CHAPTER

7

Reaching and Grasping

OUTLINE

Much of human culture takes the form it does because of what we do with our hands. We build houses, draw pictures, make bread, play musical instruments, and gesture, all because of the strength, flexibility, and precision of hand movements. Manual performance is so central to human experience that we refer to hand motions when we discuss other topics. We say, "on the one hand and on the other," "I hope this grabs your attention," "These ideas go hand in hand," "an offhand remark," and so on.

Because of the importance of manual control in human experience, several lines of research have grown around it. One is the control of drawing and writing, which will be covered in the next chapter. Another is the control of keyboard performance, which will be covered in the chapter after that. A third is the use of sign language, a topic that has been studied more from the perspective of linguistics and communications than motor control per se, so it is pointed to here but not treated in detail (Emmorey, 2002; Goldin-Meadow, 1999; Goldin-Meadow & Wagner, 2005; Poizner, Klima, & Bellugi, 1987). A fourth is the control of reaching and grasping, which will occupy some of our attention in this chapter, and is the subject of entire books (MacKenzie & Iberall, 1994; Wing, Haggard, & Flanagan, 1996).

Reaching and grasping depend on a blend of initial planning and subsequent correction. The initial planning is based on perception of the objects to be grasped and memory of what the objects afford in the way of grasping. Based on such information, one can decide whether to pick up objects with one hand or two, with a large grip or a small grip force (Gordon, Forssberg, Johansson, & Westling, 1991a,b,c), with all the fingers or only some of the fingers wrapped around the objects (Arbib, Iberall, & Lyons, 1985), and, depending on what will be done with the objects, with one or another placement of the hand on the objects (Fischman, Stodden, & Lehman, 2003; Haggard, 1998; Klatzky & Lederman, 1985; Kleinholdermann, Brenner, Franz, & Smeets, 2007; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987; Rosenbaum, Cohen, Meulenbroek, & Vaughan, 2006); see Figure 7.1.

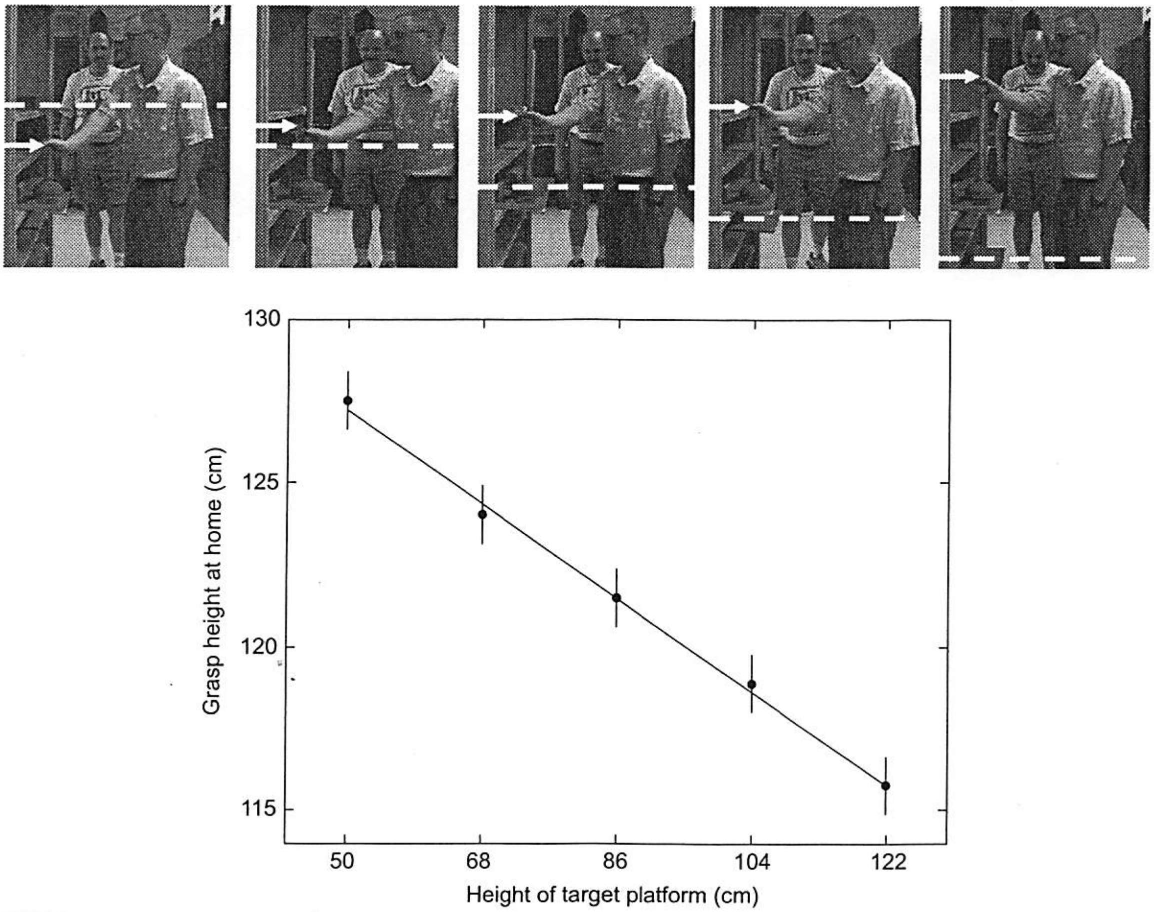

FIGURE 7.1 Grasping an object differently depending on the height to which it will be carried. Top: A subject (who gave permission to have his photo shown here) grasps a plunger on a home platform with different grasp heights (white arrows) before moving the plunger to target platforms at different heights (white dashed lines). The author of this book, also shown here, was responsible for setting up the target platforms. Bottom: Mean grasp heights (±1 SE) for home-to-target grasps. From Cohen, R. G. & Rosenbaum, D. A. (2004). Where objects are grasped reveals how grasps are planned: Generation and recall of motor plans. Experimental Brain Research, 157, 486–495. With permission.

The chapter is organized as follows. First, we will consider the development of reaching and grasping. The overarching question is at what age different aspects of reaching and grasping tend to come online. In this section, we will be concerned with more than just the extent to which grasps reflect perceptual sensitivity to physical features of objects to be grasped. We will also be concerned with the ability of infants to grasp objects differently depending on what they intend to do with the objects. Identifying the ages at which different abilities are manifested need not be taken to imply a strict stage model of development. Different babies progress at different rates, with some abilities becoming available before others in different individuals (Thelen Corbetta, Kamm, & Spencer, 1993; Thelen, Corbetta, & Spencer, 1996). Thus, describing reaching abilities in a stagewise way is meant to convey a statistical regularity, not a strict stagewise progression.

Next we will look at visual guidance. One of the issues we will consider concerns vision and movement. Given that we rely on vision to help guide our hand movements, one might expect the mappings between vision and movement to be rigid by the time one reaches adulthood. The available evidence suggests otherwise. There is a surprising degree of flexibility in the mappings between the motor system and the visual system. Similarly, there is considerable flexibility in the mappings between vision and touch. Why this is and how it is possible are matters taken up in the section on visual guidance. In this section we will also consider eye-hand coordination and how research on visually guided reaching sheds light on the distinction between two neural systems that have sparked a great deal of excitement in this field of research, the visual "what" system, and the visual "how" system.

The next section will be concerned with aiming. Here we will review work showing that aiming relies on a blend of preprogramming and error correction. A series of models has been developed to characterize this blend. That series of models has taken over a century to unfold. We will review it here in a few pages.

The fourth part of the chapter will be concerned with the equilibrium point hypothesis. The main idea here is that the motor system may have ways of specifying goal positions that eliminate the need for control of the detailed features of the movements to those goal positions.

The fifth part of the chapter will be concerned with a relatively new debate that has sprung up in human motor control: Are movements discrete or continuous? Do we, in other words, move from place to place in steps, or do we move in a smoothly flowing stream?

Sixth and finally, we will look at the coordination of the limb segments involved in reaching and grasping. When we reach for and grasp objects, we do so with our fingers, hands, and arms, and even with our torsos and legs—whatever it takes to impart the forces needed to hold, carry, and manipulate the objects being dealt with. An important principle that has emerged from this area of study is that the limb segments are controlled in a way that reflects sensitivity to their functional interdependence. Recent work on bimanual coupling suggests that this interdependence may stem largely from cognitive factors, not just lower-level aspects of movement execution. This finding highlights the tight links between motor control and mental function. Indeed, the finding that coupling between effectors is largely "in the mind" and not just "in the muscles" shows how cognitive even the most basic voluntary movements are.

Some disclaimers are in order. This chapter will not go into depth for several topics. Differences between the dominant and nondominant hands will not be covered in detail, though the nondominant hand is known to be less efficient in aiming (e.g., in performing series of peg transfers) than is the dominant hand (Annett, Annett, Hudson, & Turner, 1979). More will be said about an exciting new hypothesis concerning differences between the dominant and nondominant hands in the next chapter, Drawing and Writing.

A number of activities deserving of in-depth review will also not be surveyed as copiously as they might be, mostly to keep the length of the chapter manageable. We will not look in detail at the control of throwing (McDonald, van Emmerik, & Newell, 1989), the control of catching (Lacquaniti & Maioli, 1989; McIntyre, Zago, Berthoz, & Lacquaniti, 2001), the control of continuous tracking (Jagacinski & Flach, 2003), adaptation to artificial force fields while interacting with robots (Krakauer, Ghilardi, & Ghez, 1999), or adaptation to Coriolis forces while being immersed in slowly spinning rooms (Lackner & Dizio, 1994). Many of these topics have been covered elsewhere, often in connection with quite technical models of adaptive control (Shadmehr & Wise, 2005).

THE DEVELOPMENT OF REACHING AND GRASPING

By the time a human fetus is around 7.5 weeks of age it has fingers. By around 15 weeks of gestational age it can open and close its hand (Hooker, 1938). By around 24 weeks of age, a prematurely born infant can use its hand in the same way as a full-term baby. It can automatically take hold of an object placed in its palm—a reaction known as the grasp reflex (Twitchell, 1970). The grasp reflex is powerful enough in full-term infants that they can support their own weight (Figure 7.2). This has been taken to suggest that the grasp reflex may have originated with our tree-dwelling forebears. By around 6 months of age, the grasp reflex usually disappears (Touwen, 1971).

