system as participants reached for the poker chip. The result was that the maximum separation between the index finger and thumb during the reach was unaffected by the size of the disks around the poker chip even though the consciously perceived size of the poker chip depended on the surrounding disks. The absence of a size contrast effect for the fingers was not due to participants seeing their fingers and correcting the separation seen between them.

The results of Aglioti, DeSouza, and Goodale (1995) are consistent with the two visual system hypothesis. That said, it should be acknowledged that these results and others obtained in this tradition have generated as much heat as light. Questions have been raised about what such results actually mean theoretically (e.g., Glover, 2002) and doubts have been expressed about methodological features of the studies and the inferences the results allow (Franz, 2001; Smeets & Brenner, 2006).

Eye-Hand Coordination

Continuing this overview of research on the visual guidance of reaching and grasping, it is natural to ask about eye-hand coordination. A number of studies have shown that when people move the hand as quickly as possible from one location to another, the eyes generally make saccades to the target location shortly before the hand. Lags between the eye and hand movements typically range from 60 to 100 ms (Angel, Alston & Garland, 1970; Prablanc, Echallier & Jeannerod, 1979). Neural signals driving the eyes and hand may be delivered simultaneously, as shown by the fact that arm-muscle EMGs begin at virtually the same time as the first sign of eye movements (Biguer, Jeannerod, & Prablanc, 1982, 1985). These results suggest that the eyes and hand comprise a “pointing synergy” whose neural commands may be generated simultaneously (Jeannerod, 1988). Consistent with this hypothesis, eye movement latencies and arm movement latencies are usually positively correlated. Trial-by-trial correlations between times to start moving the eyes and times to start moving the hand can be as high as +0.8 (Herman, Herman & Maulucci, 1981).

Because the eyes can generally travel to a target more quickly than the hand, the eye generally reaches the target before the hand (Abrams, Meyer, & Kornblum, 1990; Gribble, Everling, Ford, & Mattar, 2002; Herman, Herman, & Maulucci, 1981; Reina & Schwartz, 2003). Given that the eye then dwells on the target, what is the advantage of initiating eye and hand movements together? The benefit may derive from the ability of the oculo-motor system and manual-control system to share spatial information. The eye can “point” to the target and the hand can then move to the target, drawing on information about where the gaze is directed in space. The ability to move the eyes to a target aids hand movements, even when the target cannot be seen after the eyes have carried out the saccade (Abrams, Meyer, & Kornblum, 1990). The latter result indicates that the hand has access to spatial information about where the eye is pointing.

Additional evidence for the coupling of the eye and hand comes from studies in which the eye tracks the hand during slow, ongoing hand movements. The hand can be tracked by the eyes even when the hand cannot be seen (Gauthier, Vercher, Mussa-Ivaldi, & Marchetti, 1988). A moving image projected from one’s own hand can be tracked more accurately than the projection of someone else’s hand, even when the person whose eye movements are monitored does not know which hand is the source of the image displacement (Steinbach & Held, 1968). Perhaps most remarkably, the maximum velocity of smooth pursuit eye
movements—about 40 degrees per second in the case of a conventional visual target (Westheimer, 1954)—is more than doubled (to 80 to 100 degrees per second) when the visual target is moved by the subject him- or herself (Gauthier, Vercher, Mussa-Ivaldi, & Marchetti, 1988).

What mechanism allows for such tight coupling between the eyes and hands in tracking one’s own hand movements? Presumably, when one voluntarily moves one’s hand, one can predict where the hand-driven stimulus will be. Prediction enables the oculo-motor system to anticipate the position of the moving stimulus. Tracking a conventionally driven external stimulus, by contrast, does not derive such anticipatory benefits.

Anticipation is so sophisticated that when the eye tracks the hand, if the hand causes a target to reverse direction, the eye can track the target virtually perfectly, with no measurable delay, at the reversal point (Gauthier et al., 1988). It is difficult to imagine how such near-perfect tracking could be based on a mode of control not involving some form of prediction.

As tightly coupled as the eye and hand may be, the eye and hand should also be free of one another in some circumstances. It would be unappealing to be forced to visually track one’s hand movements, for example. Young babies and children with severe cerebral palsy cannot achieve such de-coupling. If the hand happens to fall into view, visual attention is captured, and the eyes are “dragged along” by sight of the hand (Gauthier et al., 1988). In the course of normal development, such coupling can be broken if necessary and the hands can perform one task while the eyes are directed elsewhere. The importance of this observation is that eye-hand synergies are task-dependent. Such task dependency is also evident in the discovery that the way the eyes scan an array of targets differs depending on whether the observer is merely looking at the targets or is preparing to tap the targets with the finger (Epelboim et al., 1997).

Beyond these fundamental observations, some creative studies of eye-hand coordination have allowed for inferences about naturalistic performance, the relation between performing actions and watching others perform those actions, and the understanding of language.

