

The problem of serial order in behavior: Lashley's legacy

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Abstract

In a prescient paper Karl Lashley (1951) rejected reflex chaining accounts of the sequencing of behavior and argued instead for a more cognitive account in which behavioral sequences are typically controlled with central *plans*. An important feature of such plans, according to Lashley, is that they are hierarchical. Lashley offered several sources of evidence for the hierarchical organization for behavioral plans, and others afterward provided more evidence for this hypothesis. We briefly review that evidence here and then shift from a focus on the *structure* of plans (Lashley's point of concentration) to the *processes* by which plans are formed in real time. Two principles emerge from the studies we review. One is that plans are not formed from scratch for each successive movement sequence but instead are formed by making whatever changes are needed to distinguish the movement sequence to be performed next from the movement sequence that has just been performed. This plan-modification view is supported by two phenomena discovered in our laboratory: the *parameter remapping* effect, and the *handpath priming* effect. The other principle we review is that even single movements appear to be controlled with hierarchically organized plans. At the top level are the starting and goal postures. At the lower level are the intermediate states comprising the transition from the starting posture to the goal posture. The latter principle is supported by another phenomenon discovered in our lab, the *end-state comfort* effect, and by a computational model of motor planning which accounts for a large number of motor phenomena. Interestingly, the computational model

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hearkens back to a classical method of generating cartoon animations that relies on the production of *keyframes* first and the production of *interframes* (intermediate frames) second.

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1. Introduction

In 1951, Karl Lashley, a neurophysiologist at Harvard University, published a paper that has become a classic: “The Problem of Serial Order in Behavior.” The paper challenged the prevailing view of behavioral sequencing in America in the first half of the 20th Century. According to that view, expressed by Washburn (1916), Watson (1920), and other behaviorists, the functional mechanism that governs the unfolding of behavior is the *reflex chain*: Stimulation caused by movement n triggers movement $n + 1$, stimulation caused by movement $n + 1$ triggers movement $n + 2$, and so on.

Lashley argued against this view on the basis of three main lines of evidence: (1) Movements can occur even when sensory feedback is interrupted. (2) Some movement sequences occur too quickly for elements of the sequences to be triggered by feedback from the preceding elements. (3) Errors in behavior suggest internal plans for what will be done later.

To these sources of evidence, new sources have since been added: (4) The time to initiate a movement sequence can increase with the length or complexity of the sequence (e.g., Henry & Rogers, 1960; Klapp, 1977; Rosenbaum, 1987; Sternberg, Monsell, Knoll, & Wright, 1978). (5) The properties of movements occurring early in a sequence can anticipate later features (e.g., Cohen & Rosenbaum, 2004; Kent, 1983; Van der Wel & Rosenbaum, 2007). (6) Neural activity can indicate preparation of upcoming behavioral events, including upcoming behavioral events in the relatively long-term future (e.g., Aldridge, Berridge, Herman, & Zimmer, 1993; Ashe, Lungu, Basford, & Lu, 2006; Averbeck, Sohn, & Lee, 2005; Kennerley, Sakai, & Rushworth, 2004).

All of these findings substantiate Lashley’s (1951) hypothesis that the solution to the serial order problem (i.e., the solution to the problem of how behaviors are sequenced) need not be ascribed to triggers from sensory feedback. Instead, the state of the nervous system can predispose the actor to behave in particular ways in the future. The common-sense way of saying that the nervous system prepares some behaviors but not others is to say that there are *plans* for behavior. Asserting that there are plans need not imply that sensory feedback plays no role, or only a minimal role, in movement control. It is known that neural states permitting differentiation of behavior can do so on the basis of sensory feedback. For example, whether a cat extends or flexes its limb when pressure is applied to its paw depends on where the limb is in the step cycle (Forssberg, Grillner, & Rossignol, 1975).

Lashley (1951) was instrumental in promoting the notion of hierarchical organization of plans. Several lines of evidence support this notion. One is that the same behaviors can have different functional interpretations depending on the context in which they occur. Thus, the sound pattern/rajt/ can be interpreted differently depending on where it occurs in a sentence, as in this sentence used by Lashley: “The mill-wright on my right thinks it right that some conventional rite should symbolize the right of every man to write as he

pleases” [p. 116]. Such contextual dependence, Lashley argued, is only possible with functionally overarching states of the sort implied by hierarchical plans.

Other sources of evidence for hierarchical plans have since been added to Lashley’s list. One pertains to errors in behavior. Analyses of such errors, whether in the domains of speech (Dell, 1986; Garrett, 1975), typewriting (see Rosenbaum, 1991, Chapter 8), or everyday action (Norman, 1981), implicate hierarchical organization. To cite one well known example from language production, word exchanges rarely cross syntactic class boundaries: Nouns switch with nouns and verbs switch with verbs, but nouns and verbs rarely switch with each other (Garrett, 1975). In addition, phonological errors indicate dominance relations. If a sports announcer accidentally says that there are “two out and one runs” while narrating a baseball game, the “s” in “runs” is pronounced like a “z”, not like a hard “s,” as befits the plural form of “out” in English. This outcome suggests that phonological rules, or their neural equivalents, are invoked during speech.

A second source of evidence for hierarchical organization of plans comes from the timing of behavioral sequences. As mentioned above, the initiation time of a movement sequence can increase with its length. So too can the inter-response times of the sequence elements (Sternberg et al., 1978; for a recent review see Rhodes, Bullock, Verwey, Averbeck, & Page, 2004). Further, inter-response times can depend on the size of the phrase that is about to be generated. The larger the phrase, the longer the inter-response time (Collard & Povel, 1982; Rosenbaum, Kenny, & Derr, 1983). Such data have been interpreted in terms of ‘decoding’ or ‘unpacking’ hierarchical plans into their constituents.

A third source of evidence for the hierarchical organization of plans comes from the relative ease or difficulty of learning different kinds of behavioral sequences. It is easy to learn sequences such as 123, 234, 345, 456, . . . , but it is hard to learn random sequences such as 143, 256, 265, . . . (Restle, 1970; Simon, 1972). Sequences of the former kind are well described by rules, and may be compactly represented by computer programs, such as the following program written in MATLAB (see Rosenbaum, 2007),

```
for i = 1:5
  for j = 1:3
    y(i,j) = i + (j - 1);
  end
end
y
```

The output from this program is

```
y =
  1 2 3
  2 3 4
  3 4 5
  4 5 6
  5 6 7
```

Saying that a plan may be likened to a computer program need not imply that there is a little person in the head (a homunculus) ‘writing the program,’ although some critics of the cognitive approach to motor control have claimed that this is the case. 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 a *memory for what has happened*. The latter concept is not one that anyone doubts. Recent evidence linking the hippocampus, a brain area associated with memory, with the ability to imagine the future supports this analogy (Hassabis, Kumaran, Vann, & Maguire, 2007).

A fourth and final source of evidence for hierarchical plans pertains to the fact that the long-term learning of skills is naturally characterized by the process of forming ever larger hierarchical units or ‘chunks’ (Miller, 1956; for a review see Rhodes et al., 2004). According to this view, the way learners acquire new skills suggests that they learn control structures for successively larger units of behavior, with newly learned routines calling up or relying on more elementary routines (Bryan & Harter, 1897). This account has been used to interpret the observation that the growth of skill is expressed by the capacity to display increasingly complex behaviors. Thus, one learns how to play a single note on the piano and then a simple series of notes before learning to play Rachmaninov’s Fourth Piano Concerto.

The chunking perspective has also been used to account for the fact that the time to repeatedly perform a task decreases as the task is practiced more and more, with the rate of reduction decreasing as practice continues. This phenomenon is quantitatively described by the Power Law of Learning (Crossman, 1959), a law so named because the time to perform a repeatedly practiced task can be expressed mathematically as the number of times the task is practiced, raised to a numerical power. The smaller the power (i.e., the more negative the power), the greater the speeding with practice. The success of the Power Law of Learning – indeed, it is being called a Law – has been ascribed to mastering ever more inclusive routines for behavioral control (Newell & Rosenbloom, 1981).

With all this support for Lashley’s position, what more has our field contributed to Lashley’s proposal? In this paper, we present some new sources of evidence for hierarchical organization of motor plans, including results that suggest that even single movements rely on plans which are hierarchically organized. We particularly focus on investigations that have helped shed light on the *processes* by which plans are assembled. We have been led to the view that motor plans are assembled by gradually changing the control parameters that distinguish what needs to be done from what has just been done before. This view has come from work on sequential effects in performance, which we review in the next major section of this paper. Then we turn to the evidence suggesting that plans for single movements are hierarchically organized. This evidence comes from computational modeling and from a variety of behavioral and neurophysiological findings, to which we turn before the Conclusions section.

2. Sequential effects

One way to study motor planning is to study sequential effects in performance. We have found this to be a rich mine for investigating the processes underlying motor planning.