FIGURE 7.2 The grasp reflex. Still photograph from a film made by the psychologist John B. Watson in 1919. Reprinted from Boakes (1984). With permission.

Direction

Infants between the ages of 6 and 11 days can reach with rough accuracy for objects placed in different radial positions—0, 30, or 60 degrees to the right or left (Bower, Broughton, & Moore, 1970). From this result, Bower, Broughton, and Moore concluded that newborns not only have reasonably good control of their reaching movements but can also obtain directional information through vision (also see Bower, 1974).

Other studies have shown that directions of infants' reaches become more precise during the first 4 or 5 months (Hofsten, 1980; Lockman & Ashmead, 1983). By the end of this period, infants are so good at controlling the directions of their reaching and grasping movements that they can direct their hands to future positions of objects in motion, effectively "catching" the objects in midflight (Hofsten, 1980).

Distance

Distance control also improves during the first 4 or 5 months, as has been shown by identifying the distances over which infants are willing or not willing to reach. When an interesting object is out of reach, infants should refrain from reaching for it, but when the same object is within reach, infants should try, or be willing to try, to grasp it. By this logic, if distances that elicit reaches are sharply demarcated from distances that do not elicit reaches and if the boundary between the two kinds of distances approximates the length of the infant's arm, one can conclude that the infant perceives distances veridically and has information about the length of his or her arm.

Based on this logic, Bower (1972) reported that infants as young as 7 to 15 days refrain from reaching for out-of-reach objects, though the distances that elicit reaches are not sharply divided from those that do not. During subsequent development, the boundary between reachable and unreachable distances becomes sharper, until by 5 months of age, infants rarely reach for objects just beyond the maximum extent of the outstretched arm (Field, 1977; Gordon & Yonas, 1976).

Another indication of the quality of distance control is the slowing of the hand as the hand approaches an object to be grasped. By around 5 months of age, infants exhibit significant hand slowing just before contacting to-be-grabbed objects (Hofsten, 1979; White, Castle, & Held, 1964). This suggests that 5-month-old infants are sensitive to the distance and direction of the object to be grasped and of the position of the hand with respect to the object. Whether the slowing is preprogrammed or based on visual feedback is still an open question. An experiment that could resolve the question would be to study the speed with which the hand approaches a target in the dark, given that the target was visible when the hand started reaching for it. It has been established that by 9 months—but not by 5 or 7 months—infants have enough prospective control of their reaching behavior to make successful reaches when the room is darkened upon reach initiation (McCarty & Ashmead, 1999). In the McCarty and Ashmead study, infants were able to complete reaches despite being unable to see the object after reach initiation.

Orientation

As mentioned above, babies exhibit accurate control of the directions and distances of their reaches by around 5 months of age. The control of hand orientation appears to crystallize at a later age. Five-month-old babies orient their hands correctly around a vertically or horizontally oriented bar, but they orient their hands correctly only after physically contacting the bar. Nine-month-old babies, by contrast, orient their hands in anticipation of bar contact based on vision alone (Lockman, Ashmead, & Bushnell, 1984).

Why do babies younger than 9 months not orient their hands correctly before contacting objects to be grabbed? One possibility is that they cannot visually discriminate vertical and horizontal lines. Contrary to this hypothesis, however, even 2-month-olds can make this visual discrimination (Essock & Siqueland, 1981). Furthermore, 5-month-old babies can reorient their hands after physically contacting objects they wish to handle. Apparently, then, babies younger than 9 months lack a fully developed map between visually perceived orientations and corresponding hand orientations.

Size

Another control parameter that appears to be mastered only by 9 months or later is related to the size of the object being grasped. When adults reach for objects of varying size, they vary the distance between the thumb and the other fingers (Jeannerod, 1981). Infants 9 months or older do so as well, but infants younger than 9 months do not (Hofsten & Rönnqvist, 1988). It is doubtful that infants younger than 9 months are unable to visually distinguish large and small objects (Hofsten & Rönnqvist, 1988). Furthermore, infants younger than 9 months are physically able to vary their grip size, for they can spread their fingers farther apart once they have felt a large object (Hofsten & Rönnqvist, 1988). The more likely possibility is that infants younger than 9 months have not yet learned to preprogram grip size on the basis of visual information, just as infants younger than 9 months have not yet learned to preprogram hand orientation on the basis of vision.

Functional Tuning of Grasps in Infancy

Beyond recognizing the physical features of objects to be grasped and directing and shaping grasps accordingly, infants develop the ability to tune their grasps according to the functions they wish to perform. Recent research has shown that the cognitive capabilities linked to anticipatory effects in reaching and grasping appear at a relatively young age.

Claxton, Keen, and McCarty (2003) showed that 10-month-old infants reach more quickly for a ball when engaged in an activity that requires less precision (throwing the ball) than when engaged in an activity that requires more precision (fitting the ball into a tube). This outcome is reminiscent of the finding that adults reach more quickly for an object that will be used in a high-precision task than in a low-precision task (Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987).

Another series of studies by the group led by Rachel Keen (formerly known as Rachel Clifton) showed that 19- to 24-month-old infants orient their hands appropriately for grasping a spoon, but younger infants (9- to 12-month-olds) do not do so (McCarty, Clifton, & Collard, 1999; McCarty, Clifton, & Collard, 2001). Twelve-month-olds can, however, show improvements in this regard through training (McCarty & Keen, 2005).

These demonstrations show that infants come to see objects more and more accurately and reach for objects in ways that are more accurate relative to how the objects look. The demonstrations also show that infants alter the way they reach for and grasp objects depending on what they plan to do with the objects. Such anticipatory effects have been mentioned before in connection with adult prehension.

Discovering anticipatory changes in physical behavior is of great interest to cognitive psychologists (of which the author is one) because such changes reflect mental representations. Mental representations—thoughts, ideas, reminiscences, predictions, and so on—are likely to underlie tool use, for how else could one explain the purposeful use of a tool to achieve some goal? Discovering anticipatory changes in grasps among infants and monkeys therefore bears on theories of tool development (Johnson-Frey, 2003).

VISUAL GUIDANCE

Reaching for a seen object usually benefits from visual feedback. If one looks at an object to be picked up but keeps one's eyes closed while reaching for it, one's performance typically suffers. Try this for yourself. Assuming your reach turns out to be better with vision than without vision, you will be primed to wonder how visual feedback is used in the control of reaches and grasps.

In approaching this question, it is useful to recognize that visual feedback can be used more and more effectively over the course of development. At around 5 months of age, babies perform about as well when reaching for objects that are seen only briefly as when reaching for objects that are seen continually (Wishart, Bower, & Dunkeld, 1978). After 5 months, reaching benefits more and more from continuous vision until, by around 11 months, the benefit of vision approximates its best level (Figure 7.3).

Learning how to use visual feedback does not end in the first year. Adults can also learn to adjust their reaching behavior based on exposure to new visual conditions. These

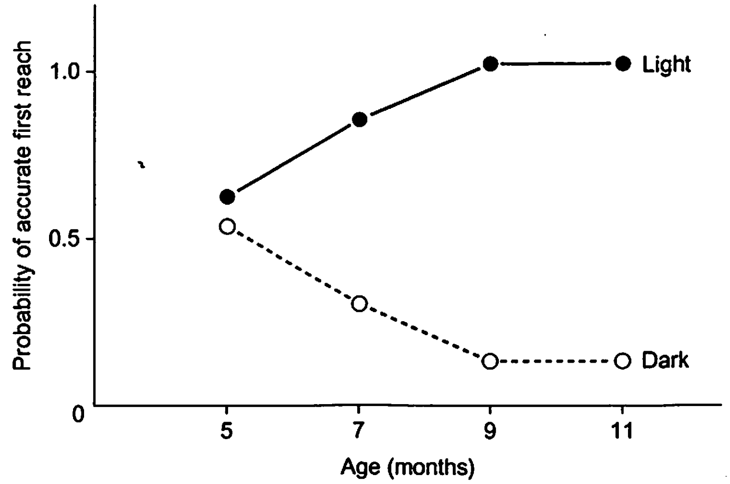

FIGURE 7.3 Accuracy of reaches made in the light (solid points and line) or dark (rings and dashed line) in babies 5–11 months of age. Data from Wishart, J. G., Bower, T. G. R., & Dunkeld, J. (1978). Reaching in the dark. Perception, 7, 507–512. With permission. Adapted from Hay (1984).

conditions can be introduced by having people observe their hand movements through a mirror (which reverses right and left) or by having people observe their hand movements through lenses or prisms that invert, displace, rotate, magnify, or minify (shrink) the image.

One of the first studies of adaptation to visual rearrangement was conducted in the late nineteenth century. The experimenter, George Stratton, wore an inverting lens for 8 days. His purpose was to learn how visual direction is appreciated given that the retinal image of the visual world is normally inverted. Stratton believed that we learn visual directions by associating visual experiences with other forms of sensory feedback, such as proprioceptive input from hand movements. Thus, if the hand is moved to the right, proprioceptive input indicates a rightward movement and allows one to identify the associated visual input as coming from the right rather than the left. Stratton reasoned that if people initially learn visual directions in this way, they should be able to learn new associations between visual and proprioceptive inputs.

Stratton's initial experiences were upsetting:

> If he saw an object off to the right, he would reach for it with his right hand and discover that he should have reached for it with left hand. He could not feed himself very well, could not tie his shoelaces without considerable difficulty, and found himself to be severely disoriented in general. His image of his own body became severely distorted. At times he felt that his head had sunk down between his shoulders, and when he moved his eyes and head the world would slide dizzyingly around [Kaufman, 1984, p. 417].

Gradually he adapted:

> As time went by, Stratton achieved more effective control over his body. He would reach with his left hand when he saw an object on the right. He could accomplish normal tasks like eating and dressing himself. His body image became almost normal, and objects did not appear to move about so much when he changed the positions of eyes and head. He even began to feel as though his left hand was on the right and his right hand was on the left. As long as this new location of his body was vivid, the world appeared to be right side up. Frequently, however, he would experience his own body as upside down in a visually right-side-up world. The visual world became the standard with which he localized his body [Kaufman, 1984, pp. 417–418].