Regarding naturalistic performance, Hayhoe and Ballard (2005) described work that took advantage of the fact that eye movement recording technology has become more portable in recent years than it was before. Whereas in the past, a researcher interested in eye movements had to have a subject sit still in a head mount or even on a bite block, eye movements can now be recorded with the subject moving freely (Figure 7.6). With this new type of apparatus, it is possible to record where people look as they engage in everyday activities like stacking blocks or making peanut butter and jelly sandwiches (Hayhoe & Ballard, 2005).

Regarding the second of the topics referred to above, namely, the relation between performing and watching others perform actions, Flanagan and Johansson (2003) found that people generated similar scanpaths when they stacked blocks or watched someone else stack the same blocks. Subjects looked at critical points where they themselves would grasp blocks for stacking, and they looked at those same critical points when they watched someone else do the “heavy lifting.” This outcome suggests a tight connection between one’s own plans for action and one’s appreciation of others’ action plans.

Regarding the third of the topics mentioned above, the understanding of language, psycholinguists have relied on eye-hand coordination to investigate speech perception.

Behind this work is the idea is that if subjects need to reach for one of two objects named in an experimental trial, subjects’ eye movements over the scene may reveal how the subjects process the heard name of the object. If there are two objects, one a piece of candy and the other a candle, for example, the subjects may only look at the object to be named after the distinguishing syllable is heard: the “y” of candy or the “le” of candle. By contrast, if there are two objects, one a piece of candy and the other a pickle, subjects may look at the object to be named earlier, at the moment of the first distinguishing phoneme. All that is needed to distinguish “pickle” from “candy” is the first phoneme. If people can distinguish words immediately after their distinguishing phonemes are heard, they should be able to move their eyes to the candy more quickly when the alternative is a pickle than when the alternative is a candle. This is just what has been found (Allopenna, Magnuson, & Tanenhaus, 1998; Tanenhaus, Spivey Knowlton, & Eberhard, 1995).
Much of the research on the control of hand movements has been concerned with the task of moving the hand from one position to another, generally as quickly and as accurately as possible. How people correct their errors has been a topic of long-standing interest.

In approaching this problem, it is useful to remember that errors arise when initial movements are incorrect. From this perspective, it is useful to note some of the errors reflect biases in the way movements are made.

Figure 7.7 shows data from a study that revealed an important feature of such biases. In this study (Gordon & Ghez, 1994), participants moved one hand from a home position to each of a number of targets. Some of the targets were near the home position and others were farther away. Participants were told that they did not have to correct their movements if the movements ended off target. Under this instruction, the distribution of endpoints for the movements could be taken to reflect the biases of the movement system.

As seen in Figure 7.7, the endpoint distributions were elliptical: The endpoints were more widely spread along the line connecting the start point to the target point than along the line perpendicular to the line connecting the start point to the target point. This result implies that participants were better at getting the direction of movement right than at getting the amplitude of movement right. From this outcome, one would expect amplitude corrections to be more strongly needed than direction corrections.

![Elliptical end-point distributions obtained when participants moved from a home position (+) to each of a number of targets (circles) but did not have to correct the movements they made. From Gordon, J., & Ghez, C. (1994). Accuracy of planar reaching movements: I. Independence of direction and extent variability. Experimental Brain Research, 99, 97-111. With permission. From http://www.ncbi.nlm.nih.gov/pubmed/7925800.](image-url)
Amplitude errors are of two main kinds. One is going farther than required. The other is going shorter than required. Going farther is more time-consuming than going shorter. It takes longer to turn back than to go farther (Vince & Welford, 1967). This outcome makes sense in terms of mechanical inertia. It may also explain why participants take longer to resolve direction uncertainty than extent uncertainty when preparing to move to targets with different directions and extents (Rosenbaum, 1980). They may pay more attention to getting direction right before movements begin than to getting amplitudes right before movements begin because direction errors are harder to correct than are amplitude errors.

Figure 7.8 shows another important finding from Gordon and Ghez (1994). This figure shows speed profiles for the movements in their task. As seen in Figure 7.8, the speed profiles are bell-shaped, with the bell shapes being larger for movements to far targets than for movements to near targets. This outcome suggests that from the start of the movements, participants moved at rates that scaled with the distance to be covered. The movements were ready in their entirety before being executed, or at least their principal features were

![Figure 7.8](Figure_7.8.png)

ready in advance, such as their lengths and directions. Before they started to move, the participants knew, at some level, just how they would do so.

This outcome helps explain why one sometimes has the uncanny feeling, while making a movement, that the movement is doomed to fail. Similarly and more positively, it helps explain why one may sense that a movement will be successful (Gray, Beilock, & Carr, 2007). A report of such a feeling was reported in the sports news while the author was working on this second edition of Human Motor Control. On the evening of April 7, 2008, the University of Kansas beat the University of Memphis for the NCAA national basketball championship. With just 2.1 seconds left in regular play and with Kansas behind Memphis by 3 points, Mario Chalmers hit a 3-pointer. The two teams went into overtime and Kansas went on to beat Memphis 75–68. In the author’s local newspaper, the Centre Daily Times, this quote from Mario Chalmers appeared the next morning: “I had a good look at it. . . . When it left my hands it felt like it was good, and it just went in.”