2.1. The parameter remapping effect

One line of studies in our lab concerned a sequential effect called the *parameter remapping effect* (Rosenbaum, Weber, Hazelett, & Hindorff, 1986). In an illustrative experiment, college undergraduates produced simple finger-tapping sequences over and over again

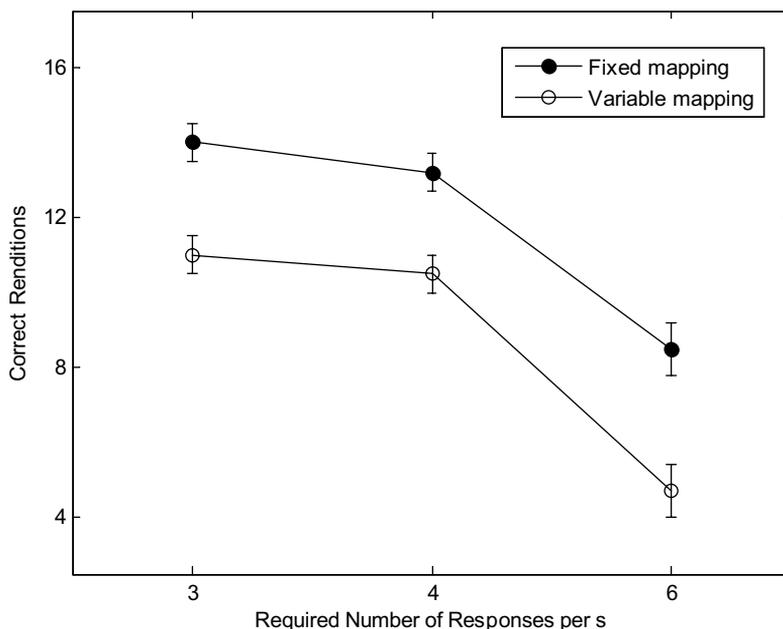


Fig. 1. Number of correct renditions of finger-tapping sequences with fixed mappings of number of taps to fingers and with variable mappings of number of taps to fingers. Adapted from Rosenbaum et al. (1986).

from memory at a rate given by a metronome (Fig. 1). Two finger-tapping sequences were used: (1) MMiimIIIi and (2) MIIimmIIM, where M and I denote the right middle and index fingers, respectively, and m and i denote the left middle and index fingers, respectively. The reader may wish to try these two sequences now.

If the reader's experience is like that of the participants in the actual experiment, sequence 1 turned out to be much harder than sequence 2. The data from the experiment are shown in Fig. 1.

What accounts for the greater difficulty of sequence 1 than sequence 2? In sequence 1, the mapping of number-of-taps to fingers changes, whereas in sequence 2 the mapping of number-of-taps to fingers remains the same. Said another way, each time a finger is used in sequence 2, the number of times it is consecutively tapped is constant, but each time a finger is used in sequence 1, the number of times it is consecutively tapped differs. If one hypothesizes that the need to change the mapping of taps to fingers (or vice versa) is a time-consuming, error-prone process, one can account for the superiority of sequence 2 over sequence 1. This hypothesized process accounts for the name of the associated phenomenon, the *parameter remapping effect*.

If the parameter remapping effect is a general phenomenon, one would expect to see it crop up in other performance contexts. Data consistent with this view are shown in Fig. 2. Here, undergraduate students recited the first n letters of the alphabet over and over again as quickly as possible under the stipulation that they always alternate between stressed and unstressed pronunciations. With this requirement, the mapping of stresses to letters remained the same when n was even but varied when n was odd. As seen in Fig. 2, when n was odd, the number of letters that could be successfully recited in 10 s was lower than the number of letters that could be successfully recited when n was even. The hardest

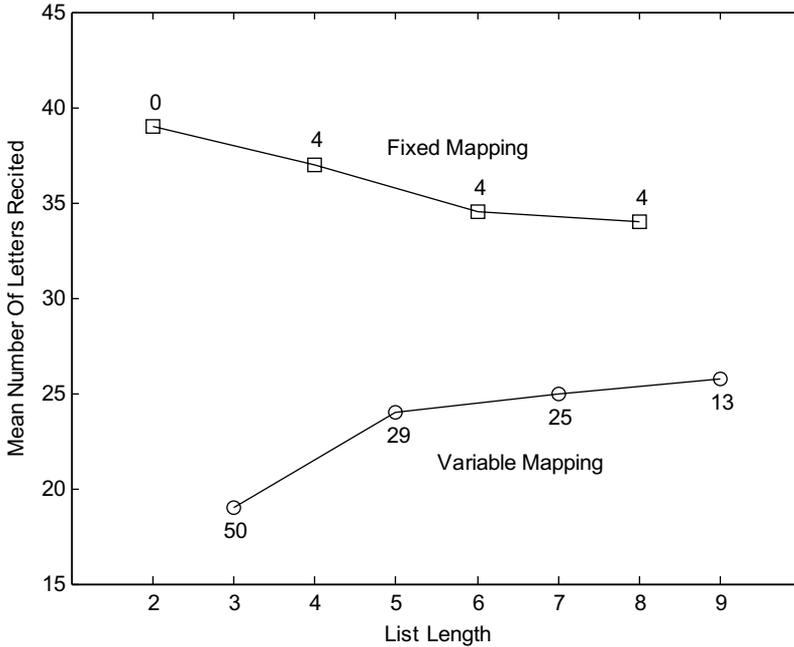


Fig. 2. Number of letters said when reciting the first n letters of the alphabet over and over again with the constraint that successive letters alternate between stressed and unstressed pronunciations. The mapping of stresses to letters was variable when n was odd but was fixed when n was even. Adapted from Rosenbaum et al. (1986).

condition was $n = 3$, which was the condition in which parameter remapping, by hypothesis, had to occur most often.

The results shown in Fig. 2 support the view that the more often the mapping of stresses to letters (or vice versa) had to be changed, the worse participants did. This outcome is consistent with the hypothesis that plans for recently performed actions are changed to enable subsequent actions.

A final demonstration of the parameter remapping effect came from observations of violinists playing two musical passages, one which proved to be easy and one which proved to be hard. (The first author was one of the violinists, and he discovered the parameter remapping effect while struggling with the hard passage along with the other amateur string players in the community orchestra he was in at the time.) The two passages are shown in Fig. 3. The easy passage had *fixed* mappings between bow directions and bow durations, whereas the hard passage had *varied* mappings between bow directions and bow durations. The passage with the fixed mappings was easy to play, but the passage with the varied mappings was hard to play. This outcome cannot be ascribed to the fact that the varied-mapping passage required alternating up and down bowstrokes, for those are just the kind of bowstrokes that beginning violinists start with. The difference in the ease of these two passages was most easily explained by saying that one passage required changes of parameter associations whereas the other did not. This outcome supports the more general hypothesis that motor planning occurs by changing features of successively needed motor plans.

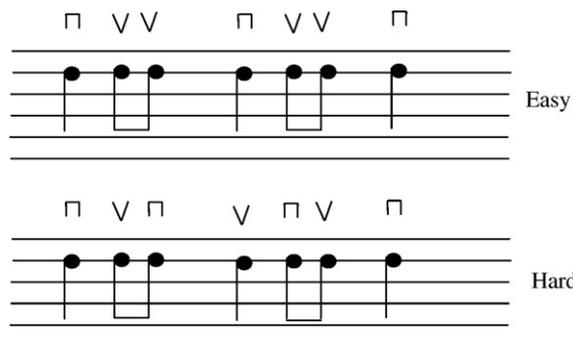


Fig. 3. Easy and hard bowing patterns. The inverted U shape denotes the down bowing direction and the caret denotes the up bowing direction.

2.2. The hand path priming effect with virtual objects

Another set of observations from our lab provides additional evidence for the view that features of recently performed movements carry over to plans for subsequent movements. These observations also broaden the domain in which such sequential effects are observed.

Fig. 4 shows the setup in which the relevant effect was found (Jax & Rosenbaum, 2007). Individual participants sat at a table and held a vertically oriented dowel with the hand in

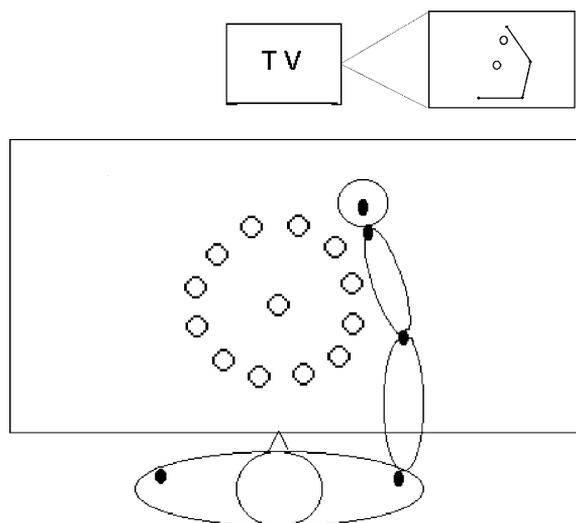


Fig. 4. Experimental setup used by Jax and Rosenbaum (2007) in their demonstration of the hand path priming effect. Participants slid a hand-held vertical dowel along a table top, causing an image of the arm to move on a TV monitor that they watched. The upper right corner of figure illustrates what participants saw, which also included one pair of targets at a time and one obstacle if an obstacle was present in a trial. The circles on the table are shown here only to indicate the positions that corresponded to the possible target locations. No circles were present on the table, and looking down on the table provided no useful information to the participants, whose hand was far from the table edge at all times.

a power grip. The dowel stood on a wide circular disk with felt on its bottom, allowing the base of the dowel to slide easily from one position to another. Affixed to the top of the dowel was an infra-red emitting diode (IRED) whose position was picked up with an OPTOTRAK motion tracking system (Northern Digital, Inc., Waterloo, Ontario, Canada). Additional IREDs were affixed to the participant's left shoulder, right shoulder, right elbow, and right wrist. These IREDs were also in view of the OPTOTRAK. Output from the OPTOTRAK went to a computer that was programmed to display a stick-figure image of the participant's right arm, which moved as the participant's right arm did and with no noticeable delay after the participant moved.

Besides seeing an image of his or her own right arm on the computer display, the participant also saw targets and, in some conditions, obstacles. The targets were displayed in the context of a center-out-and-back movement task. A circle appeared in the middle of the screen and the participant brought his or her hand marker into the circle, whereupon a circle appeared at some point on the rim of an imaginary circle around the center circle. The participant's task was to move the hand marker to the target and then return it to the center circle as quickly as possible. Participants were not prevented from looking down at the table, but there was nothing on the table to guide them in their performance of this task.