When Stratton removed the inverting lens at the end of the eighth day of the experiment, he frequently made incorrect reaching movements. However, he soon regained his normal perceptual-motor coordination. Because he could adapt to the inverting lens and then readapt to the normal environment, he showed through his research that perceptual-motor coordination is plastic.

Did Stratton adapt to the inverted lenses by finding a new correlation between vision and proprioception, as he supposed, or did he adapt by finding a new correlation between vision and actively generated motor commands or the intentions giving rise to those intentions?

To test the latter hypothesis, Held (1965) allowed observers to see the reflected image of a square in a horizontal mirror. The observers could move their hands beneath the mirror, but they could not see their hands. The observers' task was to mark the perceived corners of the square with a pencil, but because they could not see where the pencil marks were placed in relation to the square, the only way they could tell where the marks were placed was to compare the seen position of the square with the felt position of the hand. The question was how well observers could perform the task depending on the kind of training they received. One group actively moved their hands while watching their movements through a displacing prism. Another group simply looked at their hands through the displacing prism without making movements. A third group viewed their hands through the displacing prism as their hands were moved passively by the experimenter. After the training session, the three groups returned to the task of marking the corners of the square.

The results were clear. Only the active-movement group exhibited significant adaptation to the prism. The stationary group and the passive movement group did not. Thus, the group that could correlate the altered visual input created by the prisms with their own motor commands (or movement intentions) exhibited more adaptation than the groups that not could not achieve this correlation. Because the subjects in the passive-movement group received approximately the same proprioceptive feedback as the active-movement group, the results argue against Stratton's proposal that we learn to coordinate vision and touch by correlating visual and proprioceptive inputs. Rather, we learn to coordinate vision and touch by correlating visual information with motor commands or their underlying intentions.

Vision and Touch

When one learns new correlations between the way things look and the way things feel, does vision change, does touch change, or both? In the early eighteenth century, the British philosopher George Berkeley argued that touch is more trustworthy than vision because touch puts one in direct contact with the external environment. If Berkeley had been asked to predict what would change in a prism adaptation experiment, he would have said that vision changes but touch does not.

Subsequent experiments have indicated that Berkeley would have been mistaken. If anything, touch changes but vision remains the same. In one relevant experiment, subjects looked through prisms that made a straight rod appear curved (Gibson, 1933). When the subjects were asked to describe how the rod looked and felt, they reported that the rod looked curved and also felt curved. Thus, vision dominated over touch in this experiment. Similar results were obtained when subjects looked through a minifying lens at a cube lying on a cloth (Rock & Harris, 1967). The subjects in this study could reach under the cloth and feel the cube without seeing their hands. When they felt the cube, there was an objective mismatch between its felt and seen size. However, the subjects reported that the cube felt small—as small, in fact, as a physically smaller cube that was viewed normally. Thus, for these subjects, as for the subjects in Gibson's (1933) experiments, vision dominated touch.

What accounts for visual dominance? One possibility is that vision captures attention less effectively than touch does (Posner, Nissen, & Klein, 1976). Tapping someone on the shoulder, for example, is sure to get their attention, but raising one's hand—say, in a classroom—is not guaranteed to summon attention. Vision may dominate over touch, then, because touch has a greater alerting capacity.

Regardless of the exact cause of visual dominance, the phenomenon may have practical benefits. Consider the following curious observation (Tastevin, 1937, reported in Kaufman, 1984). A plaster replica of a person's finger was made to move in step with a subject's moving finger. When the subject saw the replica but not her own finger through a small window, she did not know that the finger she saw was someone else's. In a similar demonstration (Rock & Harris, 1967), a subject was told that she would be able to watch her own hand through a window, but unbeknownst to her, she actually saw the experimenter's hand through a mirror. Provided the experimenter's hand moved in synchrony with the subject's, the subject did not know that the hand being seen was someone else's.

These reports suggest a possible strategy for physical rehabilitation and training. Someone regaining control of a limb might be helped by seeing an image of that limb with greater mobility than it actually has. Giving the patient the impression of limb mobility might provide him or her with the incentive to try moving the limb on his or her own. One could also imagine a more draconian approach, where the movement one sees is *less* than the movement generated, in which case the patient might be persuaded to try harder to move.

An approach that builds on such visual changes has been taken with robotic aids to movement. Here, patients with limited mobility, typically after stroke, have been assisted in their movements toward specific targets. The idea is to get patients to move more and more independently by building on their returning movement abilities (Volpe et al., 2008).

The approach has also been pursued in a manner that relies solely on vision. The method entails showing amputees mirror images of their extant limbs (Figure 7.4). A mirror is placed so the image of the amputee's remaining limb appears where the amputated limb would be if it still existed. In some patients, witnessing the image of the remaining limb helps "unlock" the patient's phantom limb (Ramachandran & Rogers-Ramachandran, 1996). For example, one patient whose phantom hand had been in a clenched, painful position for years felt the phantom hand's fingers unfurl after experiencing the mirror treatment, and the pain associated with the phantom hand abated. This method has received quite a bit of popular press. The promise of the approach was extolled in the Science section of the *New York Times* (Angier, 2008).

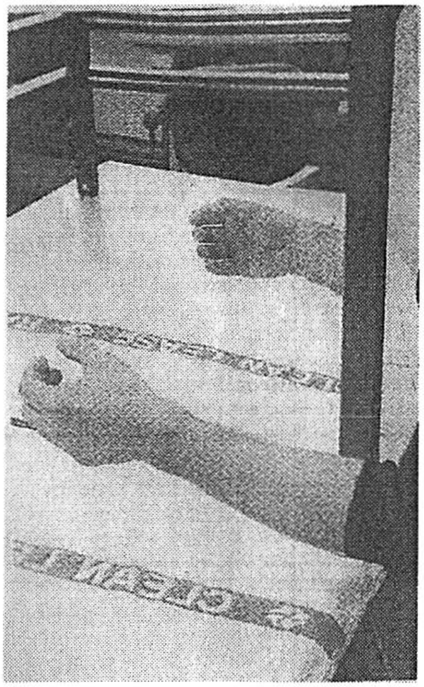

FIGURE 7.4 The one remaining hand of an amputee and the reflection of that hand in a mirror. From Angier, N. (2008). Reflections on the simple mirror. The Global Edition of The New York Times, Thursday, July 24, 2008, p. 10.

Vision for Action

No less intriguing than the effects described above are effects related to changes in perception accompanying reaching and grasping. From a conventional view of perception, one might expect perception to be the same if one were looking at a scene for the sake of recognizing objects or for the sake of acting. On the other hand, the hypothesis that there are two visual systems, one for recognition (the "what" system") and one for action (the "how" system), would allow perception to differ in these two contexts; see Figure 2.13. A number of studies have supported the two visual system hypothesis. The tack taken in these studies has been to ask whether visual illusions that arise in non-action, recognition contexts, disappear in action contexts.

An influential study done along these lines (Aglioti, DeSouza, & Goodale, 1995) relied on the fact that a circle of fixed size tends to look smaller when surrounded by large circles than when surrounded by small circles (Figure 7.5). What would happen, Aglioti, DeSouza, and Goodale asked, if instead of merely looking at the standard circle, participants reached for it? The researchers had participants reach for a poker chip surrounded by large or small disks. The participants wore infra-red emitting diodes on their index finger and thumb so the distance between the index finger and thumb could be recorded with a motion tracking

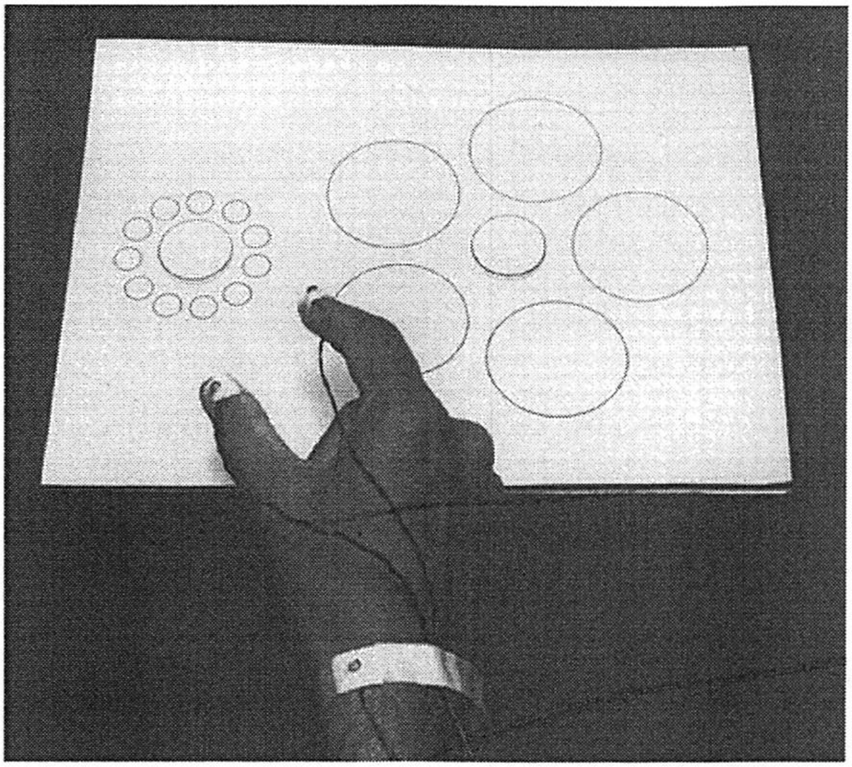

FIGURE 7.5 Reaching for a poker chip of fixed size surrounded either by small or large disks. From http://www.current-biology.com/content/article/fulltext?uid = PIIS0960982295001333&origin = SD. Original source: Aglioti, S., DeSouza, J. F., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. Current Biology, 5, 679–685. With permission.

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 100ms (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.

