2

Object Representations Used in Action and Perception

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The remarkable skill of the human hand in object manipulation tasks is not the result of rapid sensorimotor processes or powerful effector mechanisms. Rather, the secret lies in the way that the nervous system organizes and controls manipulation tasks. Skilled and dexterous object manipulation requires the ability to tailor motor commands, predictively, to the goals of the task and the physical properties of manipulated objects (Johansson and Flanagan 2009; see also Frey, this volume). Thus, the ability to estimate these properties, based on sensory cues and memory, is essential for dexterous performance. Skilled manipulation also requires the ability to predict the sensory outcomes of motor commands. By comparing predicted and actual sensory feedback, the sensorimotor system can monitor task progress and take appropriate goal-directed corrective actions if a mismatch occurs. In addition, the sensorimotor system can update information about the physical properties of objects, as well as the mechanical interaction between objects and the body, so as to reduce future mismatches. The first part of this chapter focuses on predictive control mechanisms in object manipulation tasks and the way the sensorimotor system represents the physical properties of objects.

In addition to manipulating objects, we use our hands to perceive object properties, including weight. Judgments about weight are comparative in nature rather than absolute (Ross 1969; Ellis and Lederman 1998; Flanagan et al. 2008). That is, weight judgments are biased by expectations about weight. Various weight illusions reveal this bias, including the size–weight and material–weight illusions (Ross 1969; Ellis and Lederman 1999; Flanagan et al. 2008). Thus, a small cube is judged heavier than an equally weighted large cube, and a cube covered in foam is judged heavier than a cube covered in metal, because the small and foam-covered cubes are heavier than expected based on size and surface material, respectively. Hence, expectations about object weight are essential in perceiving object weight, just as they are in controlling fingertip forces when lifting objects. The second part of this chapter examines representations of object weight used when making judgments about weight and considers the relation between these representations and those employed by the sensorimotor system when lifting objects.

PREDICTIVE AND REACTIVE CONTROL MECHANISMS IN PRECISION GRIP LIFTING

Object manipulation tasks are composed of a series of actions or phases that are often bounded by mechanical events that represent subgoals of the task (Flanagan et al. 2006; Johansson and Flanagan 2009). These events involve either the making or breaking of contact between the fingertips and an object, or between a grasped object and another object or surface. Consider, for example, the task of lifting a block using a precision grip with the tips of the index finger and thumb on either side (Fig. 2.1). In this task, contact between the digits and object marks the end of the initial reach phase, and the breaking of contact between the object and tabletop marks the end of the subsequent load phase during which the vertical load force, applied by the digits, is increased. Tactile signals associated with such mechanical contact events play an essential role in the control of object manipulation tasks. Not only do these signals confirm completion of the current action phase, they provide critical information for controlling subsequent phases (Johansson and Westling 1984; Westling and Johansson 1987; Jenmalm and Johansson 1997). For example, when the fingertip contacts an object, ensembles of tactile afferents provide rich information about the magnitude, direction, and spatial distribution of forces, the shape of the contact site, and the friction between the skin and the object (Goodwin et al. 1998; Jenmalm et al. 1998; Jenmalm et al. 2000; Birznieks et al. 2001; Johansson and Birznieks 2004; see Johansson and Flanagan, 2009 for a detailed review).

The precision grip lifting task has been used extensively to investigate both predictive and reactive sensorimotor control mechanisms in object manipulation. Using this task, Johansson and Westling (1988a) examined the control of fingertip forces when lifting objects whose weight could be accurately predicted based on previous lifts (see Fig. 2.1A). When lifting such an object just off a surface, during the load phase, people smoothly increase the vertical load force to a target level that slightly exceeds the weight of the object. Moreover, the rate at which load force is increased is proportional to weight. Thus, the load force rate function typically features a single peak that scales with weight. To ensure grasp stability, the grip force (normal to the grasp surfaces) is modulated in phase with the