There were two control conditions and one experimental condition. In one of the control conditions, no obstacle ever appeared between the center circle and target circle. In the other control condition, an obstacle *always* appeared between the center circle and target circle. When an obstacle appeared, the participant had to make circuitous movements around the obstacle. If any part of the participant's arm (or image thereof) touched the obstacle, the computer made an unpleasant sound and the participant's end-of-block score, which otherwise reflected performance time, was significantly inflated.

Of greatest interest were the experimental conditions. Here, an obstacle sometimes appeared between the center circle and target, but the obstacle's appearance was unpredictable. If an obstacle appeared, it always appeared at the moment the target came on and always stood midway between the center circle and target (as in the control condition in which an obstacle always appeared).

The question of primary interest was what would happen in trials in which an obstacle was possible but did not appear. Fig. 5 illustrates what happened in such cases and in the control conditions. The most interesting outcome occurred in the cases where an obstacle did *not* appear after an obstacle *had* appeared. Here, participants often made needlessly circuitous hand movements. Detailed analyses of participants' handpaths in such trials showed that hand path curvature depended on how often and how recently obstacles appeared. The more often and the more recently there were obstacles, the greater was the hand path curvature in the trials where no obstacle was actually shown. In addition, and of greatest interest, this *hand path priming* effect, as Jax and Rosenbaum (2007) called it, generalized over the workspace. It was not restricted to radial directions from the center to the target next to the last tested target. (Jax and Rosenbaum did not test the same target twice in a row.)

The last outcome suggests that an abstract spatio-temporal form carried over from one movement to the next. The form was abstract in that it was not tied to particular muscles or particular joint angles. Finding evidence for such abstract spatio-temporal forms is consistent with a hypothesis offered by Lashley (1951), which he expressed as follows:

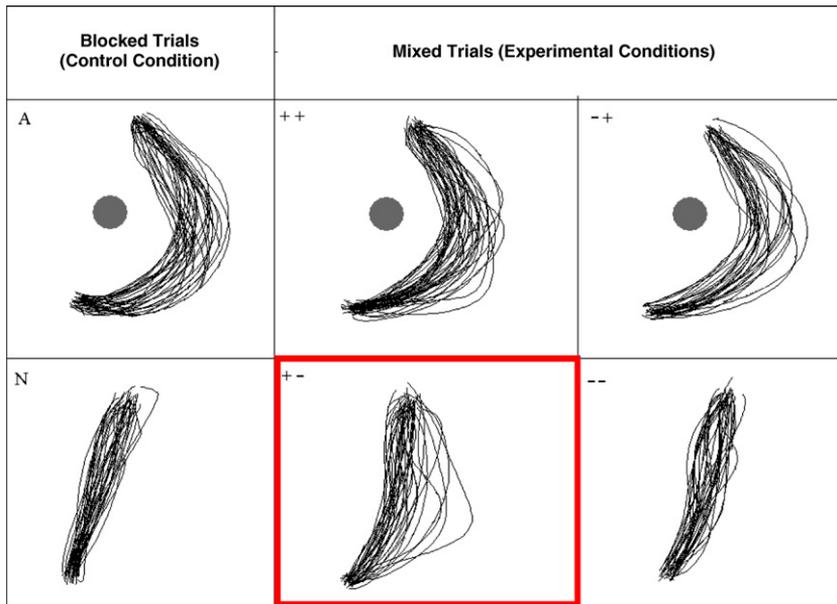


Fig. 5. Illustrative handpaths by one participant to one target when an obstacle always appeared (A) or never appeared (N) in the blocked trials (the control conditions) or when an obstacle sometimes appeared in the mixed trials (the experimental condition). The experimental condition was broken down into cases in which an obstacle did not appear after a preceding obstacle-absent trial (– –), an obstacle did appear after a preceding obstacle-absent trial (– +), an obstacle did not appear after a preceding obstacle-present trial (+ –), or an obstacle did appear after a preceding obstacle-present trial (+ +). Adapted from Jax and Rosenbaum (2007).

Patterns of coordinated movement may often be transferred directly to other motor systems than the ones practiced. In such transfer, as to the left hand for writing, an analysis of the movements show that there is not reduplication of the muscular patterns on the two sides, but a reproduction of movements in relation to the space coordinates of the body. Try upside-down mirror writing with the left hand and with eyes closed for evidence of this. The associative linkage is not of specific movements but of directions of movement. [p. 124].

The hand path priming effect helps substantiate Lashley's claim, and in so doing also supports computational models of motor control that have assumed abstract spatio-temporal forms for the generation of movement trajectories (Bullock, Bongers, Lankhorst, & Beek, 1999; Meulenbroek, Rosenbaum, Thomassen, Loukopoulos, & Vaughan, 1996).

2.3. The hand path priming effect with real rather than virtual objects

A possible objection to the findings of Jax and Rosenbaum (2007) is that their hand path priming effect may have stemmed from participants' uncertainty about target locations and obstacle locations. From trial to trial, participants did not know where a target would appear, nor, in the conditions where an obstacle could sometimes appear, where and whether it would show up. It is possible, therefore, that participants adopted a guessing strategy that led them to perform as they did.

To address this concern, Van der Wel, Fleckenstein, Jax, and Rosenbaum (2007) designed a task in which participants had complete certainty about the workspace in which they made aimed hand movements. The most important feature of the setup, shown in Fig. 6, vis à vis the earlier work by Jax and Rosenbaum (2007) was that participants could see the targets and obstacles they would deal with in every trial. The targets were large red foam dots arranged in a semi-circle on the table where movements were made, and the obstacle was a piece of cardboard standing upright between a pair of targets. The targets and obstacle were in full view of the participant before and during each experimental trial.

Participants held a vertically oriented dowel with the right hand (the dominant hand for all the participants). The dowel was made of wood, was 20.2 cm high, 3 cm in diameter, and weighed 100 g. Affixed to the dowel were IREDs whose positions were picked up by the same OPTOTRAK motion tracking system used by Jax and Rosenbaum (2007). Additional IREDs were also affixed to the obstacle.

The participant's task was not to slide the dowel from one target to another, as in the experiments of Jax and Rosenbaum (2007), but to carry the dowel, or the base of the dowel, from one target to the next in time with a metronome clicking every 600 ms. In each trial, the experimenter asked the participant to start on either the leftmost or rightmost target and to start moving when s/he felt that s/he had internalized the beat. If the participant started on the left, s/he moved from target to target in the rightward direction, all the way to the farthest target on the right, then back to the left, tapping all the targets in between, whereupon s/he returned toward the right again, and so on. If the participant started on the right, the sequence was reversed. The experimenter told the participant to keep moving until he gave an oral "stop" command.

Each participant completed two sets of conditions. In the control condition, no obstacle was present between any of the target pairs. In the experimental condition, an obstacle stood between a pair of targets, equidistant between them. The participant was asked to

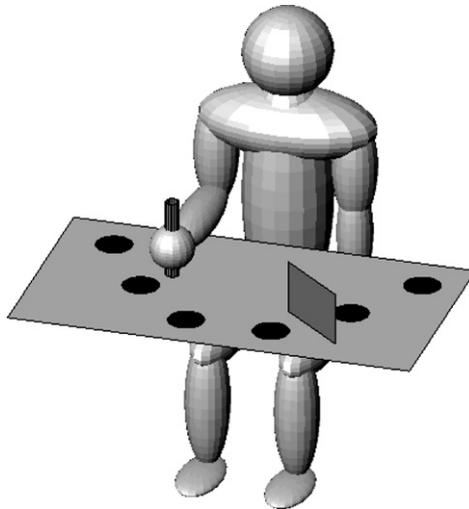


Fig. 6. Experimental setup used by Van der Wel et al. (in press). Participants held a dowel with the right hand and moved it back and forth from target to target, tapping the targets in time with a metronome. A cardboard obstacle stood between each pair of radially adjacent targets in the experimental conditions, and no obstacle was present in the control condition.

move from target to target and to move over the obstacle in time with the metronome. The location of the obstacle (i.e., the two targets between which it stood) was varied within participants to include all adjacent target pairs. Obstacles of different height (7.5 cm, 15.0 cm, or 22.5 cm) were used with different groups of participants. The question of interest was what would happen to the peak height of the movements before and after clearing an obstacle. These peak heights were compared to the same movements in the control condition, where there was no obstacle.