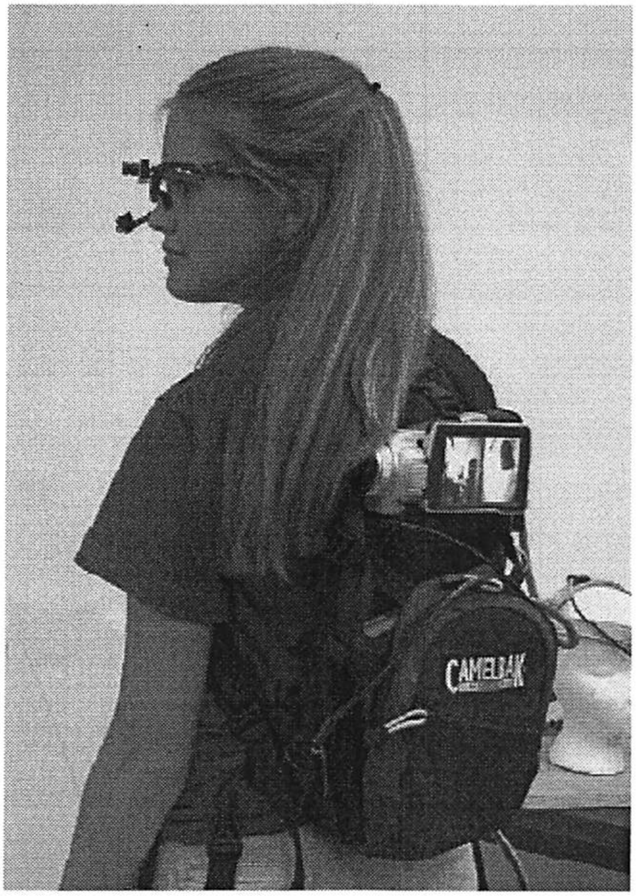

FIGURE 7.6 Portable eye-tracking system. From Hayhoe, M. & Ballard, C. (2005). Reaching in natural behavior. Trends in Cognitive Sciences, 9, 188–194. With permission. From http://www.sciencedirect.com/science?_ob = ArticleURL&_udi = B6VH9-4FM9MR7-1&_user = 209810&_rdoc = 1&_fmt = &_orig = search&_sort = d&view = c&_acct = C000014439&_version = 1&_urlVersion = 0&_userid = 209810&md5 = b9b045735ab772ace5b0edd6947afa28.

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).

AIMING

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.

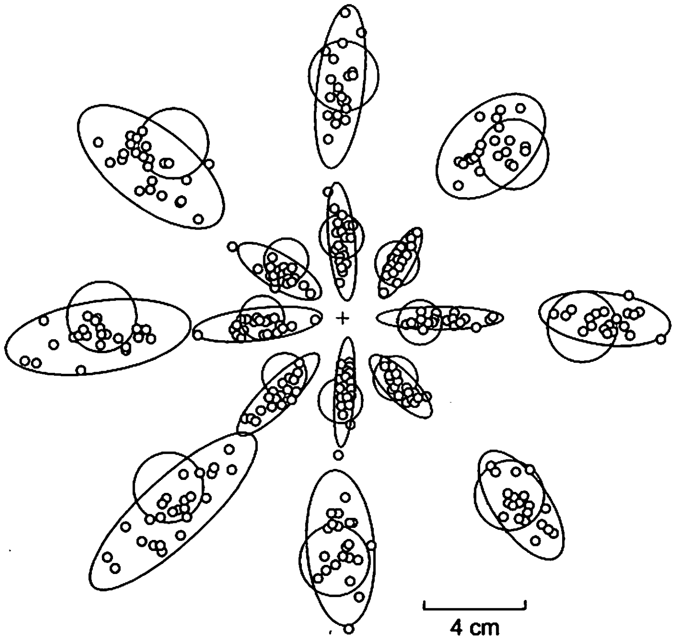

FIGURE 7.7 Elliptical end-point distributions obtained when participants moved from a home position (+) to each of a number of targets (circles) but did not have to correct the movements they made. From Gordon, J., & Ghez, C. (1994). Accuracy of planar reaching movements: I. Independence of direction and extent variability. Experimental Brain Research, 99, 97–111. With permission. From http://www.ncbi.nlm.nih.gov/pubmed/7925800.

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

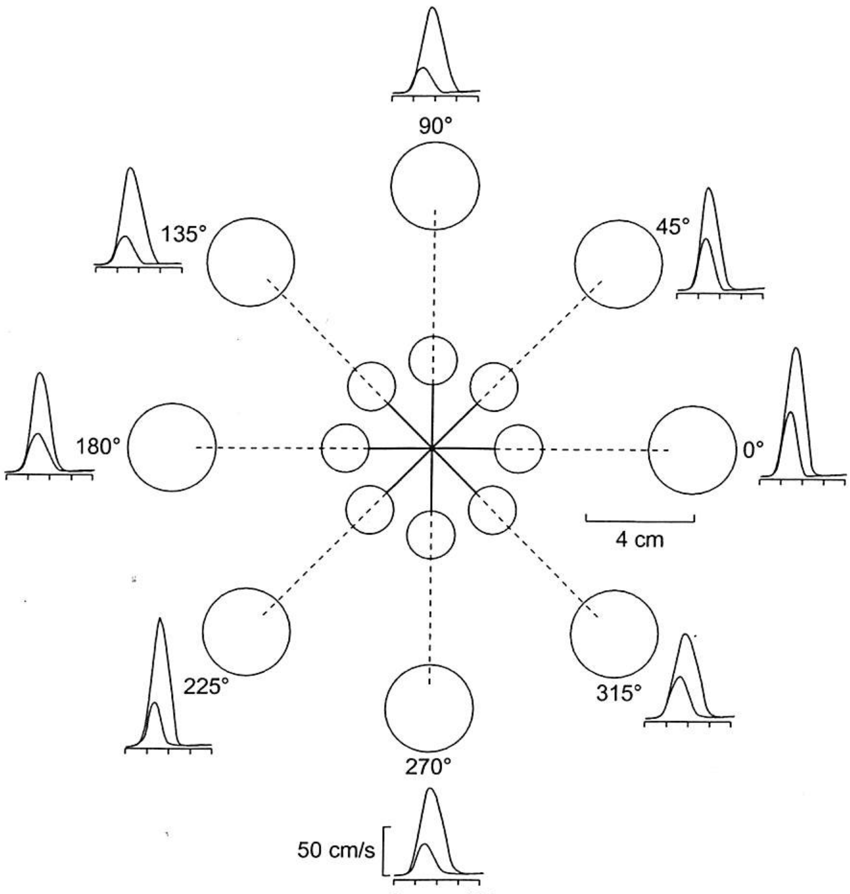

FIGURE 7.8 Speed profiles to near and far targets. From Gordon, J., & Ghez, C. (1994). Accuracy of planar reaching movements: I. Independence of direction and extent variability. Experimental Brain Research, 99, 97–111. With permission. Experimental Brain Research. From http://www.ncbi.nlm.nih.gov/pubmed/7925800.

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

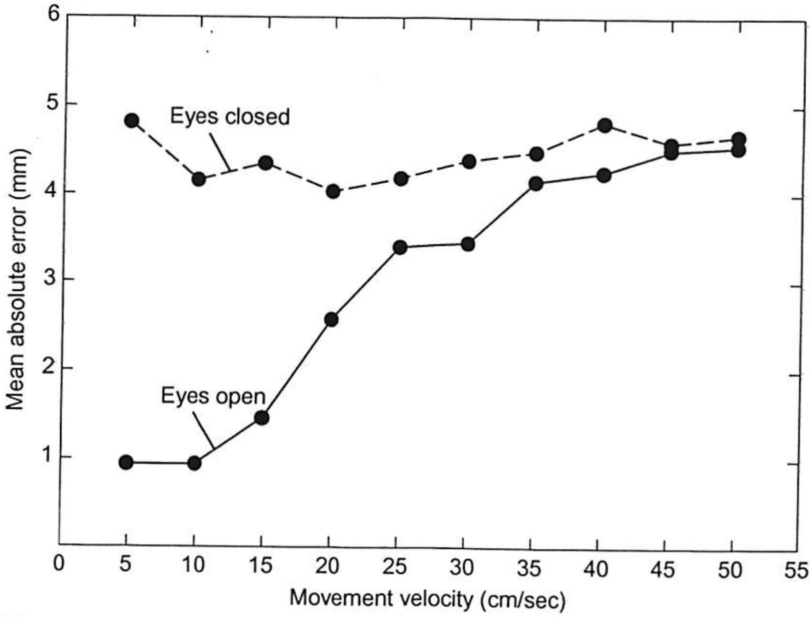

FIGURE 7.9 Mean absolute error of hand movements made by subjects with their eyes open or closed. Data from Woodworth (1899). Adapted from Woodworth, R. S. (1899). The accuracy of voluntary movement. Psychological Review, 3, 1–119. With permission.

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:

$$\mathrm{MT} = a + b\log_2(2\mathrm{A}/\mathrm{W}), \tag{7.1}$$

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 $\log_2(2\mathrm{A}/\mathrm{W})$ 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 been 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,

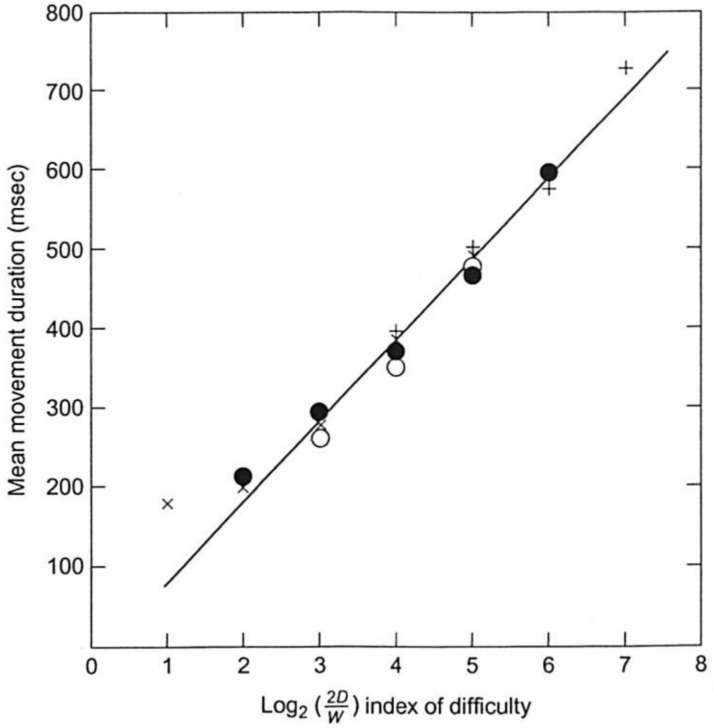

FIGURE 7.10 Movement time as a function of index of difficulty in Fitts' (1954) study. From Meyer, Smith, Kornblum, Abrams, and Wright (1990).