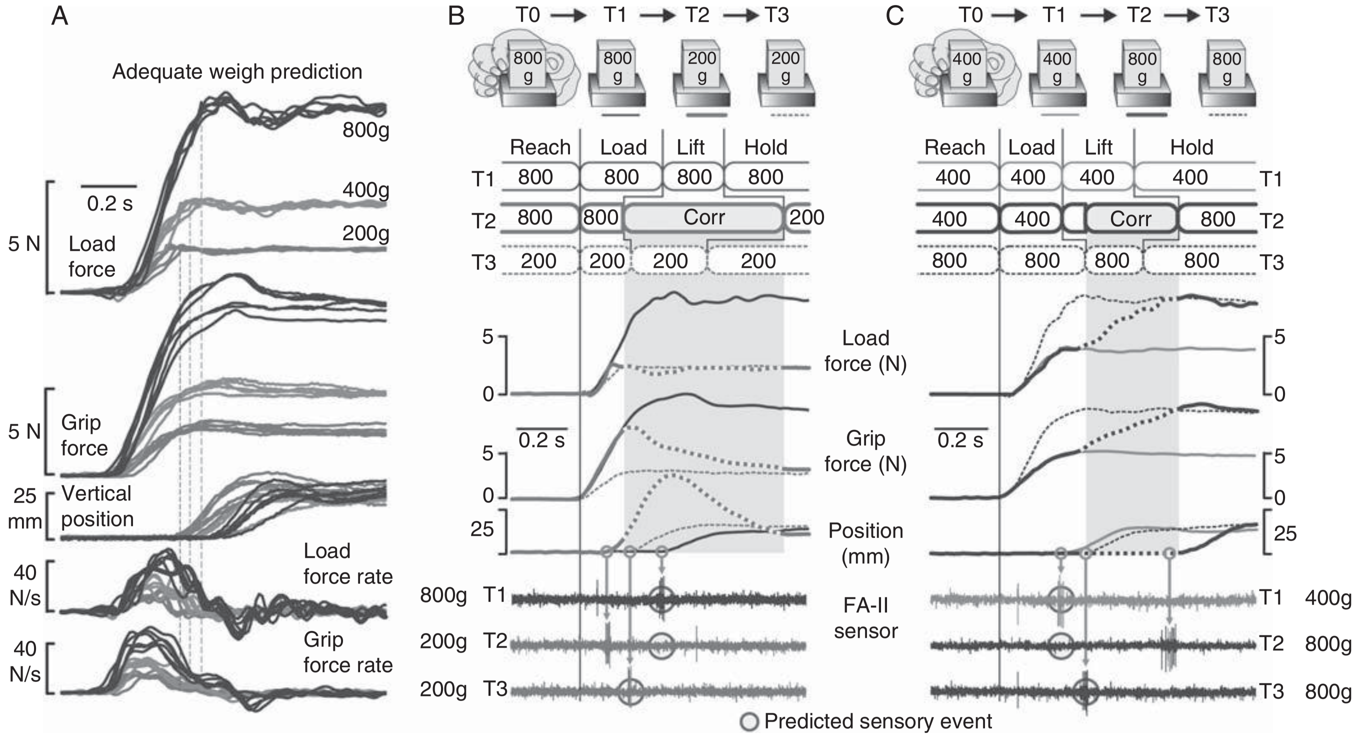

Figure 2.1 Adaptation of motor output to object weight. **A**: Fingertip forces and object position during the initial part of adequately programmed lifts with three objects of different weights (data from 24 single trials from a single participant superimposed).

load force, with a gain that depends on the friction between the digits and surface. Importantly, the increase in load force during the load phase is controlled predictively based on the expected weight of the object.

In the task used by Johansson and Westling (1988a), expectations about object weight were based on knowledge gained from previous lifts of the same object, and such knowledge has been referred to as *sensorimotor memory*. However, reasonable predictions about object weight can often be obtained, prior to the first lift, from other sources of information. Thus, Gordon and colleagues (1993) have shown that people can identify families of objects (e.g., candlestick holders, books, and loafs of bread) based on visual or haptic information and then use learned size–weight associations linked to these families to retrieve weight estimates (Gordon et al. 1991b; Gordon et al. 1991a; Gordon et al. 1991c; Mon-Williams and Murray 2000). In a recent study by Cole (2008), participants first lifted an opaque brown bottle 20 times. After a delay of 15 minutes, the participants then lifted a slightly smaller bottle that was similar in appearance. Although the participants were not aware of the change in bottle size, they nevertheless scaled their lifting forces appropriately for the smaller bottle. Based on