The main result appears in Fig. 7. Participants moved higher between targets when an obstacle was in the way than when no obstacle was in the way. More surprisingly, they

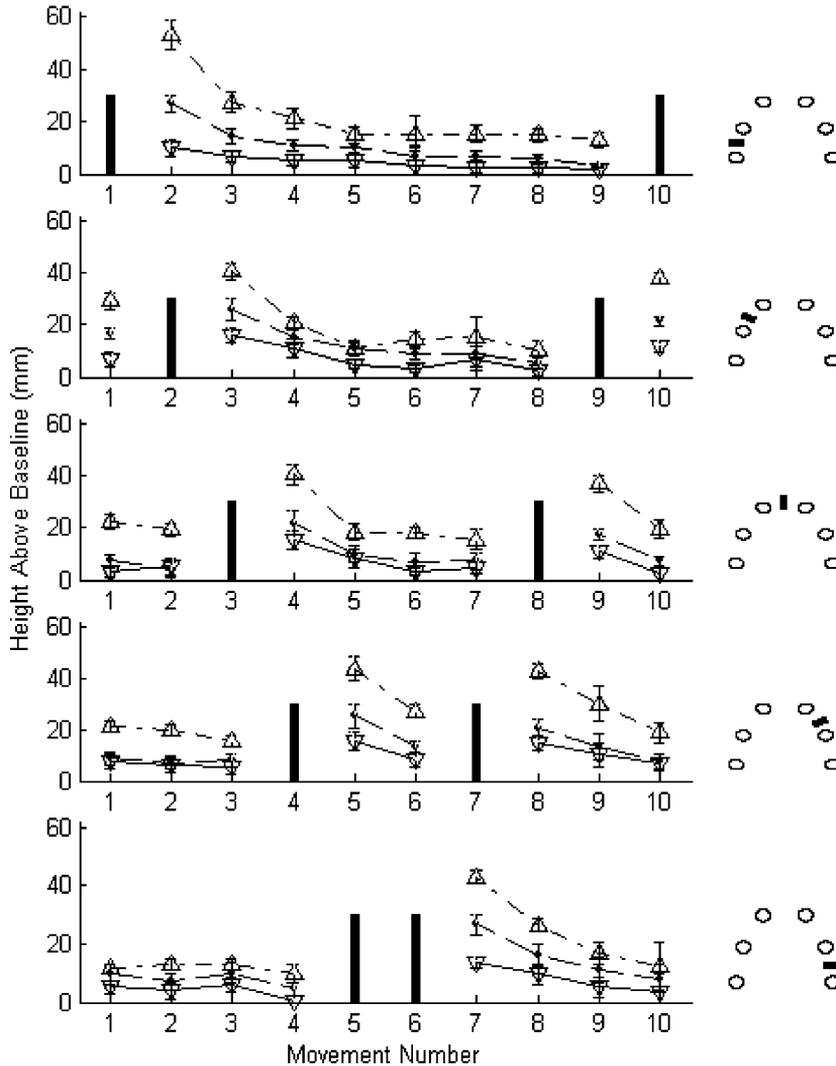


Fig. 7. Peak movement heights (in mm, ± 1 SE) above baseline for each obstacle position when clearing a low (\blacktriangledown), medium (\bullet), or high (\blacktriangle) obstacle. The black bar indicates the positions of the obstacle (also shown on the right). There were three cycles of 10 movements per trial. The movements shown are averaged across all three cycles.

moved higher *after* clearing an obstacle than when no obstacle was present for the same pair of targets in the control condition. The post-obstacle peak movement heights decreased as the obstacle was left behind. This *hand path priming* effect scaled with the height of the obstacle: The higher the obstacle, the higher the subsequent inter-target moves and the larger the number of subsequent moves that were so affected.

These results essentially replicate the hand path priming effect of Jax and Rosenbaum (2007), and they show that the results of Jax and Rosenbaum were not an artifact of uncertainty about targets or obstacles. The results of Van der Wel et al. also help substantiate Lashley's assertion that abstract spatio-temporal forms play a role in the control of serially ordered behavior. In the case of the obstacle clearing task of Van der Wel et al., the evidence for such abstract spatio-temporal forms came from the fact that higher-than-normal jump heights were observed in locations spatially removed from the obstacles.

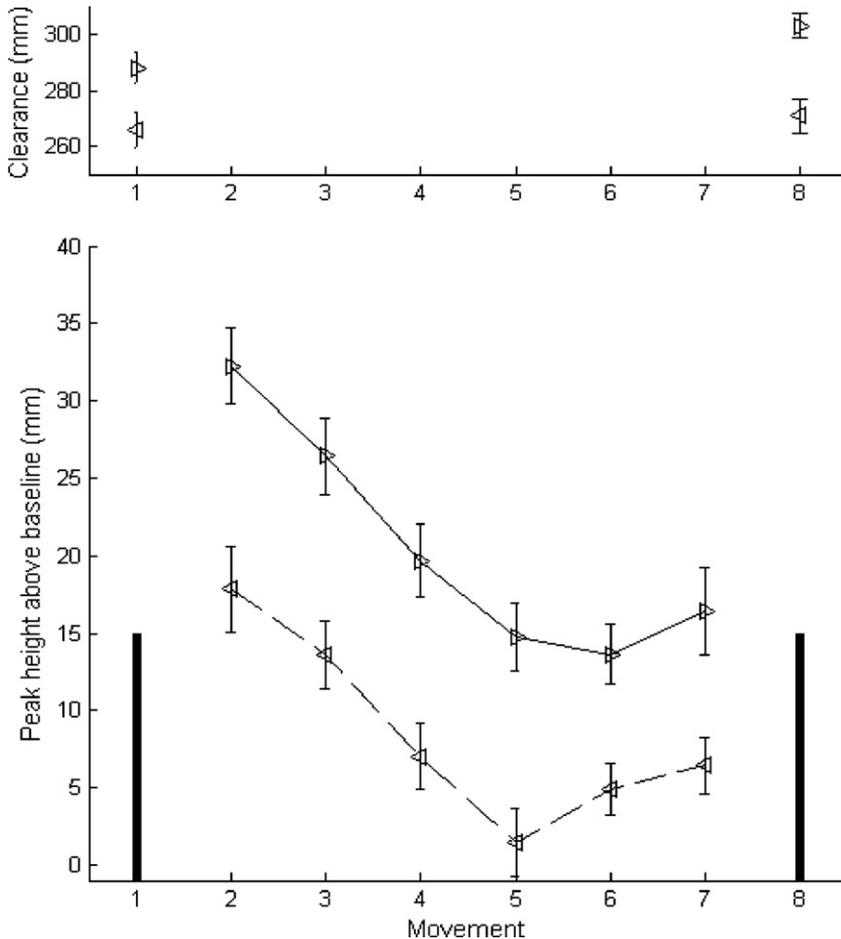


Fig. 8. Peak movement heights (in mm, ± 1 SE) above baseline when clearing an obstacle with the left hand and continuing with the right hand (>) or vice versa (<). There were three cycles of 10 movements per trial; the movements shown are averaged across all three cycles. The top panel shows the height above baseline when participants moved over the obstacle.

Another experiment by Van der Wel et al. provided further support for the abstract nature of carried-over movement forms. In that experiment, participants moved one hand over an obstacle and then continued with the other hand. To accommodate this demand, participants held two dowels, one in each hand. As shown in Fig. 8, the hand path priming effect was observed even in this inter-manual transfer task. After participants moved over the obstacle with one hand, the heights of the subsequent inter-target movements with the *other* hand were affected, indicating that the hand path priming effect did not depend on simple properties of muscle activation, but operated instead at a higher level.

Another feature of the results shown in Fig. 8 lends further support to this conclusion. Obstacle clearances were higher for the left hand than for the right hand, but the subsequent movements were higher with the right hand than the left. This outcome suggests a true carry-over of the spatial form of the successive movements.

3. Posture-based planning model

3.1. Motor equivalence in handwriting

The foregoing conclusions not only reveal how successive movements are generated. They also have implications for our understanding of the capacity to achieve the same physical tasks in essentially the same ways when using different effectors. Such ‘motor equivalence’ is often discussed in the context of handwriting. People can write their names or other scripts in ways that preserve their individual writing styles when they write with different muscle groups – for example, when using the fingers, hand, forearm, foot, or mouth (Raibert, 1977). Such capabilities suggest that writers have at their disposal memories of the abstract spatio-temporal forms they wish to produce.

Meulenbroek et al. (1996) built a computational model of writing that relied on this idea. In their model, writing was conceived as a series of aiming movements made *to* and *through* spatial targets (Fig. 9). The spatial targets *to* which movements were made were points of minimal speed, whereas the spatial targets *through* which movements were points of maximal speed. Meulenbroek et al. (1996) assumed that a set of such targets can be mentally represented in such a way that the set can be mentally projected onto a writing surface. The larger the desired writing, the larger the projection. Previous research has provided objective psychophysical evidence that people can indeed project visual images onto external surfaces and control the sizes of those projected images (Kosslyn, 1980).

As seen in Fig. 9, it was possible to simulate the kinematics of pen tip motion with this model. When the model was used to generate a written letter such as the cursive letter ‘e,’ represented as a series of appropriate ‘to-and-through’ targets, the tangential velocity profile of the simulated pen tip was similar to that obtained from human writing (Fig. 10). When the simulated writing was done with the hand and fingers on a horizontal surface or with the shoulder and elbow on a vertical surface, the form of the written output was similar in the two cases, although the simulated joint kinematics were very different, just as they must be for the body to accommodate writing in these two situations.