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 submoves. 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 submoves 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 submoves 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

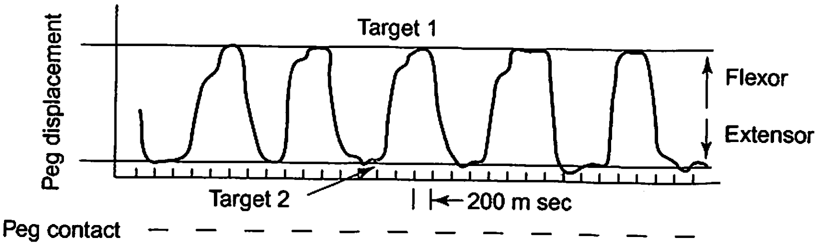

FIGURE 7.11 Peg displacement as a function of time in an aiming task performed under a microscope. The "plateaus" prior to the targets reflect momentary slowing of the hand. Data from Langolf, G. D., Chaffin, D. B., & Foulke, J. A. (1976). An investigation of Fitts' Law using a wide range of movement amplitudes. Journal of Motor Behavior, 8, 113–128. With permission. Adapted from Smyth, M. M. (1984). Memory for movements. In M. M. Smyth & A. M. Wing (Eds.), The psychology of human movement (pp. 83–117). London: Academic Press. With permission.

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 200ms, a time that was unlikely to permit much current control. The targets were between 10 and 30cm 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:

$$W_e = k(D/T), \tag{7.2}$$

which can be rearranged as

$$T = k(D/W_e). \tag{7.3}$$

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,

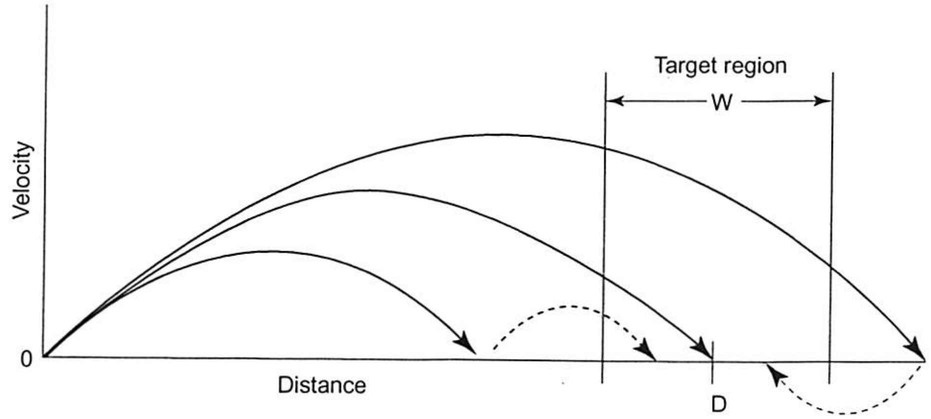

FIGURE 7.12 Representative sequences of submovements toward the target region assumed in the optimized initial impulse model of Meyer, Abrams, Kornblum, Wright, and Smith (1988). From Meyer et al. (1988). Optimality in human motor performance: Ideal control of rapid aimed movements. Psychological Review, 95, 340–370. Copyright © 1988 by the American Psychological Association. Adapted by permission.

$$S_i = k(D_i / T_i), \tag{7.4}$$

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.

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.

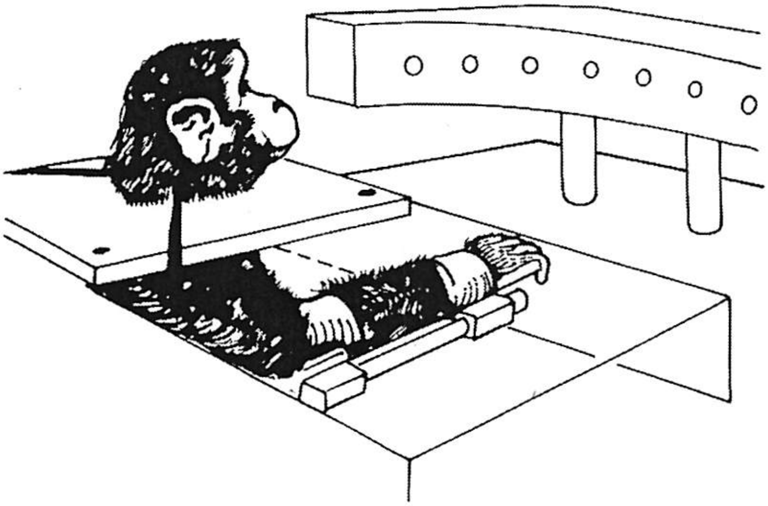

FIGURE 7.13 Experimental arrangement used by Polit and Bizzi. From Polit, A. & Bizzi, E. (1979). Characteristics of motor programs underlying arm movements in monkeys. Journal of Neurophysiology, 42, 183–194. Reprinted by permission of the American Physiological Society.

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.

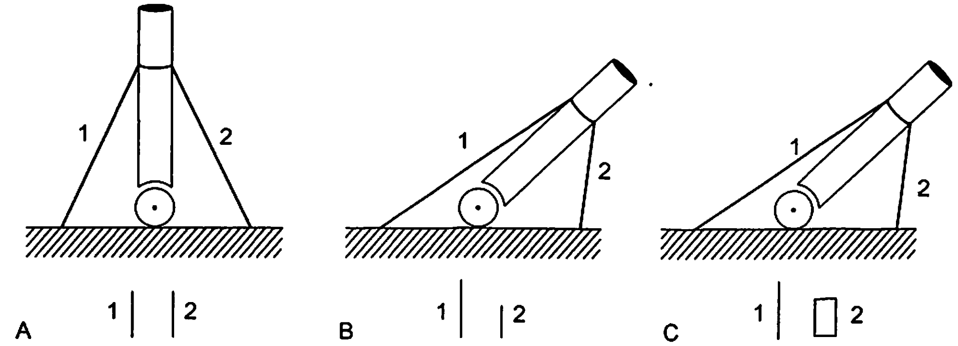

FIGURE 7.14 Illustration of the mass-spring model with a hinged cylinder and two rubber bands. (A) Resting lengths and stiffnesses of the rubber bands are equal. (B) Resting length of rubber band 1 is less than the resting length of rubber band 2 but the stiffnesses are equal. (C) Resting lengths of the rubber bands are equal but the stiffness of rubber band 2 is greater than the stiffness of rubber band 1 (indicated by the thicknesses of the bands in the rest position).

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 a 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 on 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 (Buchanen, 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?

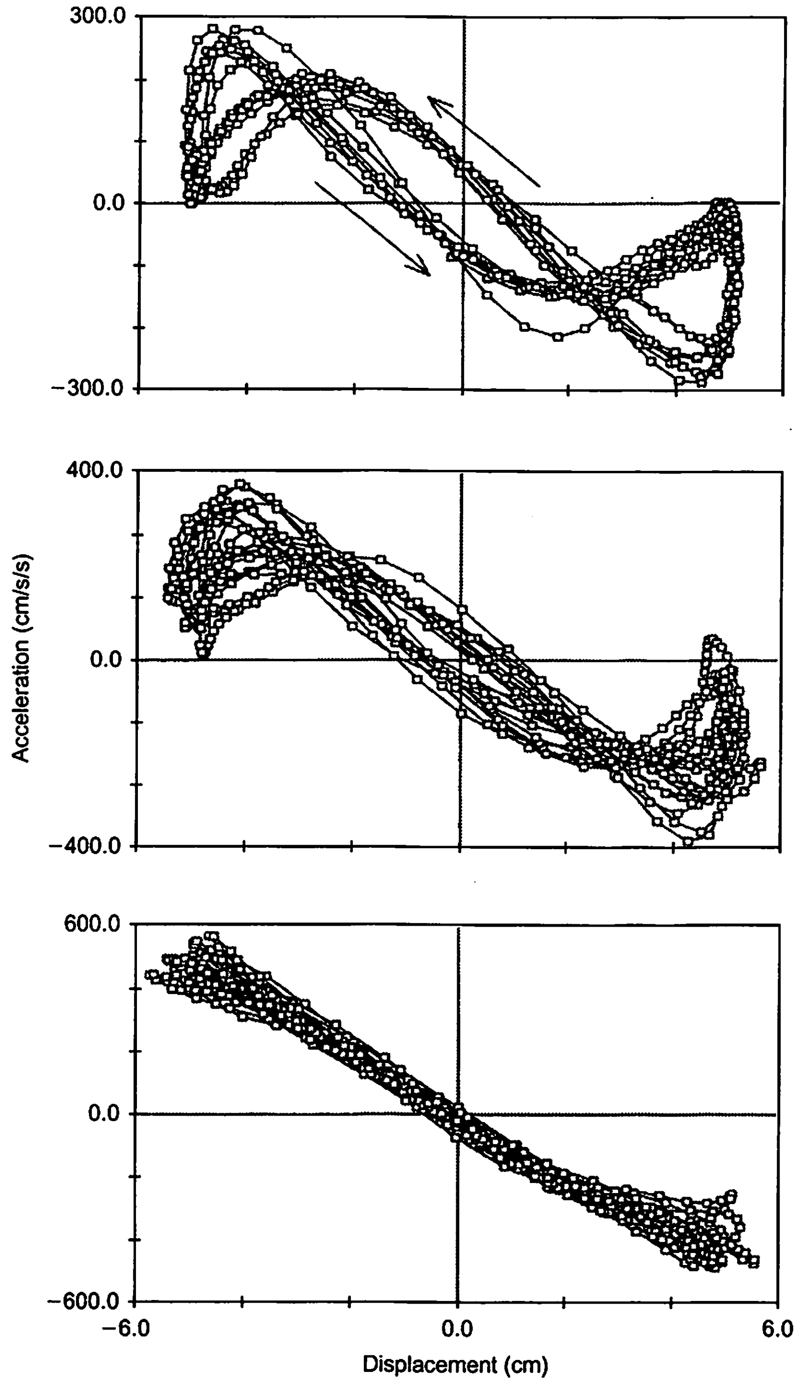

FIGURE 7.15 Acceleration as a function of displacement for back-and-forth aiming movements with a low (top panel), medium (middle panel), and high (bottom panel) index of difficulty. From Guiard, Y. (1993). On Fitts's and Hooke's laws: Simple harmonic movement in upper-limb cyclical aiming. Acta Psychological, 82, 139–159(1993). With permission.