Figure 2.1 (*Continued*) **B** and **C**: Force adjustments and single unit tactile afferent responses to unexpected changes in object weight. Gray circles and vertical lines indicate the instance of lift-off for each trial and the arrowheads point at the signals generated by the lift-off in a FA-II (Pacinian) afferent. The circles behind the nerve traces indicate the corresponding predicted sensory events. **B**: Three successive trials (T1–3) in which the subject lifted an 800 (*blue curves*), a 200 (*red solid curves*), and then the 200 g object again (*red dashed curves*). The forces in T1 were adequately programmed for the prevailing weight because the participant had previously lifted the 800 g object (T0). The forces in T2 were erroneously programmed for the previously lifted 800 g object. In T2, sensory information indicating lift-off occurred earlier than expected, which triggered a corrective action (*yellow-dashed red curves*) terminating the strong force drive and bringing the object back to the intended position. **C**: Three successive trials (T1–3) in which the subject lifted a 400 (*green curves*), an 800 (*blue solid curves*), and then an 800 g object again (*blue dashed curves*). The forces in T2 were erroneously programmed for a 400 g object and the absence of sensory information at the expected lift-off time elicited a corrective action (*yellow-dashed blue curves*) that involved additional force increases until terminated by sensory input signaling lift-off. **B** and **C**: The top diagrams represent sequential action-phase controllers parameterized for different weights. Corrective actions ("Corr") were triggered about 100 ms after a mismatch between predicted and actual sensory information related to lift-off and were linked to an updating of weight parameterization in the remainder of the trial and the next trial. Modified from Johansson, R.S., and J.R. Flanagan. 2009. Coding and use of tactile signals from the fingertips in object manipulation tasks. *Nature Reviews Neuroscience* 10: 345–59, with permission of the publisher. (See color plate.)

these results, Cole (2008) concluded that people automatically make use of visual size cues in addition to memory of object density to scale lift forces when lifting. However, because not all families of objects have constant density, a more general conclusion would be that people learn size–weight maps for families of objects. It has been argued that predictions about the load force (and grip force) required to lift an object are based on an internal model that captures the mechanical properties (e.g., weight) of the object (Johansson and Westling 1988a; Kawato 1999; Imamizu et al. 2000; Wolpert and Ghahramani 2000; Wolpert and Flanagan 2001; Flanagan et al. 2006; see also Imamizu, this volume). However, these results suggest that people do not typically store the weights of individual objects in memory but instead store a more general representation (i.e., a size–weight map) associated with a family of objects. As noted, people appear to learn different size–weight maps for different families of objects such as books, loafs of bread, and candlestick holders (Gordon et al. 1993). Presumably, people can also use object material to estimate size–weight maps and learn associations between material and size–weight maps through experience (Wetenkamp 1933; Ross 1969). Thus, we learn that objects made of Styrofoam and objects made of stainless steel have very different densities or size–weight maps.

Although we rely on weight predictions for smooth and dexterous lifting, there are inevitably instances where our predictions go awry, and this can often result in pronounced performance errors. These errors are signaled by mismatches between actual sensory events and expected events that form part of the sensory plan of the task; that is, the sequence of sensory events expected as the phases of the task unfold (Johansson and Flanagan 2009). Moreover, these mismatches give rise to intelligent, phase-dependent corrective responses. These mechanisms have been well documented for erroneous weight predictions (Johansson and Westling 1988a) and are illustrated in Figures 2.1B and C. Figure 2.1B shows load and grip forces, the vertical position of the object, and predicted and actual sensory events from a fast-adapting type II (FA-II) tactile afferent for three successive trials (T1–T3) where the weight of the object changes, unexpectedly, from 800 to 200 grams in the second trial (T2). The figure also depicts the different phases of the lift for each trial and the expected weight in each phase. When the object being lifted is lighter than predicted and the load phase of the lift is programmed for a heavier weight (T2 in Figure 2.1B), the object lifts off earlier than expected and is lifted higher than intended. The sensory events elicited by the lift-off occur before the predicted sensory events of the sensory plan (Johansson and Flanagan 2009). This mismatch automatically triggers a learned corrective action, or smart reflex, that involves termination of the load phase force followed by corrective motor commands that bring the object back to the intended position. Due to the substantial delays in sensorimotor control loops, this corrective action, which takes ~100 ms to initiate, cannot prevent an overshoot in the lifting movement. Figure 2.1C is similar to Figure 2.1B, and shows three successive trials in which the weight of the object changes, unexpectedly, from 200 to 800 grams in the second trial (T2). When the object is heavier than expected (T2 in Figure 2.1C), the object does not lift off at the expected time because the load force increase is targeted for a lighter weight. In this case, the sensory events elicited by lift-off neither occur before nor at the point predicted by the sensory plan. This mismatch, resulting from the absence of an expected sensory event, triggers a different learned corrective action that involves slow, probing increases in fingertip forces until terminated, reactively, by sensory events signaling lift-off.