3.2. Keyframes and interframes

What assumptions about body motion were made to generate the simulations of Meulenbroek et al. (1996)? The most important one was embodied in the distinction between

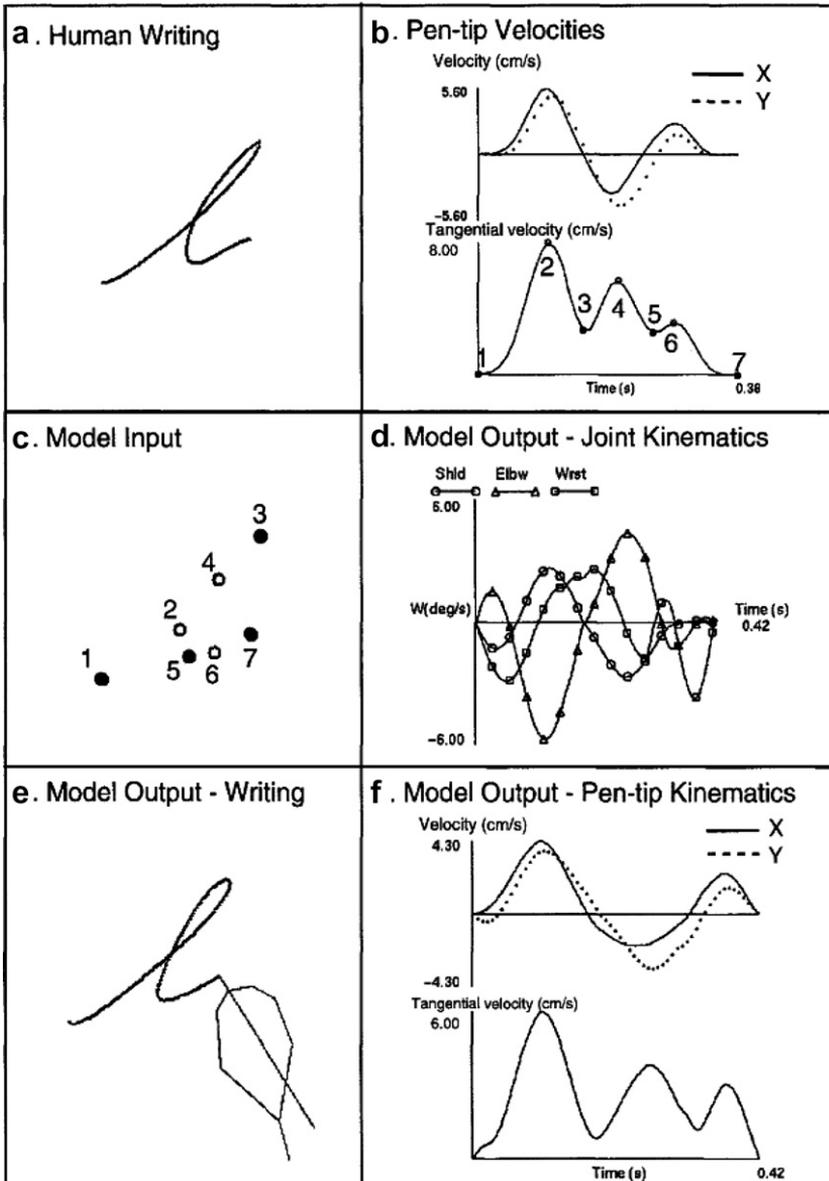


Fig. 9. Human and simulated writing. (a) Written output from a human participant. (b) Pentip velocities and tangential velocities. (c) Targets to which movements are made (solid points) and targets through which movements are made (empty points). (d) Joint kinematics from the model. (e) Simulated writing. (f) Simulated pen-tip velocities and tangential velocities. From Meulenbroek et al. (1996).

keyframes and *interframes* (Fig. 11). This distinction was first discovered by cartoon animators. They found that it made sense to draw keyframes (i.e., critical frames) and then to draw interframes (i.e., successive frames between the keyframes). In modern times, computer animators have used similar methods (Pullen & Bregler, 2002).

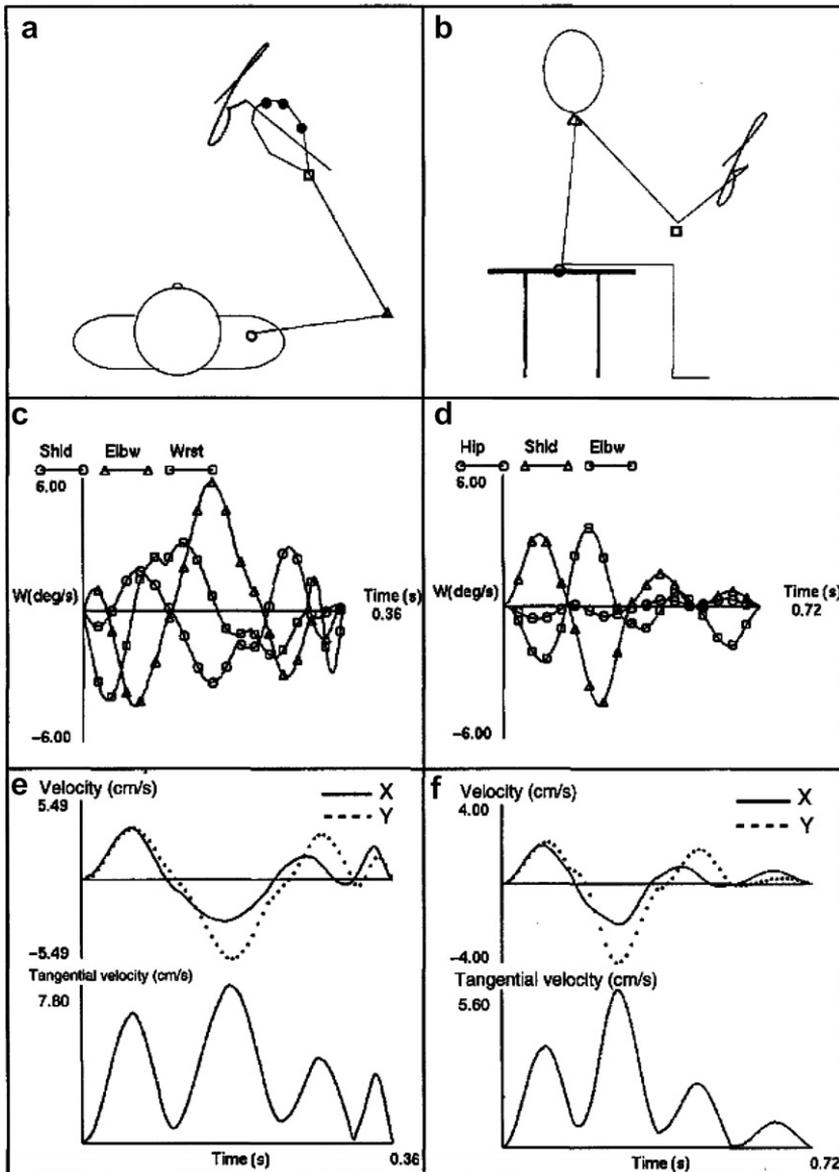


Fig. 10. Simulated writing. (a) Writing in the horizontal plane. (b) Writing in the vertical plane. (c) Simulated joint angles for horizontal writing. (d) Simulated joint angles for vertical writing. (e) Simulated velocities and tangential velocities for horizontal writing. (f) Simulated velocities and tangential velocities for vertical writing. From Meulenbroek et al. (1996).

One of the most intriguing features of keyframes and interframes is that interframes contain less information than keyframes do. Interframes only contain successive differences between the keyframes around them. For this reason, computer files that store movies that have been generated with keyframes and interframes (stored in *.mpg* format) use

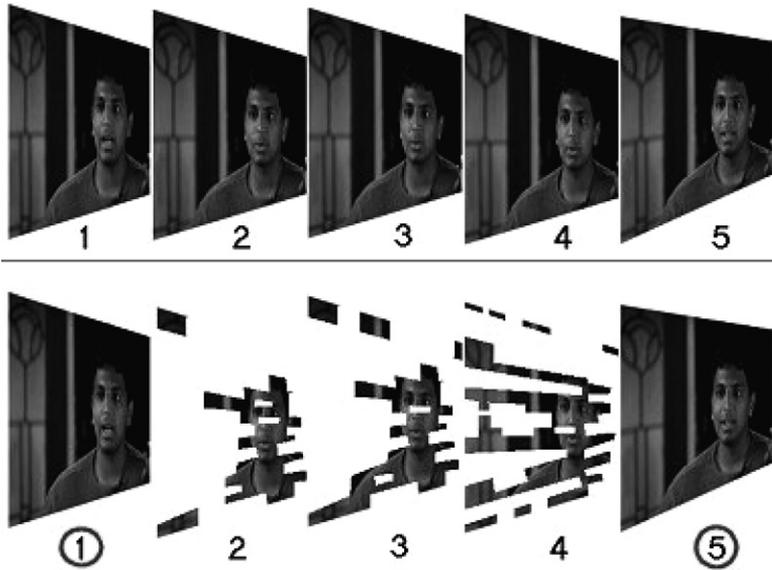


Fig. 11. Two methods of computer animation. Top panel: Storing every frame completely. Bottom panel: using keyframes along with interframes that only contain successive differences between the surrounding keyframes. From public domain website <http://nickyguides.digital-digest.com/keyframes.htm>.

much less memory than computer files that store movies as series of complete images (stored in *.avi* format).

Another intriguing feature of keyframes and interframes is that they essentially rely on the method of planning that we have been led to in our research on sequential effects. We have suggested that plans for what to do next are represented through a series of differences between what was done before and what must follow.

3.3. *Why distinguish between goal postures and movements?*

Keyframes and interframes were used in the simulations of Meulenbroek et al. (1996), with the necessary keyframes (goal postures) and interframes (movements) being found by satisfying task constraints defined by the tasks at hand (see Meulenbroek et al., 1996 for details). The assumption that there are goal postures and movements in the context of computer simulations raises the question of whether such differences have biological and psychological credibility. We review our reasons for believing that they do below, having done so in more detail elsewhere (Jax, Rosenbaum, Vaughan, & Meulenbroek, 2003; Rosenbaum, Cohen, Meulenbroek, & Vaughan, 2006).

3.3.1. *Memory for position versus memory for movement*

One reason for sanctioning the functional distinction between goal postures and movements is that memory for position is much better than memory for movement. As shown originally by Marteniuk and Roy (1972) and then replicated and extended by others (see Smyth, 1984, for review), people are good at reproducing body positions they recently

occupied but are poor at reproducing features of the body movements they made to get there.

3.3.2. *Kinematic regularities*

A second reason to believe in the functional distinction between goal postures and movements is that positioning movements display kinematic regularities which depend on actors' having advance information about the final position to be adopted. For example, hand speed profiles for positioning movements are typically bell-shaped and scale with the distance to be covered (Hogan, 1984). This result is most easily explained by assuming, among other things, that the final position is known in advance of movement.