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

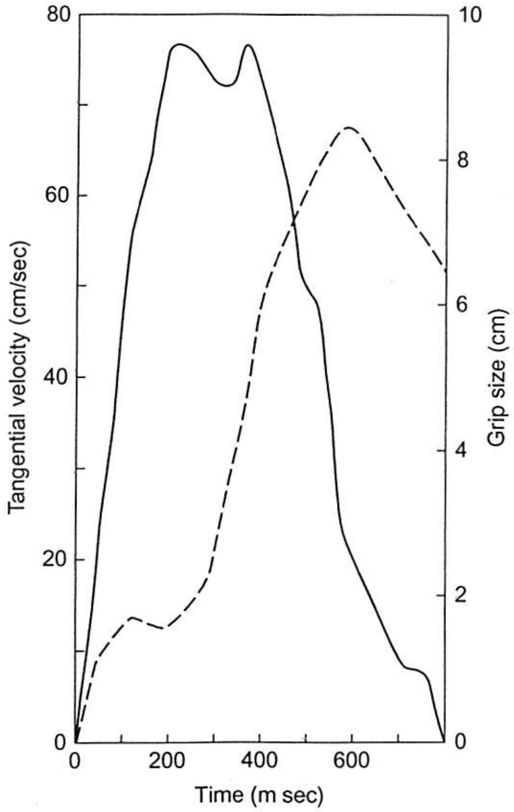

FIGURE 7.16 Tangential velocity of the hand (solid line) and grip size (dashed line) as a function of time. From Jeannerod, M. (1984). The timing of natural prehension movement. Journal of Motor Behavior, 26, 3, 235–254. With permission.

performance (Meulenbroek, Rosenbaum, Jansen, Vaughan, & Vogt, 2001; Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001; Smeets & Brenner, 2002).

Hand-Space versus Joint-Space Planning

As the hand moves to pick up an object, the angles of the shoulder and elbow joints usually change. Muscle torques are applied at these joints to cause the arm to move. The muscle torques are selected on the basis of a chosen path for the hand to follow through extrapersonal space.

In robotics, determining how the endpoint of a system of hinged levers is displaced when certain torques are applied to the levers is called the *forward dynamics* problem. The *inverse dynamics* problem is the problem of determining the torques that should be applied to the levers given that the endpoint of the levers is supposed to traverse some path. The inverse dynamics problem is the one that is usually required in motor control. One reason why it is interesting to ask how the joint angles of the arm change during aiming movements is to learn how the motor system solves the inverse dynamics problem.

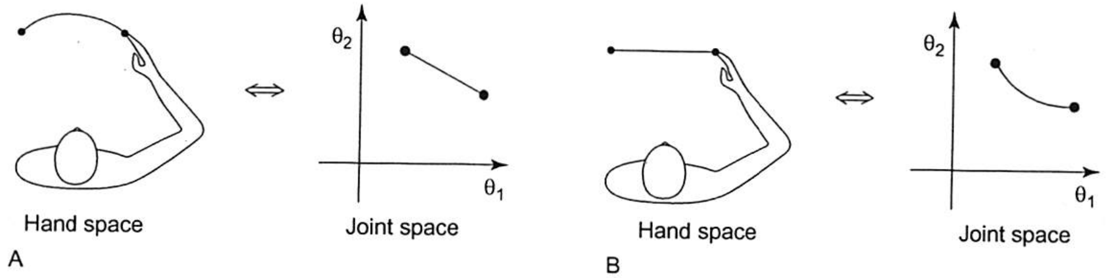

FIGURE 7.17 Trajectories expected if hand movements are planned in joint space (A) or in hand space (B). From Hollerbach, J. M. & Atkeson, C. G. (1986). Characterization of joint-interpolated arm movements. In H. Heuer & C. Fromm (Ed.), Generation and modulation of action patterns (pp. 41–54). Berlin: Springer-Verlag. With permission.

Suppose the inverse dynamics problem is so hard for the motor system that it effectively sidesteps it. Suppose that instead of selecting a direct path for the hand to follow on its way to a target, the motor system actually selects a set of muscle torques and then, perhaps after some trial and error in the planning process, allows the hand to get to the target through a path that may be straight or may just as well be curved. If this strategy were used, one would expect considerable simplicity in the pattern of joint angles that occur during aimed hand movements but considerable complexity in the patterns of associated hand paths. By contrast, if the motor system had no difficulty with the inverse dynamics problem, and so could select direct hand paths and then find the muscle torques that would produce them, one would expect simple hand paths but complex joint angle patterns. The question, then, is whether the motor system plans movements with respect to *joint* space, which uses the intrinsic coordinates of the body, or *hand* space, which uses the extrinsic coordinates of the external surroundings.

Figure 7.17 illustrates possible consequences of joint-space or hand-space planning. If planning is based on the extrinsic coordinates of hand space, the hand would be expected to move in a straight line. Conversely, if planning used the intrinsic coordinates of joint space, then joint angles, or the function relating joint angles to time, would be expected to follow a straight line. Note that only one of these outcomes is possible. If the hand moves in a straight line, the joint angles cannot do so, and if the joint angles move in a straight line, the hand cannot do so.

Data bearing on this distinction were collected by Morasso (1981). He recorded hand trajectories on a two-dimensional surface when people pointed to targets. He found that subjects' hands tended to move in straight lines, but their joints went through complex angular changes. Even when subjects were told to draw curved lines, detailed analyses of their hand trajectories suggested that they actually generated series of straight-line segments (Abend, Bizzi, & Morasso, 1982). These results suggest that the nervous system can in fact plan hand movements in extrinsic coordinates. Once it has done so, it determines the muscles torques that should act on the joints.

Not all investigators are convinced that planning is achieved in hand space, however. Hollerbach, Moore, and Atkeson (1986) proposed a way of directly controlling the joints that can yield straight-line hand trajectories. Their method simply entailed varying the onset times for the motions of the joints, allowing all the joints to stop together at the end of the movement. This method can yield approximately straight hand paths given appropriate onset delays

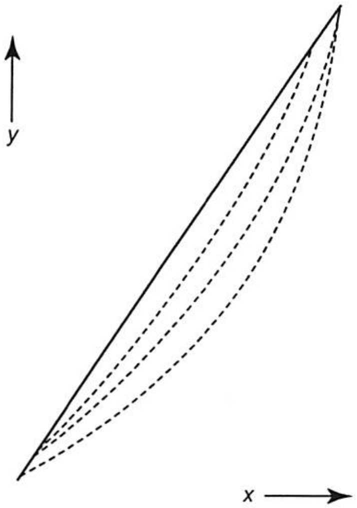

FIGURE 7.18 Motion of the hand in the x and y dimensions when the onsets of elbow and shoulder motion are staggered to varying degrees. From Hollerbach, J. M., Moore, S. P., & Atkeson, C. G. (1987). Workspace effect in arm movement kinematics derived by joint interpolation. In G. N. Gantchev, B. Dimitrov, & P. Gatev (Eds.), Motor Control (pp. 197–208). Plenum. With permission.

(see Figure 7.18). Moreover, consistent with the staggered-time proposal of Hollerbach, Moore, and Atkeson, the motions of the joints of the arm actually appear to be timed so all the joints do in fact reach their final positions simultaneously (Kaminski & Gentile, 1986).

Another source of evidence that there may be joint-based planning is the observation that during the performance of simple pointing movements, invariant relations can be observed among the joints. Soechting and Lacquaniti (1981) studied how people perform the simple act of pointing to a target. Initially, the subjects stood with their arms hanging freely at their sides. When they felt ready to do so, they pointed to the target, located on a vertical surface directly in front of them. Soechting and Lacquaniti found that the peak angular velocities of the elbow and shoulder joints were reached at the same time. In addition, the ratio of the peak velocities of the two joints equaled the ratio of the radial distances that the joints covered. Such regular relations would not be expected if the planning system did not take the joints into account.

A similar result was reported by Kots and Syrovegnin (1966), who recorded the angular positions of the wrist and elbow during the two tasks shown in Figure 2.4. In one task, which can be called the *congruent articulation* task, subjects attempted to flex the wrist while flexing the elbow or they attempted to extend the wrist while extending the elbow. In the other task, which can be called the *incongruent articulation* task, subjects attempted to flex the wrist while extending the elbow or flex the elbow while extending the wrist. Kots and Syrovegnin (1966) found that in the congruent articulation task, the beginnings and ends of the joint motions occurred nearly simultaneously. However, in the incongruent articulation task, the motions of the joints were not well synchronized. Apparently, the elbow and wrist joints were controlled via some sort of coordinative structure (Turvey, 1977) or synergy (Latash, 2008b). Such a structure can help reduce the number of degrees of freedom that must be individually controlled (Bernstein, 1967). One would not expect such simplifying structures if arm motions could simply be controlled by directing the hand to move in straight lines in external space.

Moving Two Hands at Once

Do coordinative structures also apply to the coordination of the joints of one arm? Consider the child's game of rubbing the stomach and patting the head. Because this ostensibly simple task is actually quite difficult—it is hard to keep the shape of one hand's movement from infiltrating the other's—one may suppose that there are coordinative structures for the two arms as well.