The results shown in Figures 2.1B and C demonstrate that the sensorimotor system reacts to both the presence of an unpredicted sensory event and the absence of a predicted sensory event. Moreover, the nature of the corrective actions triggered by these mismatches depends on the phase of the action and is built into the controller for that phase (see "action phase controllers" in Figure 2.1). This phase-dependent use of sensory feedback provides a nice example of optimal, or at least intelligent, feedback control that is central to recent computational models of sensorimotor control (Todorov and Jordan 2002; Scott 2004; Todorov 2004). In addition to triggering corrective actions, these sensory mismatches lead to an updating of memory representations related to object weight, which in turn improves predictive control in subsequent action phases and tasks involving the same object. Thus, for example, in the third trials (T3) shown in Figures 2.1B and C, increases in load force and grip force are tailored for the 200 and 800 g objects, respectively. In the absence of strong visual or haptic cues about object weight, this updating generally occurs in a single trial (as shown in Figures 2.1B and C). However, in the presence of misleading size cues about weight, repeated lifts may be required for complete updating (Gordon et al. 1991b; Flanagan and Beltzner 2000; Flanagan et al. 2008).

Although sensory feedback is continuously predicted and monitored throughout all action phases involved in a manipulation task, tactile signals associated with mechanical contact events play an especially important role in the control of object manipulation tasks. The example shown in Figure 2.1 focuses on tactile signals related to object lift off. However, distinct tactile signals also encode other mechanical events. For example, whereas FA-II afferents quickly and reliably signal the transient mechanical events that occur when an object is lifted off or placed on a surface, slow-adapting type I (SA-I) and especially fast-adapting type I (FA-I) afferents signal making and breaking of contact between the digits and the object (Westling and Johansson 1987; see Johansson and Flanagan, 2009 for a review). We have argued that these mechanical events, which mark the completion of task phases, serve as critical sensorimotor control points in object manipulation tasks (Johansson et al. 2001; Flanagan et al. 2006). By comparing predicted and actual tactile signals linked to mechanical events, the central nervous system can evaluate whether task subgoals (such as object grasp and lift-off) have been successfully completed and can launch appropriate corrective actions as needed. Moreover, information about object properties provided by tactile signals, including texture, shape, and weight, can be used to parameterize subsequent action phases (e.g., Johansson and Westling 1984; Johansson and Westling 1988a; Jenmalm and Johansson 1997; Jenmalm et al. 1998). Thus, when lifting an object aloft, information about the friction between the skin and object surface obtained as the digits contact the object at the end of the grasp phase can be used to determine the appropriate ratio of grip force to load force during the subsequent load, lift, and hold phases (Johansson and Westling 1984). Importantly, mechanical events related to task subgoals also give rise to distinct signals in other sensory modalities including vision, audition, and proprioception. Thus, the comparison of predicted and actual sensory signals related to mechanical events and task subgoals can occur in multiple sensory modalities. Furthermore, that fact that the same events give rise to discrete sensory signals in multiple modalities means that these events provide an opportunity for multisensory alignment.

When lifting objects, grip force is increased in synchrony with and in proportion to load force (Figure 2.1A), and the rate of change of grip force, relative to the rate of change of load force, is tailored to the expected frictional conditions between the skin and the contact surface (Johansson and Westling 1984). Recently, it has been suggested that the modulation of grip force with changes in load force, seen in precision grip lifting and many other manipulation tasks, arises mechanically from the compression of finger pads rather than neural control mechanisms (Pilon et al. 2007). However, we know with certainty that this conjecture (for which the authors provide no evidence) is simply incorrect. There is clear and very strong evidence that neural mechanisms drive the coupling between grip force and load force and that the contribution of mechanical factors is minimal. Because we have recently discussed this issue in detail (Flanagan et al. 2009), we will only briefly deal with it here, taking advantage of the data shown in Figure 2.1B. As noted earlier, when a participant expects to lift an 800 g object but actually lifts a 200 g weight (cf. T2 in the figure), the object lifts off earlier than expected. Due to biomechanical factors, including muscle shortening, there is a rapid cessation of load force increase at the moment of lift-off. However, grip force continues to increases for some 100 ms after lift-off (before it decreases due to a reflex-mediated mechanism triggered by the earlier than expected lift-off). For the first 100 ms or so after lift-off, the grip force profile is indistinguishable from the profile observed when the participant both expects and receives the 800 g object (compare T1 and T2 in Figure 2.1B). Thus, for a critical 100 ms window there is a clear dissociation between changes in grip force and changes in load force, and grip force is unaffected by dramatic changes in load force. Similar dissociations between changes in grip force and changes in load force have been demonstrated in a number of different tasks in which load forces are unpredictably decreased or increased (Cole and Abbs 1988; Johansson and Westling 1988b; Johansson et al. 1992; Flanagan and Wing 1993; Häger-Ross et al. 1996; Blakemore et al. 1998; Turrell et al. 1999; Witney et al. 1999; Delevoye-Turrell et al. 2003; Hermsdorfer and Blankenfeld 2008). These results clearly demonstrate that load force and grip force are not mechanically coupled, and show that both anticipatory and reactive changes in grip force are achieved through neural control mechanisms.