Woodworth’s Pioneering Study

We turn now to error correction itself. How well can people aim for targets? Pioneering work on aiming was done by Woodworth (1899) for his doctoral dissertation at Columbia University. Woodworth was impressed by the speed and accuracy with which construction workers hammered nails. He wondered how these workers could achieve the speed and accuracy they did. To answer this question, he set up an experiment in which people moved a stylus back and forth through a slit, reversing the direction of the movements at two visually marked locations. Woodworth recorded subjects’ movements by allowing the pencil to draw a line on a paper roll that turned beneath the work surface. (Computers and other electronic data-recording devices were not yet available.) Subjects were asked to make the back-and-forth movements at different rates specified by a metronome. In one set of conditions, subjects made the movements with their eyes open. In another set of conditions, they made the movements with their eyes closed.

Woodworth’s results are shown in Figure 7.9. The dependent measure was mean absolute error, defined as the mean absolute value of the distance between the point where the pencil reversed direction and where it should have reversed direction (the target). The independent measure was the mean movement velocity. As seen in Figure 7.9, when subjects had their eyes closed, their mean absolute error remained more or less constant as velocity increased. When subjects had their eyes open, their mean absolute error decreased as velocity decreased.

Woodworth accounted for these results by saying that in the eyes-closed condition subjects’ movements were entirely preprogrammed, being guided by what he called the initial impulse. By contrast, in the eyes-open condition, the subjects’ movements were preprogrammed but could be corrected with visual feedback, or what Woodworth called current control. Woodworth hypothesized that the first part of an aiming movement is achieved through initial impulse control and the later parts are achieved with current control. He based this hypothesis on observations of participants making large, quick, target-directed movements followed by smaller, slower, target-capturing movements.

By Woodworth’s way of thinking, if a movement is made in too short a time for current control to be possible, the movements should be just as error-prone if visual feedback is
FIGURE 7.9 Mean absolute error of hand movements made by subjects with their eyes open or closed. Data from Woodworth (1899). Adapted from Woodworth, R. S. (1899). The accuracy of voluntary movement. Psychological Review, 3, 1–119. With permission.

present or not. Conversely, if a movement is made in enough time for current control to be possible, the movements should more accurate if visual feedback is present than if not. Seeing where along the required velocity axis there is a transition from no benefit of visual feedback to some benefit of visual feedback lets one estimate the critical velocity for using visual feedback. Because a single distance was used in Woodworth’s experiment, the critical velocity could be translated to a critical time (since velocity equals distance divided by time). Woodworth estimated the critical time for visual feedback to be a fifth of a second.

Later research largely confirmed Woodworth’s estimate. It did so based on the following logic. Suppose it takes \( t \) ms to process visual feedback. Movements that take longer than \( t \) ms should then be impaired if visual feedback is suddenly withdrawn, but movements that take less than \( t \) ms should be carried out equally well regardless of whether visual feedback is available or not. This reasoning allowed Keele and Posner (1968) to estimate \( t \). They trained subjects to move a stylus from a home position to a target position in different amounts of time: 150 ms, 250 ms, 350 ms, or 450 ms, +10% for each target time. In a block of trials, the subject repeatedly tried to make the movement within the target time, but on some trials the room lights went off unpredictably as soon as the movement began. Aiming accuracy was affected by the presence or absence of visual feedback only when movements took about 200 ms or more. From this outcome, Keele and Posner (1968) concluded that it takes about 200 ms to use vision to correct aiming movements. Subsequent research has suggested that visually based corrections may take less time than Keele and Posner (1968) proposed (Carlton, 1981; Zelaznik, Hawkins, & Kisselburgh, 1983). Nonetheless, it is safe to say that the time for the visual feedback loop is between 100 ms and 200 ms.
Fitts' Law

The idea that aiming movements have an initial, ballistic phase followed by a feedback-based homing-in phase has been pursued with a number of methods. One is to have subjects move a stylus back and forth between two targets as quickly as possible, where the distance between the targets and the widths of the targets varies (Fitts, 1954). The time to bring the stylus from one target to another increases with the distance between the targets. It also increases as the targets become narrower. This relation was summarized by Fitts (1954) as follows:

$$MT = a + b \log_2(2A/W),$$

(7.1)

where $MT$ denotes movement time, $A$ denotes the amplitude (or distance) between the centers of the targets, $W$ denotes the width of the target, and $a$ and $b$ are empirical constants. The term $\log_2(2A/W)$ is called the index of difficulty, or ID.