A number of investigators have sought to provide detailed descriptions of the interactions between the two arms. As noted in Chapter 2, the German physiologist Erich von Holst (see von Holst, 1973) recorded the activities of the two arms of human subjects as the subjects oscillated their arms at different relative frequencies: 1:1, 1:2, 2:3, and so forth. Only at relative frequencies of 1:1 and 1:2 could the two arms move in a stable fashion over repeated oscillations.

Interactions between the two arms also arise when people point to two targets at once. Kelso and colleagues (Kelso, Putnam, & Goodman, 1983; Kelso, Southard, & Goodman, 1979) took advantage of the fact that the time to move the hand to a target depends on the target's index of difficulty, or ID, as discussed earlier in connection with Fitts' law. Kelso and co-workers asked what would happen if each hand had to move to a target with a different ID. If each hand could be controlled independently, then each hand's movement time should have only depended on the ID of the target to which it moved. In fact, the movement times of the two hands tended to be approximately equal, even when the IDs of the two targets differed. Specifically, the hand that had an easier targeting task (a lower ID) slowed down so its movement time matched the other hand's. Because subjects were not instructed to synchronize the movements of their two hands, their tendency to do so derived from the operation of some mechanism governing two-hand movements.

What is the nature of this mechanism? One possibility is that each arm is controlled with one or more oscillators, and the oscillators for the two arms are functionally coupled (Haken & Kelso, 1985). This hypothesis is attractive because coupled oscillators are likely to underlie locomotion (see Chapter 5) and the arms were used for walking earlier in evolution. Evidence has been obtained for oscillator control of arm movements in studies where subjects first let one arm dangle freely, then press the arm against a rigid surface, and then dangle the arm freely again (Craske & Craske, 1986). When the arm hangs freely before being pressed against the wall, it displays some oscillation, as would be expected from the fact that the arm, when suspended from the shoulder, can be viewed as a pendulum (Fenn, 1938). More importantly, when the arm dangles freely after being pressed against the wall, it oscillates in the plane of the applied pressure. Craske and Craske (1986) suggested that oscillators responsible for the initial direction of motion become fatigued or adapt during strenuous arm-pressing. Later, when those oscillators are unable to contribute as much as they normally do, the observed direction of oscillation changes. Try this exercise yourself if you wish.

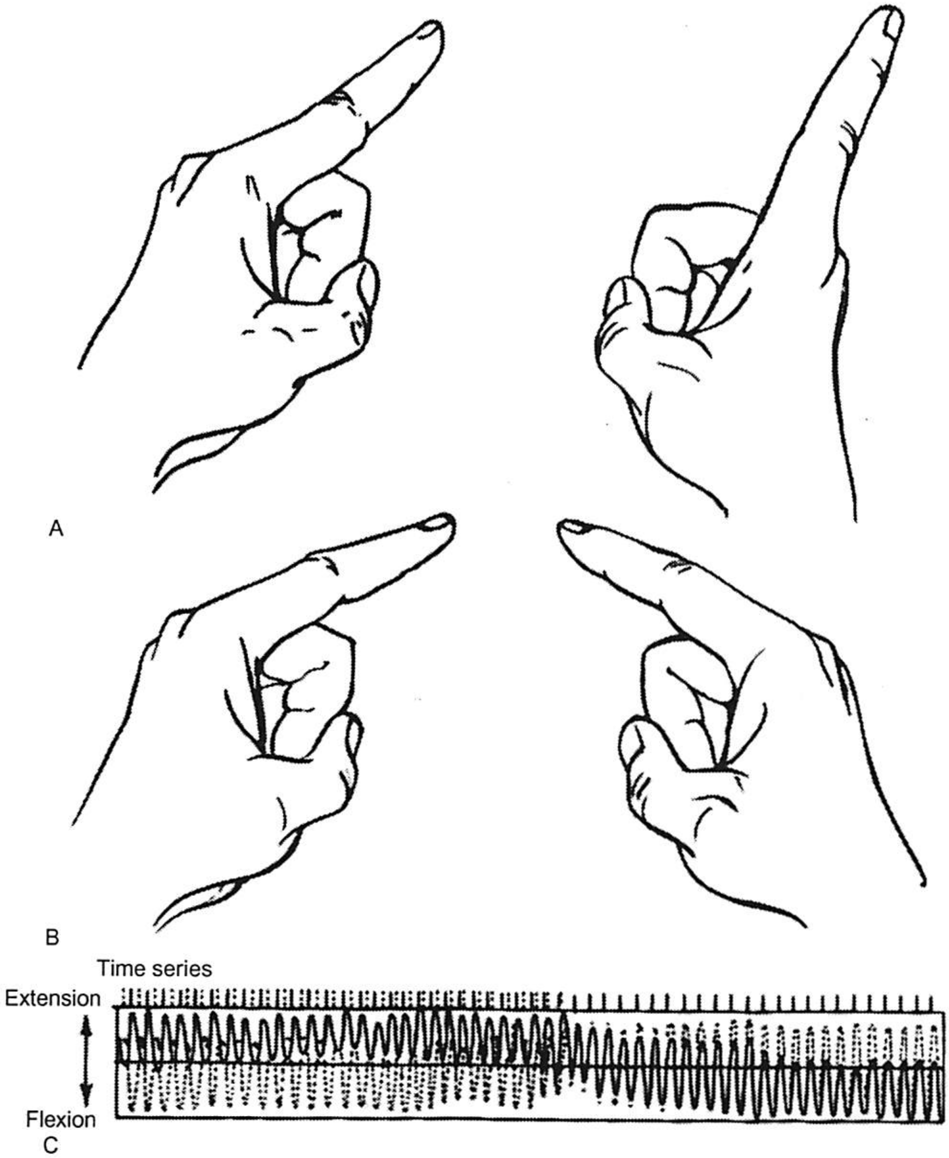

FIGURE 7.19 Coupling of the two index fingers. (A) At low frequency, the two fingers can stay in anti-phase (one finger extending while the other flexes). (B) At high frequency, only an in-phase relation can be maintained (both fingers flex or extend). (C) Time series showing the transition from anti-phase to in-phase relation as oscillation frequency increases. Positions of right finger appear as a solid line. Positions of left finger appear as a dotted line. From Haken, H., Kelso, J. A. S., & Bunz, H. (1985). A theoretical model of phase transitions in human hand movements. Biological Cybernetics, 51, 347–356. With permission.

Another observation that accords with the oscillator hypothesis is another you can make yourself. Position your two index fingers as in Figure 7.19 so your left index finger flexes and you right index finger extends. Now allow the fingers to reverse position, so the right index finger flexes and the left index finger extends. Alternate between these two positions, slowly at first, but then at higher and higher rates. Keep going faster and faster until your fingers move as quickly as possible. What you may notice is that your fingers switch from an anti-phase pattern, where one finger flexes while the other finger extends, to an in-phase pattern, where both fingers flex together or extend together. The switch only occurs from anti-phase to in-phase patterns. If you start at a slow rate with the fingers in-phase, speeding up does not cause a switch to anti-phase coupling. This phenomenon has been investigated in detail by Haken, Kelso, and Bunz (1985), who modeled the switch in terms of nonlinear, coupled oscillators.

Regardless of whether coupling between the hands is due to nonlinear coupled oscillators or some other mechanism, a question that has intrigued motor control researchers concerns the locus of the interactions. Is it in the neuro-muscular periphery—for example, in the spinal cord—or is it in higher centers? These alternatives are not mutually exclusive.

Several sources of evidence indicate that the locus of bimanual coupling is in higher rather than lower levels of motor control. One source of evidence concerns split-brain patients. Research with such patients has shown that they can achieve greater spatial independence between the hands than normal individuals can (Franz, Eliassen, Ivry, & Gazzaniga, 1996). This outcome would not be expected if bimanual coupling resided in the spinal cord because in split-brain patients it is the corpus callosum, the bridge between the two cortical hemispheres, that is severed surgically (to relieve the spread of severe epileptic seizures).

Another source of evidence for a higher rather than a lower level of control as the source of bimanual coupling comes from Franz, Zelaznik, Swinnen, and Walter (2001), who asked participants to move their two hands in synchrony in the frontal plane so the two hands behaved in different ways (Figure 7.20). In one condition, the two hands reached their *zeniths* at the same time (top-top). In another condition, the two hands reached their *nadirs* at the same time (bottom-bottom). In another pair of conditions one hand reached its zenith while the other hand reached its nadir (top-bottom or bottom-top).

One of these four conditions was dramatically harder than the others. In the bottom-top condition, when the arcs drawn by the two hands came together rather than going apart, participants basically "fell apart." Their movements became chaotic. Because there was no obvious biomechanical reason for this breakdown, and because the participants commented

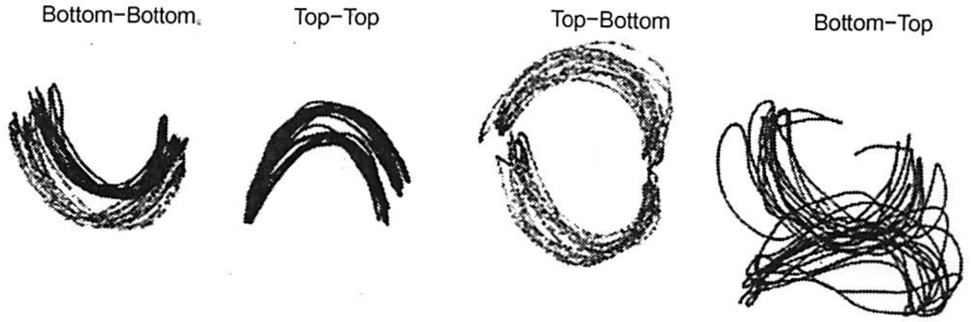

FIGURE 7.20 Motions of the two hands in the four conditions studied by Franz, Zelaznik, Swinnen, and Walter (2001). From Franz, E. A., Zelaznik, H. N., Swinnen, S., & Walter, C. (2001). Spatial conceptual influences on the coordination of bimanual actions: When a dual task becomes a single task. Journal of Motor Behavior, 33, 103–112. With permission.