Prediction, Control, and Internal Models

In numerous studies, we and others have examined the coupling of grip force and load force while moving objects held in a precision grip, where the direction of movement is orthogonal to the grip axis (e.g., Flanagan et al. 1993b; Flanagan and Wing 1993; Flanagan and Wing 1995; Flanagan and Wing 1997; Blakemore et al. 1998; Danion 2004; Descoins et al. 2006; Danion and Sarlegna 2007). This work has shown that grip force is modulated in phase with changes in acceleration-dependent loads that arise when moving inertial loads. Furthermore, grip force is modulated in phase with load force when moving objects with different dynamics specifying the relation between forces applied to the object and its motion (Flanagan and Wing 1997). Figure 2.2A shows single-trial kinematic and force records obtained in a task in which the participant moved a grasped object, instrumented with force sensors, in a horizontal direction between two positions. The object was attached to a linear motor that could be servo-controlled to create inertial, viscous, and elastic loads that depended on acceleration, velocity, and position of the object, respectively. After experiencing each of these loads for a few trials, participants were able to generate smooth movements that were roughly similar, in terms of kinematics, for the three loads. Of course, by design, the load force profiles produced during these movements were very different. The key finding was that the grip force was modulated in phase with load force for all loads.

The result shown in Figure 2.2A indicates that the sensorimotor system knows about, and cares about, object dynamics. When moving a hand-held object, the mapping between arm motor commands and load forces depends on the dynamics of the object. Therefore, to predict accurately the load forces that arise during movement, the sensorimotor system needs to take the dynamics of the object in account. In other words, the sensorimotor system must have stored knowledge, or an internal model, that captures the mechanical behavior of the object while interacting with the hand. Moreover, the sensorimotor must also take into account (i.e., have an internal model of) the dynamics of the arm. The ability of the sensorimotor system to account for arm dynamics is illustrated in Figure 2.2B, which shows fingertip forces recorded in a task in which participants slid an object, instrumented with a force sensor, across a near-frictionless horizontal surface

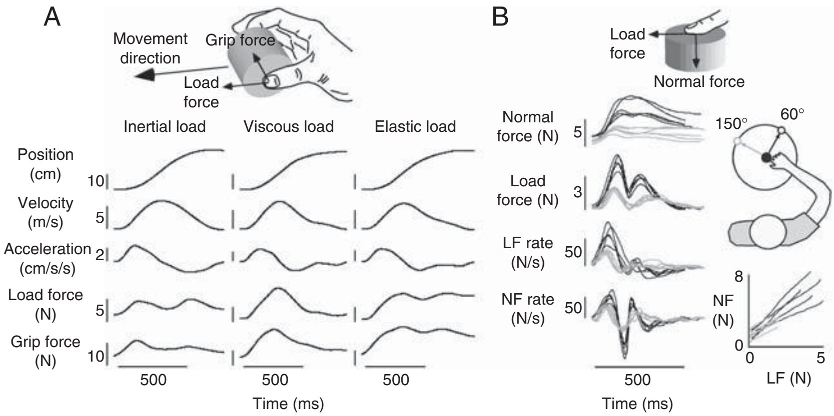

Figure 2.2 Anticipatory adjustments in grip force for movement-related changes in load force. **A**: Single kinematic and force records from one subject moving a hand-held object with three different loads. For all three loads, grip force changes in parallel with fluctuations in load force measured as the resultant load tangential to the grasp surface. All calibration bars start at zero. **B**: Normal and load forces records (data superimposed from ten single trials from a single participant) when sliding an object across a frictionless horizontal surface to one of two targets located at 60 degrees (*red traces*) or 150 degrees (*blue traces*). Subjects held the object, instrumented with a force sensor, beneath the index finger. The lower right panel shows normal force plotted as a function of tangential force from movement onset to the initial peak load force (same ten trials). Modified from Flanagan, J.R., and A.M. Wing. 1997. The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads. *Journal of Neuroscience* 17: 1519–28; and Flanagan, J.R., and S. Lolley. 2001. The inertial anisotropy of the arm is accurately predicted during movement planning. *Journal of Neuroscience* 21: 1361–69, with permission of the publisher.