Equation 7.1 says that MT increases linearly with ID, a claim that has been confirmed experimentally (Figure 7.10). In fact, Equation 7.1 has been found to do such a good job predicting movement times for so many aiming tasks that it has come to be called Fitts' law (Keele, 1968). Fitts' law is one of the few laws in psychology.

Other tasks where Equation 7.1 applies include discrete ("one-shot") aiming movements (Fitts & Peterson, 1964), transferring pegs over a distance to be inserted into a hole (Annet,
Golby, & Kay, 1958), moving a joystick or turning a handle to move a cursor on a screen (Jagacinski, Repperger, Moran, Ward, & Glass, 1980; Meyer, Smith, & Wright, 1982), throwing darts at a target (Kerr & Langolf, 1977), carrying out aiming movements under water (Kerr, 1973), and manipulating objects under a microscope (Langolf, Chaffin, & Foulke, 1976).

Some mathematical variants of Fitts’ law have been proposed (Beamish, Bhatti, Mackenzie, & Wu, 2006; Kvalseth, 1980; Plamondon & Alimi, 1997), but the main idea behind Fitts’ law has never been questioned, namely, that the farther one has to go and the tighter the accuracy constraints of the target, the longer the movement takes, provided one tries to go as quickly as possible.

Fitts’ law or variants of Fitts’ law (Elliott, Helsen, & Chua, 2001) have also been pursued by considering other related tasks, including moving around obstacles (Jax, Rosenbaum, & Vaughan, 2007) and moving through restricted pathways (Accot & Zhai, 2001). People can engage in motor imagery in accordance with Fitts’ law (Decety & Jeannerod, 1995; Sirigu et al., 1996) and can see actions as possible or impossible depending on whether those actions are consistent with Fitts’ law (Grosjean, Knoblich, & Shiffrar, 2007). Fitts’ law can also be violated when extraneous targets are present in the workspace (Adam, Mol, Pratt, & Fischer, 2006), and decisions about optimal movement choices, as defined by Fitts’ law, can be made in some tasks (Augustyn & Rosenbaum, 2006), but not others (Young, Chau, & Pratt, 2008).

**Iterative Corrections Model**

How can one explain the main relation suggested by Fitts’ law? One idea, embodied in the *iterative corrections* model of Crossman and Goodeve (1963/1983; Keele, 1968), is that Fitts’ law is mainly attributable to current control. According to this model, an aiming movement consists of a series of discrete submovements, each of which is triggered by feedback that the target has yet to be attained. By hypothesis, each submove takes the hand (or a handheld stylus) a fixed proportion of the distance to the target. For example, if the hand is 20 cm from the center of the target and each submove takes the hand 50% closer to the center of the target, then the first submove brings the hand 10 cm from the target center, the second submove brings the hand 5 cm from the target center, the third submove brings the hand 2.5 cm from the target center, and so on. As the width of the target decreases, the hand falls within the target later in the series of submovements. Similarly, as the distance of the target increases (for a given target width), the first submove for which the hand falls within the target is also delayed. Qualitatively, then, the model accounts for the relationships implied by Fitts’ law. Quantitatively, the model predicts a linear increase of total movement time with index of difficulty (Fitts’ law), provided one assumes that each correction takes a constant amount of time (Keele, 1968).

The iterative corrections model has been supported by detailed analyses of movement trajectories. Discrete submovements of the sort assumed in the model have been recorded (Annett, Golby, & Kay, 1958; Carlton, 1981; Crossman & Goodeve, 1963/1983; Jagacinski et al., 1980; Langolf, Chaffin, & Foulke, 1976; Woodworth, 1899). A representative example is shown in Figure 7.11.

Further research has shown, however, that the iterative corrections model is a bit off target. When discrete submovements are present, they appear as distinct peaks in the function relating velocity to time, yet one does not always see these distinct velocity peaks (Langolf et al., 1976). In addition, when distinct submovements are detectable, they do not have constant

durations (Jagacinski et al., 1980; Langolf et al., 1976), nor do they travel constant proportions of the distance remaining to the target (Jagacinski et al., 1980). These problems have led investigators to seek an alternative to the iterative corrections model.

**Impulse Variability Model**

One alternative says that Fitts’ law represents the initial impulse phase of movement rather than the current control phase (Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979). The experiments that led to this model differed from the kinds of experiments that Fitts (1954) conducted. Whereas Fitts had his participants get to a defined target area in as little time as possible, Schmidt et al. had their subjects get to a target within a prescribed amount of time, trying to minimize the spatial variability of the movement endpoints. Specifically, subjects in the experiments of Schmidt et al. were supposed to move within 200 ms, a time that was unlikely to permit much current control. The targets were between 10 and 30 cm from the home position. A single movement was made in each trial. The measure of interest was the spatial variability of the movement endpoints.

Schmidt et al. observed that the standard deviation of the endpoints, denoted $W_e$, increased with the distance, $D$, to be covered and decreased with the duration, $T$, of the movement:

$$W_e = k(D/T),$$

which can be rearranged as

$$T = k(D/W_e).$$

This relation between time, distance, and effective target width is similar to Fitts’ law.