An early, influential proposal about such profiles was that positioning movements obey a 'minimum jerk' principle. According to this proposal (Hogan, 1984), the time series of end-effector positions adopted by a limb in moving from one static position to another minimizes mean squared jerk. (Jerk is the third time derivative of position, velocity is the first time derivative, and acceleration is the second time derivative.) There has been debate about the minimum jerk principle, but speed profiles of manual positioning movements are broadly consistent with any such optimization principle, which requires, for its implementation, information about initial and final positions (Todorov, 2004). Interestingly, one such optimization model asserts that minimizing variability of final positions is the main organizing principle behind positioning control (Harris & Wolpert, 1998).

3.3.3. *Data consistent with the equilibrium point hypothesis*

A third reason to distinguish between goal postures and movements is that many studies have yielded data consistent with the equilibrium point hypothesis of motor control (e.g., Feldman & Latash, 2005). The equilibrium point hypothesis states, in its most general form, that when a movement is completed, the neuromotor system reaches a state of equilibrium it was not in when the movement was started.

The equilibrium point hypothesis is controversial, and different versions of it have been proposed. Nevertheless, a number of studies have yielded data consistent with it, expressed in the general way given above (e.g., Feldman & Latash, 2005). For example, in a classic study, Polit and Bizzi (1979) showed that deafferented monkeys could point to visual targets even when the monkeys could not see, hear, or feel their movements. Most remarkably, the monkeys could still do this even if the pointing limb was mechanically perturbed at the start of the movements. This result is consistent with a form of the equilibrium point hypothesis in which muscle stiffness is centrally regulated to cause muscle antagonist forces and torques to sum to zero. To the extent that such a method relies on the functional dissociation between goal positions and movements, the data from this study lend further support for the dissociation between movements on the one hand and positions on the other.

3.3.4. *Goal posture neurons*

A fourth reason to advocate the distinction between goal postures and movements is that evidence has been adduced for the neurophysiological representation of goal postures in the monkey motor- and premotor-cortex (Graziano, Taylor, & Moore, 2002). When cells in these regions are stimulated for about half a second, monkeys adopt postures that depend on where the stimulation is applied, but not on the monkeys' initial postures. The

latter result rules out the possibility that the stimulation merely causes particular muscles to contract. Other studies indicate that movements per se are also neurally represented.

3.3.5. Noncommutativity of joint rotations

A fifth and (for here) final reason to distinguish between goal postures and movements is that specifying goal postures in advance of movements helps obviate a problem that would exist otherwise. The problem relates to the fact that the order in which joints rotate in 3-space affects the final position that is adopted. The technical term for this dependency of final position on rotation order is *noncommutativity*. When operations are commutative, the order in which they are carried out has no effect on the result. (Addition is an example of a commutative process: $3 + 2 = 2 + 3$.) When operations are noncommutative, however, the order in which they are carried out *does* have an effect on the result. This is the case for rotations about three orthogonal axes.

The problem that noncommutativity poses for positioning movements is that it becomes cumbersome to keep track of all the rotation orders needed to bring an effector to a desired spatial position (see [Gielen, Vrijenhoek, & Flash, 1997](#)). A proposed solution to this problem is to hypothesize unique associations between 3D spatial positions and effector orientations. Franciscus Donders, the famous Dutch physiologist of the 19th Century, found that this principle holds for the eye. According to Donders' Law, the position of the eye in its orbit is unique for any gaze angle. Thus, when the gaze is straight ahead, for example, the eye's degree of rotation about the straight-ahead axis is always the same. This is true for all other gaze angles as well ([Fetter, Misslisch, & Tweed, 1997](#)).

Some investigators have suggested that stereotyped orientations may also characterize the outstretched arm ([Gielen et al., 1997](#)). If the outstretched arm is extended straight ahead, for example, it would be odd to keep the thumb pointing down rather than up and at an approximately 45° in the medial ('inward') direction. Stereotyped effector orientations such as this would seem to simplify the motor planning problem.

The posture-based motion planning theory has two things to say about the claim that stereotyped effector orientations simplify motor planning. First, as will be seen in later in this article, Donders' Law as applied to arm positions is strongly violated. Second, hypothesizing goal postures for movements leads naturally to the idea that movements from starting postures to goal postures are not achieved by successively rotating limb segments or other effectors around their respective rotation axes in a sequential manner. Rather, the rotations – to the extent they are observable and are not just mathematical fictions – occur simultaneously or nearly simultaneously.

Simultaneity of joint rotations for positioning movements occurs when the associated movements can be represented, for graphical purposes, as straight-line interpolations in joint space from starting postures to goal postures ([Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, & Engelbrecht, 1995](#); [Soechting, Buneo, Herrmann, & Flanders, 1995](#)). Such straight-line interpolations are the most natural way to conceive of movements within the framework of the posture-based motion planning theory. Complete simultaneity of joint rotations does not always occur, of course ([Atkeson & Hollerbach, 1985](#)), and indeed *should not* occur when the movement path must be shaped to generate desired forms (as in writing, drawing, or avoiding obstacles), or when it is important to transfer momentum efficiently from one part of the body to another (as in throwing a ball). So far, the posture-based motion planning theory does not address momentum or other kinetic variables, but in principle should be able to do so by treating kinetic costs the

way it treats kinematic and other costs. For a discussion of the posture-based theory's treatment of cost reduction, see Rosenbaum, Carlson and Gilmore (2001).

3.4. Prehension

Having defended the distinction between goal postures and movements, we turn next to the question of what else the posture-based motion planning theory can explain. One class of phenomena the theory can explain concerns the kinematics of the arm, hand, and fingers in prehension.

Beginning with seminal studies by Jeannerod (1981, 1984), a challenge for the field of motor control has been to account for the way the arm, hand, and fingers are coordinated when people (and nonhuman animals) reach for and grasp objects. By relying on the idea that goal postures are established separately from movements to them, it has been possible to account for most of the detailed, quantitative features of such coordination (Rosenbaum et al., 2001).

An illustrative simulation is shown in Fig. 12. Here, an avatar reaches for a virtual cylinder after identifying the goal posture to be adopted (Rosenbaum et al., 2001). The avatar's tangential velocity and finger spread corresponded to what has been reported in the literature (see Rosenbaum et al., 2001, for review).

Fig. 13 shows a more technically advanced simulation. Here the avatar was confronted with the challenge of not only reaching for a virtual cylinder, but also avoiding a collision with a virtual obstacle, as in the experiments of Jax and Rosenbaum (2007). By assuming that combinations of goal postures are used to shape movements as well as define the endpoints of movements, it was possible to generate realistic obstacle-avoidance movements. Careful comparison of those simulated movements with actual obstacle-avoidance movements made by human participants showed that the model did essentially as well at predicting the kinematics of any participant's behavior as did the kinematics of any other

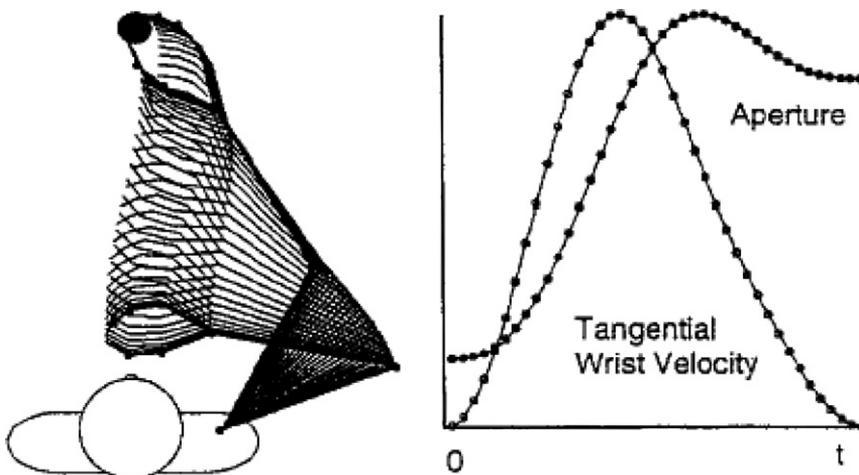


Fig. 12. Simulated prehension. Left panel: Simulated reach for a virtual cylinder. Right panel: Resulting time series of tangential velocities for the wrist, and aperture size as a function of time, t . From Rosenbaum et al. (2001).

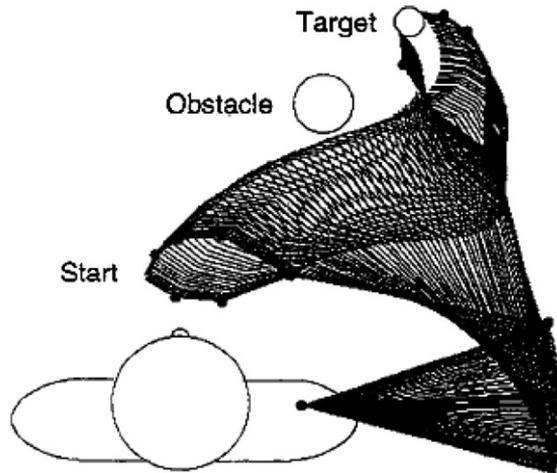


Fig. 13. Simulated reaching for a virtual object after reaching around a virtual obstacle. From Rosenbaum et al. (2001).

participant in the sample (Rosenbaum et al., 2001; Vaughan, Rosenbaum, & Meulenbroek, 2001). At the same time, some variants of the model did appreciably *worse* at pre-

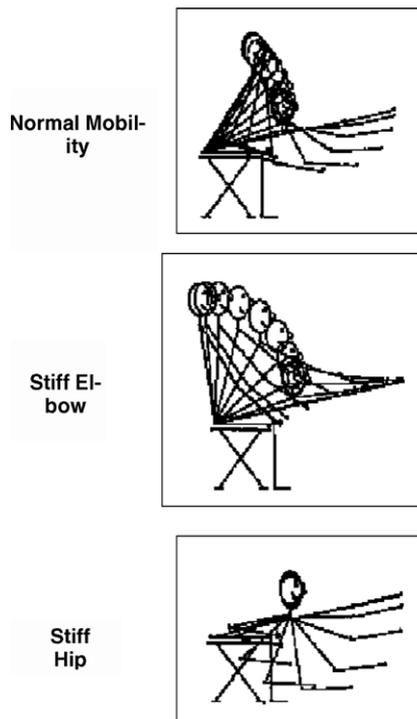


Fig. 14. Simulated reaching when the joints have normal mobility, when the elbow is stiff, and when the hip is stiff. From Rosenbaum et al. (1995).

dicting the kinematics of participants' obstacle circumventions than did any other participants (Vaughan et al., 2001). The latter outcome indicates that the model was not simply so powerful that it could never be rejected. Some forms of the model could be rejected, but all the surviving variants assumed separate representations of goal postures and movements to those goal postures.

