers, J. J. (1998). Has ecological psychology delivered what it promised? In J. Piek (Ed.), *Motor behavior and human skill* (pp. 385–402). Champaign, IL: Human Kinetics.
Summers, J. J. (2004). The cognitivist's revenge? *Journal of Motor Behavior, 36*, 392–394.
Teulings, H.-L., Thomassen, A. J. W. M., & van Galen, G. P. (1986). Invariants in handwriting: The information contained in the motor program. In H. S. R. Kao, G. P. van Galen, & R. Hoosain (Eds.), *Graphonomics: Contemporary research in handwriting* (pp. 305–315). Amsterdam: North-Holland.
Thelen, E., & Smith, L. B. (1994). *A dynamical systems approach to the development of cognition and action*. Cambridge, MA: MIT Press.
Turvey, M. T., Fitch, H. L., & Tuller, B. (1982). *The Bernstein perspective: 1. The problems of degrees of freedom and context-conditioned variability. Human motor behavior: An introduction*. Hillsdale, NJ: Lawrence Erlbaum Associates.
Valls-Solé, J., Rothwell, J. C., Goulart, F., Cossu, G., & Munoz, E. (1999). Patterned ballistic movements triggered by a startle in healthy humans. *Journal of Physiology, 516*, 931–938.
Wickens, J., Hyland, B., & Anson, G. (1994). Cortical cell assemblies: A possible mechanism for motor programs. *Journal of Motor Behavior, 26*, 66–82.
Wikipedia, (Wikipedia http://en.wikipedia.org/wiki/Klaus_St%C3%B6rtebeker) Erwin-Rosenthal, 2008.
Woodworth, R. S. (1899). The accuracy of voluntary movement. *Psychological Review, 3* [Monograph Supplement No. 2].
Woodworth, R. S. (1938). Reaction time. In: *Experimental Psychology* (pp. 298–339). New York: Henry Hold and Co.
Wundt, W. (1912). Lectures on human and animal psychology. George Allen & Company Ltd (London) and The Macmillan Company (New York) [Translated from the Second German Edition by J. E. Creighton & E. B. Titchener (1912)].