What property of the motor system could give rise to this relation? Schmidt et al. proposed that rapid arm movements are achieved by, in effect, flinging the arm toward a target. The flinging is achieved with a neuro-motor impulse delivered to the arm muscles. The impulse causes the muscles to exert a burst of force for the first half of the movement time. During the second half of the movement time, the limb coasts (moves passively) toward the target.
A further assumption is that there is variability in the forces driving the arm toward the target as well as variability in the time during which the forces are produced. The standard deviation of the force is assumed to be proportional to the amount of force, and the standard deviation of the time during which impulses are delivered is assumed to be proportional to the time during which the impulses are delivered. Thus, if more force is used to cover a larger distance, more force variability results, and if more time is spent propelling the limb toward the target, more time variability results as well. Because time and force can be independently controlled in the model, the participant’s challenge is to find the time and force that minimize the variability of both factors. According to Schmidt et al., Fitts’ law represents the solution to this problem.

The impulse variability model has much to recommend it, at least as a model of rapid movements. It recognizes the inherent variability of neuro-motor processes, and it represents this variability in simple terms.

Schmidt et al. tested their assumptions about force and time variability by having subjects make isometric movements, producing different magnitudes of force for varying amounts of times. As predicted by the model, standard deviation of force was proportional to the force produced, and standard deviation of time was proportional to the time spent moving.

As encouraging as these results were for the impulse variability model, the model cannot account for all the effects observed in rapid aiming tasks. Submoves based on feedback are often observed, as noted in the last section, yet the impulse variability model makes no provision for feedback-based correction. Furthermore, questions have been raised about the model’s assumptions concerning force and time variability (Newell & Carlton, 1988). Finally, some questions were raised about the way Schmidt et al. derived Fitts’ law from their underlying assumptions, although Fitts’ law can be derived in a less controversial manner if the assumptions are refined (Meyer, Smith, & Wright, 1982).

**Optimized Initial Impulse Model**

So far, we have considered two ways of explaining Fitts’ law. One, the iterative corrections model, explains Fitts’ law solely in terms of current control. The other, the impulse variability model, explains Fitts’ law solely in terms of initial impulse. Neither model fully accounts for the data on manual aiming, so one is left hoping for a better model. Such a model was proposed by Meyer, Abrams, Kornblum, Wright, and Smith (1988). Their *optimized initial impulse* model is a hybrid of the iterative corrections model and the impulse variability model.

The starting point for the optimized initial impulse model is shown in Figure 7.12. By hypothesis, the subject makes a first movement toward the target. If the movement lands within the target, the task is completed, but if the movement lands outside the target, another movement is necessary. The second movement can either land within the target or not. If the second movement does not reach the target, another movement must be made, and so forth. The subject’s task is to reach the target as quickly as possible, so ideally s/he should make just one, high-velocity movement directly to the target. The problem is that, according to the model, the spatial accuracy of movements is imperfect. The standard deviation, $S_i$, of the endpoint of any movement $i$ is assumed to increase with the distance, $D_i$, covered by that movement and to decrease with its duration, $T_i$, that is,
\[ S_i = k(D_i / T_i) \]  \hspace{1cm} (7.4)

where \( k \) is a constant. The subject therefore faces a dilemma. To get to the target as quickly as possible, s/he could make a movement with a long distance (large \( D \)) and short time (small \( T \)), but this would result in a large standard deviation (\( S \) in Equation 7.4) and a low probability of hitting the target. Alternatively, the subject could make a movement with a long duration (\( T \) in Equation 7.4) and s/he could make a series of short movements (small values of \( D \)) and be sure of hitting the target, but the total movement time would be very long. The best thing to do, then, is to find the balance of \( D \)'s and \( T \)'s that minimizes the total movement time. According to Meyer et al. (1988), Fitts' law represents such an optimal balance.

The optimized initial impulse model is interesting not just because it does a good job of accounting for data from aiming studies, but also because it implies that even when people engage in a task as mundane as bringing the hand to a target, they employ sophisticated strategies to optimize performance. This conclusion reinforces the point that has been made repeatedly in this book and that is arguably the most important general principle of all of motor control research, namely, that even simple motor tasks that appear on first glance to be computationally trivial are far from it.

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**EQUILIBRIUM POINT HYPOTHESIS**

In the research reviewed above, subjects were instructed to move very quickly. Not all aiming movements are performed this way, however. When movements are performed at slower rates, are they controlled through heavy reliance on feedback? An experiment reported by Polit and Bizzi (1978) provided surprising feedback on this question.
Polit and Bizzi (1978) investigated monkeys' pointing responses to target lights (Figure 7.13). On any given trial, one of the lights was turned on and the monkey was supposed to point to the illuminated light, holding its arm there for 1 second to receive a sip of juice. The monkey could not see its arm, so it received no visual feedback about the position of its arm relative to the light. The position of the arm was recorded with a splint attached to a vertical axle. The axle rotated when the monkey's arm moved, and the angular position of the axle was recorded. The axle could also be turned with a torque motor. When the torque motor came on, it caused the monkey's arm to be displaced. The torque motor was turned on unpredictably from trial to trial but usually came on after the target light was illuminated and before the monkey moved its arm.