3.5. *Compensating for changes in joint mobility*

Another capability that the theory can explain is immediate compensation for changes in joint mobility (Fig. 14). It is easy to account for immediate compensation for reduced joint mobility under the aegis of the goal-posture/movement distinction. If it becomes hard to bend the elbow, for example, a goal posture can be found that entails little elbow rotation (Fig. 14, middle panel). Similarly, if it becomes hard to bend the hip, a goal posture can be found that entails little hip rotation (Fig. 14, bottom panel). Such compensation is less easily achieved through other means (Mussa-Ivaldi, Morasso, & Zaccaria, 1988).

4. End-state comfort

In the previous section, we said that Donders' Law as applied to arm positions is strongly violated. In this section, we review the evidence to which we referred (also see Soechting et al., 1995). The observations to be reviewed were important in the original postulation of the posture-based motion planning theory (Rosenbaum, Engelbrecht, Bushe, & Loukopoulos, 1993), and for present purposes are important for joining the discussion of the serial ordering of complex behavioral sequences (the focus of Lashley's (1951) article and of the opening sections of this article) with the discussion of the control of individual positioning movements (the focus of the previous section).

4.1. *Grasp orientations*

As mentioned in the last section, it would be odd to keep one's thumb pointing down rather than pointing up at an about 45° in the medial ('inward') direction if one were holding one's arm outstretched. Nevertheless, this is just the posture that participants (university students) in our lab adopted when they reached out to turn a handle so a pointer at one end would rotate 180° from an initial, downward position to a final, upward position (Rosenbaum et al., 1993). The data are shown in Fig. 15. Participants deliberately put their arms in awkward postures (thumb down) when they grasped the handle. Doing so had a fortuitous effect: When the 180° handle rotation ended, the thumb pointed up, at or near the most comfortable position.

Why did participants sacrifice initial comfort for end-state comfort (hence the name of this effect)? The reason, as shown in subsequent research, was that they sought to optimize the degree of control they could achieve in the *series* of adopted positions.

In one follow-up experiment, no aiming was required to get the pointer to the final position. This was made possible by rigging the handle with a latch that caught when the final position was reached (Rosenbaum, Van Heugten, & Caldwell, 1996). In this situation, many participants did what no participants did in the normal (no latch) situation: They took hold of the handle in a comfortable posture and ended the task in an uncomfortable

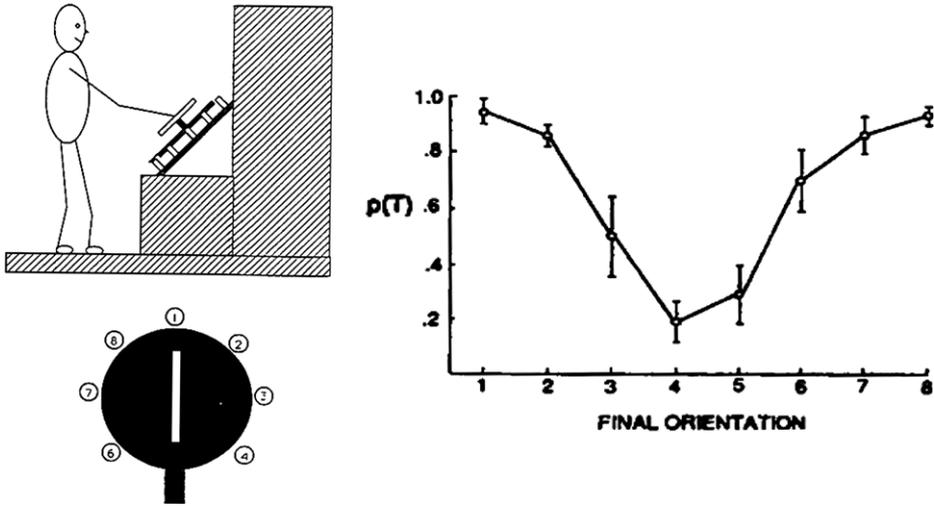


Fig. 15. Handle rotation task (top left) and handle as seen by the participant (bottom left). Probability, $p(T)$, of grasping the handle with the thumb toward the pointer (dark tab extending from the wheel on which the handle was attached) as a function of final pointer orientation (right panel). From Rosenbaum et al. (1993).

posture. This outcome suggests that participants only minimized awkwardness at the end of the handle rotation task if the task demanded it. If the start of the task and the end of the task were equally difficult (or approximately so), participants started comfortably or started uncomfortably with about equal probability.

4.2. Grasp heights

A similar set of outcomes was obtained in other experiments that examined *where* objects are grasped rather than *how* objects are grasped. Cohen and Rosenbaum (2004) asked participants to reach out in order to take hold of the handle of a standard toilet plunger and move it from one position to another. At first, the plunger stood on a platform of fixed height (at chest height for most participants). Then the plunger was brought to a platform to the side of the initial platform. The target platform could occupy any of 5 possible heights, from quite low (near the participant's knees) to quite high (near the participant's face). (The platform heights were not scaled to the individual participant's heights.) The main finding was that the grasp height on the handle was inversely related to the height to which the plunger would be brought (Fig. 16). Participants took hold of the plunger lower when they were going to bring it to a high position than when they were going to bring it to a low position. Apparently, participants sought to avoid awkward final postures, for if they always took hold of the plunger at the same height no matter where it would be brought next, they would have ended with high hand positions when the target platform was high and low hand positions when the target platform was low. Their ability to anticipate this possibility caused them to adjust their grasp heights accordingly. This grasp height effect is another manifestation of the end-state comfort effect.

Two other findings that used this general procedure are also worth reporting. One was that when participants were asked to return the plunger to the home platform, they tended

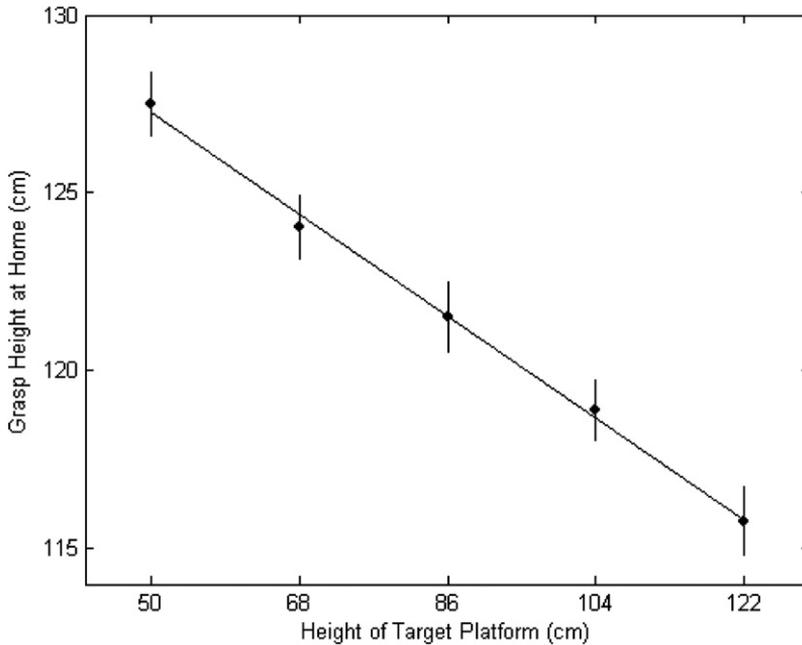


Fig. 16. Grasp height on the plunger handle as a function of the height of the target platform to which the plunger would be brought. Adapted from Cohen and Rosenbaum (2004).

to grab it where they had grabbed it before (Cohen & Rosenbaum, 2004). This outcome reinforces the claim made earlier in this article that people tend to reuse just-used motor plans. For more information about this phenomenon, see Weigelt et al. (in press).

The other finding was that grasp heights depended on how much precision was required to complete the placement task. In the relevant experiment (Rosenbaum, Halloran, & Cohen, 2007), participants were again asked to move a plunger from one standing position to another, and from a platform of fixed height to a platform of variable height. What distinguished this experiment from the previous ones was that the base of the plunger had to be lifted from a wide or narrow ring and then had to be placed into a wide or narrow ring. When the ring on the home platform was wide not much precision was required to lift the plunger from the platform, but when the ring on the home platform was narrow quite a bit of precision was required to remove the plunger from the platform. Similarly, when the ring on the target platform was wide not much precision was required to place the plunger on the platform, but when the ring on the target platform was narrow quite a bit of precision was required to place the plunger there. In these conditions the grasp height effect of Cohen and Rosenbaum (2004) was replicated: Again, grasp heights were inversely related to target heights. However, the grasp height was modulated by the precision requirements for lifting *and* for placing. Whenever the base of the plunger had to pass through a narrow ring, regardless of whether that narrow ring was on the start platform or on the target platform, participants grasped the plunger lower than when neither ring was narrow. The fact that participants adjusted their grasp heights according to the precision demands of starting and ending the task shows that participants could anticipate the demands of both phases of the task.