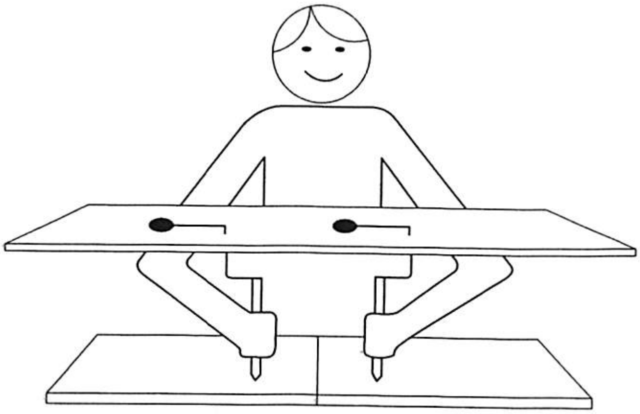

FIGURE 7.21 The crank-gear-flag setup used by Mechsner, Kerzel, Knoblich, and Prinz (2001) and two target configurations. From Mechsner, F., Kerzel, D., Knoblich, G. & Prinz, W. (2001). Perceptual basis of bimanual coordination. Nature, 414, 69–73. With permission.

on how hard it was to conceptualize the movements in this particular condition, Franz, Zelaznik, Swinnen, and Walter ascribed the participants' difficulty in the bottom-top condition to a conceptual failure rather than to a failure of movement execution per se.

If conceptual failures make some bimanual actions difficult, conceptual advantages might make other bimanual actions easy. Support for this possibility came from Mechsner, Kerzel, Knoblich, and Prinz (2001). In one of their experiments, they had participants turn cranks beneath a table (Figure 7.21). Rotation of the cranks caused two flags to turn above the table surface, and the flags were observed by the participants as they turned the cranks. The especially clever feature of the setup was that the cranks were linked to the flags through gears. This made it possible for the required ratios of the two hands' motions to be whatever the experimenters wanted for a given flag phase lag. For example, to have the two flags come together in the middle of the workspace at the same time—what can be called a zero-degree phase lag—the crank handles could be turned with the same phase lag or some other phase lag depending on the gears installed at the time. Through this methodology, Mechsner et al. showed that it was not the physical turning of the cranks that predicted the ease or difficulty of performance but rather the simplicity of the perceptual display that participants had before them. For example, even if it took a frequency ratio of 4:3 to make the two flags reach the center of the workspace at the same time, participants had no trouble generating that frequency ratio. Normally, however, they found it difficult to do so.

Other studies have similarly shown that it is the difficulty of perception or conception that accounts for bimanual coupling in humans. Diedrichsen, Hazeltine, Kennerley, and Ivry (2000) and Kunde and Weigelt (2005) showed that the cognitive representations of goals to be achieved with the two hands accounted more fully for difficulties of bimanual coordination than did the sheer physical demands of coordination. Similarly, Rosenbaum, Dawson, and Challis (2006) showed that when participants made two-hand movements by haptically tracking two moving objects—letting each hand stay in contact with a moving object through gentle touch—the participants could move their two hands essentially independently with no training. Haptic tracking was chosen as an experimental preparation by this group of investigators because it was thought that haptic tracking might bypass the intentional system responsible for macroscopic movement planning (establishing the general shape and timing of the movements to be performed). Finding that the two hands could move independently via haptic tracking, along with the other lines of work reviewed here, suggest that cognitive factors play a major role in interlimb coordination (see also Lee, Blandin, & Proteau, 1996; Oliveira & Ivry, 2008).

SUMMARY

1. Hand movements occur *in utero*. Later, by 5 months of age postpartum, infants can reliably control the direction and distance of reaches and grasps. By around 9 months, they can reliably control the orientation and size of their reaches and grasps. By around 10 months of age, they can adjust their movement speed depending on task demands. Later still, they can grasp objects differently depending on what they intend to do with the objects.
2. The use of visual feedback is susceptible to experience. As shown in the late nineteenth century, people can adapt to inverting lenses. Adaptation to such visual distortion is achieved by correlating changes of visual input with actively generated movements.
3. Vision dominates touch. Relevant illusions may have practical benefits in physical therapy.
4. Vision for action may use a different neural subsystem than vision for recognition of objects.
5. The eye and hand are tightly coupled in visually guided manual aiming tasks. Studies of eye-hand coordination have shed light on language processing and other functions.
6. When aiming for targets, amplitude errors tend to be larger than direction errors. However, speed profiles tend to scale with the distance to be covered.
7. Manual aiming for a target is often achieved in two phases, an initial ballistic phase and a secondary homing-in phase. The time for vision to be used in aiming is between 100 ms and 200 ms.
8. One domain where feedback processing has been studied in detail is manual aiming. In the so-called Fitts' task, the subject moves the hand to a spatial target, usually as quickly as possible. Fitts (1954) introduced a formula for the time needed to reach a target depending on the distance of the target from the starting position and the target's diameter: The time to reach a target increases with the distance of the target from the start position and decreases with the target's width. Because Fitts' formula does an excellent job of accounting for movement time data from a wide range of tasks, it has been called Fitts' law.
9. Several explanations have been offered for Fitts' law. The iterative corrections model says that the law mainly reflects corrections for movement errors. The impulse variability model says that the law mainly reflects the initial impulse that drives the limb toward the target. The optimized initial impulse model, which is the most successful model to date, says that both factors are important.
10. According to the equilibrium point hypothesis, a way to move a limb from one position to another is to take advantage of the spring-like properties of muscle. There are two

ways to exploit these spring-like properties—change the resting lengths of the muscle or change the stiffness of one muscle relative to the other. Several studies suggest that one or the other of these methods may be used. Treating muscles as springs may be economical from a computational standpoint. However, challenges have been raised to the equilibrium point hypothesis.

11. Another question is whether positioning movements are discrete or continuous. Data have been marshaled on both sides.
12. During reaching and grasping, two distinct phases of movement can be identified—the transport phase, during which the hand is brought toward the object, and the grasp phase, during which the fingers enclose the object. The transport and grasp phases may be controlled by different brain areas, and their underlying control mechanisms appear to develop at different rates. Some dependencies exist between the two phases.
13. Although it is convenient when studying reaching and grasping to view the hand as a single moving point, the hand is only one part of a complex set of joints. The hand often follows a straight path when people point to objects, an outcome that has been taken to suggest that movements are planned in the extrinsic coordinates of hand (or extra-personal) space rather than in the intrinsic coordinates of joint (or intra-personal) space. The fact that people exhibit straight-line hand trajectories suggests that the motor system does not compromise hand trajectories when it solves the inverse dynamics problem—the problem of determining the muscle torques that bring an end effector (such as the hand) through a desired trajectory. However, regularities in the relations of joint positions during aiming movements suggest that there may be some joint-based planning.
14. Simultaneous flexion of the wrist and elbow is easier than flexion of the wrist and extension of the elbow, or extension of the wrist and flexion of the elbow. The greater ease with which people can simultaneously flex (or extend) the wrist and elbow suggests that there are coordinative structures for the two joints. Such coordinative structures can reduce the number of degrees of freedom to be independently managed by the manual control system.
15. Coordinative structures also characterize interactions between the two arms and hands. For example, there is a tendency for the two hands to begin and end aiming movements simultaneously. Similarly, when the left and right index fingers flex and extend simultaneously, as the oscillation frequency increases, there is a tendency for the fingers only to flex together and only to extend together. Coupling between the hands appears to be centrally based rather than peripherally based.

Further Reading

Aiming movements can be perturbed by extraneous visual stimuli. See Tipper et al. (1992, 1997), Welsh and Elliott (2004), Welsh and Pratt (2008), and Finkbeiner, Song, and Nakayama (2008).

The latter study pertained to psycholinguistic influences on reaching. For other studies on this topic, see Glover, Rosenbaum, Graham, and Dixon (2004), Spivey (2007), and van der Wel et al. (2009).

Shapes of hand paths for manual positioning tasks carry over from one task to the next. See Jax and Rosenbaum (2007) and van der Wel, Fleckenstein, Jax, and Rosenbaum (2007) for data concerning such hand-path priming, as these authors called it.

Prism adaptation research has progressed, thanks in part to the work of Redding and Wallace (1997, 2008).

Coupling of grasping and fore-aft motion of the forearm has been demonstrated by Flanagan and colleagues (Flanagan, Tresilian, & Wing, 1993).

Complementing studies of unimanual grasps on objects to be moved are studies of bimanual grasps on objects to be moved (Hughes & Franz, 2007).

Researchers have studied reaching and grasping in virtual reality (Zahariev & MacKenzie, 2007) and in surgery, including surgical contexts where visual feedback magnifies the workspace or reveals tissue that is not directly visible, as in endooscopic procedures (Zheng, Verjee, Lomax, & MacKenzie, 2005). A leading investigator in this area is Christine MacKenzie of Simon Fraser University (http://www.sfu.ca/hmsl/mackenzie/).

The analysis of aiming in two spatial dimensions (aiming within a plane) has been generalized to aiming in three dimensions (aiming in open space). See MacKenzie, Marteniuk, and Dugas (1987) and Hansen, Elliott, and Khan (2008).

Sabes and Jordan (1997) suggested that people reach around obstacles in ways that take into account resistance to unexpected perturbations.

Work has been done on socially mediated reaching and grasping. See Mason and MacKenzie (2005) for a study of grip forces in passing objects from one person to another. Mottet, Guiard, Ferrand, and Bootsma (2001) studied two-person performance of the Fitts aiming task.

Shadmehr and Wise (2005) provided a mathematically in-depth treatment of reaching, grasping, and related topics.

An integrated treatment of hand function can be found in Jones and Lederman (2006).

A monograph on cognition and tool use was authored by Baber (2003).

Using a handheld tool benefits from wielding the tool. Wielding—holding an object and shaking or rotating it—provides useful information about the object's physical properties. See Carello and Turvey (2004).

This chapter covered the development of reaching in infancy. Reaching has also been studied in the elderly. See Pratt, Chasteen, and Abrams (1994) and Liao, Jagacinski, and Greenberg (1997).

For a superb review of research on aiming, see Elliott, Helsen, and Chua (2001).