The question Polit and Bizzi (1978) sought to answer was what would happen to the accuracy of pointing when the arm was displaced. For monkeys with normal proprioceptive feedback, pointing accuracy was high, consistent with the notion that when the monkey felt its arm being displaced, it introduced appropriate compensatory responses. However, an additional aspect of the experiment suggested that feedback was not the only source of information that monkeys relied on. After the initial phase of the experiment (described above), the dorsal roots of the monkey's spinal cord were severed. These fibers supply sensory feedback to the central nervous system (see Chapter 3). Thus, cutting the dorsal roots prevented the monkey from feeling anything below the neck, as confirmed in behavioral and physiological tests. Given this state of affairs, one would expect the monkey to be unable to compensate for the perturbation. Yet it could do so. When the monkey was again supposed to point to the target lights, it could do so accurately, even after the perturbation was applied.

How can this surprising result be explained? Polit and Bizzi (1978) appealed to the notion that muscles act like springs (Asatryan & Feldman, 1965; Crossman & Goodeve, 1963/1983). To appreciate the analogy, consider the following experiment, which you can set up yourself.
Take two identical rubber bands and attach one to one side of a hinged board and the other to the other side of the board, as shown in Figure 7.14. Orient the board parallel to the ground so the forces provided by the rubber bands are orthogonal to (perpendicular to) the force of gravity. Now pull the board to one side and release it. It will swing back and forth for a while and then come to rest at approximately 90 degrees. Next, try releasing the board from different starting positions. It will return to the same final position. This demonstrates that a spring system can achieve the same final position regardless of its starting position—a property known as equifinality. If the primate arm were controlled like the simple spring system of Figure 7.14, it too would be able to arrive at the same final position regardless of the position from which it starts, and it could do so even without feedback.

Unlike the board in Figure 7.14, a biological arm can get to different final positions. Can a simple spring system achieve different final positions? There are two ways it can. You can demonstrate one of these methods with a hinged board and two rubber bands of different length but the same stiffness. (You can make two such rubber bands by cutting one rubber band into two pieces of unequal length). Attach the two rubber bands to either side of the hinged board and again try releasing the board from different starting positions. Again the board will always end up at the same final position, but this time the final position will not be at 90 degrees. Instead, it will be in the direction of the shorter rubber band (see Figure 7.14B). In general, the board will end at the position where the opposing forces of the two rubber bands balance out, at the equilibrium position. If the left rubber band has a shorter resting length than the right rubber band, the board will end up pointing to the left. If the right rubber band has a shorter resting length than the left rubber band, the board will end up pointing to the right. The greater the discrepancy between the resting lengths of the two rubber bands, the more extreme the board’s final position will be. This follows from the fact that, for ideal springs, the tension exerted by a spring is proportional to the distance it is stretched from its resting position, a principle known as Hooke’s law. Because it is possible to obtain different equilibrium positions by changing the resting lengths of opposing springs, the biological motor system might achieve different limb positions by altering the resting lengths of the opposing muscles acting on the limb (Berkenblit, Feldman, & Fucson, 1986).
Another way to achieve different final positions with a simple spring system is to vary the stiffnesses of the springs (see Figure 7.14C). You can observe this effect by using two rubber bands of equal length but different stiffnesses. Use three identical rubber bands and place two on one side of the board for this purpose. Displace the board and let it swing freely. It will end up in the direction of the stiffer rubber band. In general, the stiffer the rubber band on one side relative to the other, the farther away from 90 degrees the board’s final position will be. This outcome suggests that another way for a biological motor system to vary a limb’s final position is to vary the stiffnesses of the limb’s opposing muscles (Polit & Bizzi, 1978, 1979).

Why might it be advantageous for the motor system to treat muscles as springs? The main reason is that regulating muscle resting length or muscle stiffness is a simple way of directing a limb from one position to another. If the limb naturally behaves as an equilibrium point system, it is sensible for the motor system to treat it as such. If the motor system could not exploit the spring-like nature of muscle, it might be necessary to specify the entire trajectory of the limb, which could be onerous. Treating the limb as an equilibrium point system affords the possibility of significantly reducing the computational demands of trajectory planning.