On the basis of these data, [Rosenbaum et al. \(2007\)](#) argued that participants had essentially as much information about the postures they would adopt upon ending the task (placing the plunger on the target platform) as they had about the postures they would adopt upon starting the task (lifting the plunger from its home platform). The latter inference is surprising in view of the fact that the placement event had to occur farther in the future than the lifting event and had to be based on less immediately available visual information (i.e., the plunger was visible in its initial state but not in its final state). Nonetheless, the conclusion is sensible from the perspective of the general theoretical perspective offered here, that participants can represent goal positions before they start to move.

4.3. Phylogeny and ontogeny of the end-state comfort effect

A final remark about the end-state comfort concerns its phylogenetic and ontogenetic roots. If the control of positioning movements relies on anticipation of end states, one would expect such anticipation in other species that make positioning movements. Evidence consistent with this suggestion was recently obtained in a study of cotton-top tamarin monkeys (*Saguinus oedipus*). In the study ([Fig. 17](#)), [Weiss, Wark, and Rosenbaum \(in press\)](#) presented tamarins with a plastic champagne glass with its base removed. The glass was placed in an apparatus with two metal bars and a flat platform surface that allowed the investigators to suspend the cup in either an upright or an inverted position. Inside the cup, in full view of the subject, was a marshmallow, a favorite treat of tamarins. To get the marshmallow, the tamarin had to pull on the stem of the glass to free the glass from the device. This could be done in one of two ways – with an upright grip (i.e., thumb pointing up) or with an inverted grip (i.e., thumb pointing down).

[Weiss et al. \(in press\)](#) found that when the glass was presented in an upright orientation, the monkeys tended to pull on the stem with an upright grip, but when the glass was presented in an inverted orientation, the monkeys tended to pull on the stem with an inverted grasp. These two grasps afforded comfortable final positions when the monkeys held the

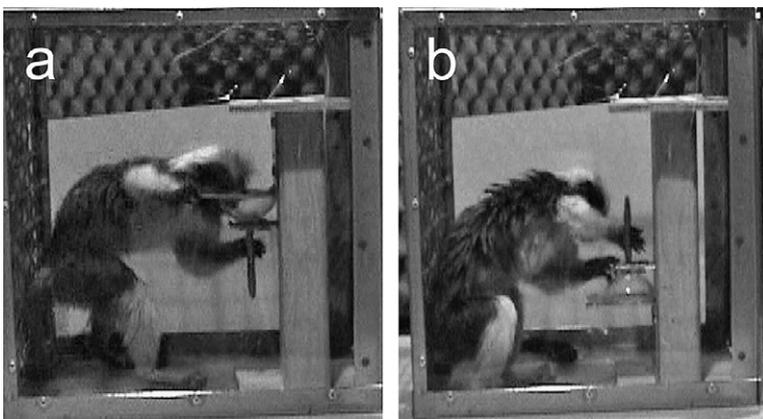


Fig. 17. Tamarin monkey showing the end-state comfort effect. (a) The monkey grasps the stem of the upright glass with an overhand grasp. (b) The same monkey grasps the stem of the inverted glass with an underhand grasp. Once the glass is pulled out of the apparatus, the monkey can take a marshmallow out of the glass with its other hand. From [Weiss et al. \(in press\)](#).

stem of the glass with one hand and took the marshmallow from inside the glass with the other hand.

The fact that the tamarins used an inverted grasp (a posture they seldom adopted spontaneously) – to extricate the inverted glass from the apparatus suggests that they had the cognitive machinery to represent future body positions and compute optimal *series* of body positions. Similar optimization is also seen in anticipatory co-articulation in speech, where the way a syllable is produced often depends on what syllable will follow (Kent, 1983; Ladefoged, 1993). The observation that tamarins demonstrate the end-state comfort effect while lacking language or tool use abilities suggests that the cognitive and computational machinery underlying the end-state comfort effect is part of the scaffolding for more complex behaviors. This view fits with other developments in animal cognition research (e.g., Terrace, 2005).

What about the ontogeny of the end-state comfort effect? To date, there is little research addressing this question, although preliminary data collected by Matthias Weigelt of the University of Bielefeld (M. Weigelt, personal communication, February 2007) suggest that the end-state comfort effect is observed in children aged 4–5 but is not reliably seen in younger children. More rudimentary anticipatory effects do appear in prehension at a younger age. One series of studies demonstrated that 19–24 month-old infants orient their hands appropriately for the task of grasping a spoon, whereas younger infants (9–12 month-olds) do not exhibit such task-appropriate hand orientations (McCarty, Clifton, & Collard, 1999, 2001). Additional training can facilitate performance in 12 month olds, however (McCarty & Keen, 2005). In addition, Claxton, Keen, and McCarty (2003) found that 10-month old infants reach more quickly for a ball when engaging in an activity that requires less precision (throwing) than when engaging in an activity requiring more precision (fitting the ball into a tube).

Together, these demonstrations show that anticipatory abilities in reaching and grasping begin to emerge around the first year of life. The observation that the end-state comfort effect does not appear until later in development suggests that this ability requires relatively sophisticated anticipation and planning.

5. Conclusions

Karl Lashley (1951) challenged researchers of his day to give up the view of behavioral sequencing that prevailed at the time (reflex chaining). He also implicitly challenged researchers of succeeding generations to fill in the gaps in the understanding of the serial ordering of behavior. In the present article, we have reported our and others' attempts to take up that challenge. We have done so by briefly reviewing findings that have supported Lashley's hypothesis that there are hierarchically organized plans for behavior. Then we turned to research suggesting that the 'micro-plans' for the control of individual reaching movements are hierarchically organized as well, a view that was anticipated in the early days of cartoon animation when animators appreciated the distinction between keyframes and interframes. We indicated that a computational model of motor planning which relies on this distinction enables simulation of a broad range of phenomena and accounts of a number of findings in the motor control literature.

With respect to the question of how behavioral plans are assembled in real time, we suggested on the basis of our and others' research that plans for behavioral sequences are not formed *de novo* for each successive behavioral sequence, but instead are altered

to accommodate differences between just completed sequences and sequences to be performed next. We noted that several lines of evidence are consistent with this view. We now add that the plan-change method of plan formation is computationally economical. It is presumably easier just to deal with differences than always to build new structures.

Another attraction of the plan-change approach is that it makes sense in terms of the continuity of behavior. The physical transitions that our bodies go through are continuous in the sense that the state space of the body can never jump to some remote point from where it was at the last moment. Similar rules may apply to cognition as well. Although we may have the sense that we switch thoughts discontinuously from one task to another, it is unlikely that mental changes occur this way. Consistent with the continuity view, measurable costs are associated with switching from one task to another. This task switch effect (see Monsell, 2003, for review), suggests that moving through ‘mental space’ is continuous rather than discontinuous. A great deal of other recent research suggests that mental states that may seem discrete are in fact continuous (Spivey & Dale, 2004, 2006).

Saying that plans are formed through plan modification may help explain why there is working memory (Baddeley, 1986). If it supposed that a single plan is successively modified to permit successive behaviors, one can say that the memory one is working on at a given time is the plan that is being currently modified. Consistent with this proposal, it has been shown that people’s ability to perform more than one task at a time, including two-hand movement sequences, is constrained by how well the participants can conceptualize the two patterns as one (Franz, Zelaznik, Swinnen, & Walter, 2001; Mechsner, Kerzel, Knoblich, & Prinz, 2001). This finding fits with the idea that what one can do motorically depends on what one can conceive of mentally. Also consistent with this proposal is the fact that bypassing the cognitive controller for bimanual motion enables people to move their two hands independently with no practice at all. The relevant method is to have participants maintain felt contact with two moving objects at once, a new task called *haptic tracking* (Rosenbaum, Dawson, & Challis, 2006).

Limits on the size of working memory can also be conceived in terms of limits on the number of plan changes that can be made per unit time or, equivalently, the speed at which one can move from one point to another in ‘plan space.’ Data consistent with the notion of a limited size of working memory are well known, and there are comparable data for a limited size of motoric working memory (Inhoff & Gordon, 1997; Logan, 1983; Rosenbaum, 1990). Such data can be understood as a limit on the rate at which plan changes can be made, as illustrated above in connection with the parameter remapping effect and the hand path priming effect.

Finally, if plans for movement sequences are cognitive objects like any other, then it is noteworthy that sequential effects of the kind reviewed here in the motor domain are manifested in virtually all other domains of cognition, perception, and performance. The parameter remapping effect and the hand path priming effect are reminiscent of other sequential effects in psychology, such as the famous Luchins water-pouring study (Luchins, 1942), reported in every cognitive psychology textbook. Here, people who are primed to pour water into and out of beakers in particular orders have a hard time switching to a different pouring procedure when one is appropriate. The fact that the same sorts of inertial effects exist in the domains of intellectual problem solving and in motor performance calls into question the utility of drawing a deep divide between these two domains (Rosenbaum et al., 2001; Schmidt & Bjork, 1992). In general, the research reviewed here points to a unified rather than a divided conception of perception, cognition, and action.

In this connection, it is noteworthy that lately, scientists have suggested that action plays a stronger role in perception than was previously thought (e.g., Proffitt, Creem, & Zosh, 2001), that perception plays a stronger role in action than was previously thought (Hommel, Musseler, Aschersleben, & Prinz, 2001), and that action plays a stronger role in cognition than was previously thought (Glenberg & Kaschak, 2002; Zwaan & Taylor, 2006). The work reviewed here suggests that cognition also plays a stronger role in action than was thought before.

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