Assuming that the study reported by Polit and Bizzi (1978, 1979) demonstrates reliance on an equilibrium point strategy for monkey limb control, what evidence is there that the equilibrium point model applies to human performance? One source of information is an experiment in which human patients who lacked sensory feedback from their fingers moved a finger from one position to another without being able to see their finger move (Kelso & Holt, 1980). After performing this task, the patients were asked to reproduce the movement they had just performed, passing the finger either over the same distance or to the same location as in the first task. Location reproduction should be possible, according to the equilibrium point model, even if the position of the finger cannot be sensed and even if the finger is passively displaced while moving toward the target. Distance reproduction, however, should be difficult, particularly if the finger is perturbed by an external force. The results supported the equilibrium point model. Although the patients could not feel their finger, they could bring the finger from one location to another, even when the finger was momentarily displaced by a torque motor. When the same patients were asked to cover the same distance as in the first task, their performance was significantly worse than when they were asked to reach the same location. This result suggests that subjects were not simply clever about finding ways of compensating for their handicaps.

Because the study of human patients by Kelso and Holt (1980) is like the study of monkeys by Polit and Bizzi (1978, 1979), one might think that the equilibrium point model can only be demonstrated with feedback-deprived subjects who must compensate for unexpected limb displacements. The model’s success is more widespread, however. When a person with normal proprioception is asked to use the forearm to drag a load over a horizontal surface to a target, if the load is suddenly released and the subject does not attempt to compensate, the resulting hand trajectories are as predicted by the mass-spring model (Asatryan & Feldman, 1965). Furthermore, a computer simulation of the equilibrium point model (Cooke, 1980) predicts a characteristic of rapid aimed hand movements that has been obtained in several studies—a bell-shaped speed profile, with the peak of the curve near the midpoint of the displacement (Abend, Bizzi, & Morasso, 1982; Cooke, 1980).
There has been debate about the equilibrium point hypothesis, however. One point of contention is whether muscle resting lengths or stiffnesses are regulated to bring limbs to new positions. Bizzi and colleagues favored the stiffness regulation view, and in support of this hypothesis, they argued that even in the absence of afferent feedback it is possible to identify cells in the spinal cord (of the frog) that when stimulated drive the leg to well-defined positions (Bizzi, Mussa-Ivaldi, & Giszter, 1991).

Feldman and colleagues favored the resting length view, arguing that a well-established mechanism can be used for regulating muscle resting length. That mechanism is changing the threshold for the muscle stretch reflex (Feldman & Latash, 2005). Feldman and colleagues contended that the results obtained by Bizzi et al. are compatible with this interpretation. A demonstration you can try for yourself to perhaps convince you that Feldman and colleagues are correct is to squeeze an object—a can of soda, say—and then pull the object out from between your squeezing fingers. Your fingers will quickly come to rest at a position within the now-absent object. This position corresponds to the resting lengths your muscles adopted while you held the can.

Others have argued that neither the stiffness view nor the resting length view is correct. Kawato and colleagues questioned the equilibrium point hypothesis altogether, based on research indicating that participants have much finer control of limb trajectories than might be expected if the equilibrium point hypothesis were correct (Gomi & Kawato, 1996). Burdet, Osu, Franklin, Milner, and Kawato (2001) argued that it is not as difficult to learn to control limb trajectories as advocates of the equilibrium point hypothesis assert. Burdet et al. showed that even in the face of highly unstable dynamics (forces and torques acting on the limb), people could learn to make adaptive movements. Thus, the subjects of Burdet et al. could do quite well on a task that, according to proponents of the equilibrium point hypothesis, should be impossible or at least very difficult.

**DISCRETE VERSUS CONTINUOUS MOVEMENTS**

Implicit in the foregoing discussion of the equilibrium point hypothesis is the assumption that movements are discrete: A movement is made to an endpoint, then the next movement is made to its endpoint, and so on. According to the equilibrium point hypothesis, if casual observation suggests that someone is moving in a smoothly flowing fashion, the underlying control is actually discrete, such that one starts before another ends. So are reaching movements fundamentally discrete or fundamentally continuous? Are they discrete with overlap that makes them appear continuous, or are they continuous with stops that make them appear discrete?

Again, as might be imagined, this has been a topic of debate in the motor control community. Evidence has been offered for the view that continuous-appearing movements may in fact arise from cascading discrete movements. Much of this evidence has relied on demonstrations that complex movement sequences with apparently seamless transitions can in fact be decomposed into overlapping submovements. Work on the optimized initial impulse model took this tack (Meyer et al., 1990), as did studies of infant reaching movements (Berthier, 1996) and corrective movements by human adults (Henis & Flash, 1995).
Henis and Flash (1995) asked what would happen when participants try to bring the hand to one target but then had to bring the hand to some other target that suddenly appeared. In their experiment, Henis and Flash had participants make horizontal planar arm movements with the preferred hand, displacing a stylus from a start location to a target location. In the control trials, a single target location appeared and participants were supposed to make direct movements to that target. In the experimental trials, the first target was extinguished and a different target appeared at either of two equally likely locations. Henis and Flash found that the observed kinematics of the hand could best be explained with a discrete cascade model. According to the model, two independent movements simply add together if a second target appears. One movement corresponds to the initially planned displacement from the start position (A) to the first target (B). The second movement corresponds to the displacement from the first target (B) to the second target (C). How the movements add—where in the movement from A to B the movement from B to C is added—depends on the timing of the second target relative to the motion of the hand away from the home position. An interesting feature of this model was that it avoided an appeal to the idea that participants aborted the first movement if a second target appeared. Rather, the second movement was simply added to the first and the first movement was allowed to run its course. This strategy is always guaranteed to work, provided the two movements are carried out correctly, because the two movements comprise two vectors that, when added, are guaranteed to bring the hand from its start position to the necessary end position.

Henis and Flash’s model is noteworthy because it illustrates how seemingly continuous kinematics can arise from discrete control. Yet it does not follow that all continuous kinematics arise this way. In an influential study that pushed things in the other direction, Guiard (1993) asked whether the back-and-forth movements observed in the Fitts’ reciprocal aiming task are in fact discrete. Guiard studied the kinematics of the hand in back-and-forth aiming tasks with varying indices of difficulty (IDs). Guiard found, as shown in Figure 7.15 (bottom panel), that when ID was high (a difficult aiming task), the function relating acceleration to displacement was essentially a straight line, or more properly, a series of points that ascended and descended along a line that was approximately straight. However, as ID decreased (aiming became easier), the function relating acceleration to displacement contained loops in the vicinity of each target. Guiard (1993) took these results to suggest that the normal way of moving is to move continuously rather than in a discrete point-to-point fashion.

Others have chimed in in favor of Guiard’s all-is-continuous view (Mottet & Bootsma, 1999; Schöner, 1990). Others have argued that there are, in fact, two distinct modes of controlling movements—the discrete way and the continuous way (Buchanan, Park, & Shea, 2006; Hogan & Sternad, 2007; van Mourik & Beek, 2004). Investigators are still sorting out the issue.

INTERSEGMENTAL COORDINATION

In the last section we considered the question of whether motions of the hand, treated as a single point, are part of one continuous stream or discrete displacements chained together. How, we asked, are series of movements coordinated?
We turn now to coordination of a somewhat different kind, coordination of different limb segments acting simultaneously. The limb segments to be considered are the hand, fingers, wrist, elbow, and shoulder. Because most people have two hands, the question of coordination naturally also extends to the analysis of two-hand motions. However, it is important to remember that while coordination can be studied in terms of the effectors that are usually involved in reaching and grasping, coordination need not be studied only in those terms. One might grasp an object with one’s mouth, for example, which is not at all unusual if one is a bird, dog, or baby. Whatever principles apply to coordination of the canonical effectors for reaching and grasping—the fingers, hand, wrist, elbow, and shoulder—those principles might also apply to the coordination of other effectors. A general theory of coordination ought to accommodate coordination of any effectors, even effectors that extend to tools.

Transport and Grasp Phases

Reaching for an object and taking hold of it appear to take place in two distinct phases—a transport phase and a grasp phase. During the transport phase, the hand is carried toward the object. During the grasp phase, the fingers are wrapped around the object. These two phases appear to be controlled by different areas of the brain. Damage to the pyramidal tract (see Chapter 3) results in impairments of fine finger control, including impairments in grasping objects. Damage to the extra-pyramidal tract results in impairments of gross arm movements, including damage to hand transports prior to object manipulation (Kuypers, 1973). Developmentally, the pyramidal tract also matures after the extra-pyramidal tract (Lawrence & Hopkins, 1972), which may explain why fine finger control is possible only after gross arm movements come to be controlled relatively skillfully. Behavioral studies also support the hypothesis that the transport phase and grasp phase are governed separately. Changing the size of an object to be grasped does not affect the rate at which the arm is moved but does affect the maximum separation between the thumb and index finger as the hand approaches the to-be-grasped object (Jeannerod, 1981, 1984).

There is some dependency between the grasp and transport phases, however. The maximum separation between the thumb and index finger when the hand is brought toward an object depends on the speed with which the grasp must be completed. Thus, when subjects try to reach for objects quickly, they spread their fingers farther apart than when they try to reach for the same objects at a leisurely pace (Wing, Turton, & Fraser, 1986). Greater finger widening increases the likelihood of capturing the object when the hand travels at high speed.

Another kind of dependency between transport and grasp concerns the timing of the opening and closing of the hand and the speed with which the hand is transported. As reported by Jeannerod (1981, 1984), the distance between the thumb and index finger is usually greatest when the hand begins the final, slow-approach phase of the movement (see Figure 7.16). Even individuals with prosthetic hands exhibit this effect (Fraser & Wing, 1981). The coincidence of maximal finger widening and the start of the slow-approach phase may reflect a tendency to time-lock related behavioral events. Having the events occur simultaneously reduces the number of degrees of freedom that must be independently controlled by the motor system. Models have been developed for such timing in reaching and grasping.