from a central target position to targets located in different directions (Flanagan and Lolley 2001). Movements to the 60-degree target (*black traces*) primarily involve rotation of the forearm about the elbow, and therefore encounter relatively low inertia; whereas movements to the 150-degree (*gray traces*) target involve rotation of the entire arm about the shoulder, and therefore encounter relatively high inertia. Because of this difference in inertia, the acceleration of the hand (and object) is greater for the 60-degree target, in comparison to the 150-degree target, and greater load forces and load force rates are observed. Importantly, the differences in load force and load force rate across the two movement directions is matched by similar differences in normal force and normal force rate. Once again, we see that grip force (i.e., the normal force) is modulated in phase with, and thus anticipates, changes in load force. The bottom right panel of Figure 2.2B further illustrates the coupling between the grip and load forces by showing normal force plotted as a function of load force from movement onset to the initial peak of the load force. These results clearly show that the sensorimotor system takes the inertial properties of the arm into account when predicting and generating required grip forces. Such prediction could be achieved by using a copy of the arm motor command (i.e., efference copy) together with internal models of the object and arm, and information about the configuration of the arm and object (Kawato 1999; Wolpert and Ghahramani 2000; Wolpert and Flanagan 2001; Flanagan et al. 2006).

The term *forward model* refers to an internal model (i.e., a neural process) that can be used to predict the consequences of motor commands. Thus, a forward model pertaining to object dynamics could be used to predict load forces that arise when moving grasped objects. However, internal models pertaining to object dynamics can also be used to estimate the motor commands required to achieve desired sensory consequences. Such models are referred to as *inverse models*. Work examining adaptation of reaching movements to hand-held objects with novel dynamics (i.e., force fields) has clearly established that the sensorimotor system can learn, and store in memory, knowledge of object dynamics that can be used to generate motor commands under appropriate conditions (e.g., Shadmehr and Mussa-Ivaldi 1994; Brashers-Krug et al. 1996; Gandolfo et al. 1996; Conditt et al. 1997; Shadmehr and Brashers-Krug 1997; Thoroughman and Shadmehr 2000; Lackner and DiZio 2005; Cothros et al. 2006).

It is important to point out that internal models of objects, as defined by most researchers in the field, are not necessarily complete or veridical representations of the dynamics of the object. Indeed, most studies examining how people adapt to novel loads have shown that learning is action and context specific (e.g., Thoroughman and Shadmehr 2000; Wang and Sainburg 2004; Nozaki et al. 2006). For example, studies examining reach adaptation to loads applied to the hand have shown limited transfer of learning when the object—or force field linked to the object—is rotated relative to the arm (Shadmehr and Mussa-Ivaldi 1994; Malfait et al. 2002). These results suggest that people do not learn the full dynamics of objects with novel loads but instead learn a mapping between object motion and context- and action-specific motor commands (Shadmehr and Moussavi 2000; Mah and Mussa-Ivaldi 2003). It is an open question whether, with sufficient practice in manipulating an object with novel dynamics, people form a single internal model that approximates the true dynamics of the object or a set of internal models tailored to specific contexts and actions (Ahmed et al. 2008).

Some researchers consider the concept of an internal model to be so general that it is unhelpful or even vacuous. However, it is important to understand the context in which this concept first gained momentum in the field of motor control. In the 1980s, researchers at the Massachusetts Institute of Technology (MIT) and elsewhere began to use concepts from robots in an effort to understand human motion planning and control. One of the important insights obtained from work in robotics is that motor learning and control are improved if the controller has knowledge about the dynamics of the system it controls (Atkeson 1989). At the same time, proponents of the equilibrium-point hypothesis, including the first author of this chapter, argued that the sensorimotor control system did not need to know about the detailed dynamics of the arm (Flash 1987; Feldman et al. 1990; Flanagan et al. 1993a; see also Latash, this volume). According to the latter view, smooth movements arise as a natural consequence of simple shifts in the equilibrium position of a limb, and there is no need to plan a movement trajectory or consider dynamics in order to convert the planned trajectory into motor commands. As noted earlier, subsequent work on trajectory adaptation and anticipatory grip force control when moving hand-held loads has shown that the sensorimotor system does learn and make use of detailed knowledge of arm and object dynamics. However, the question of whether the system plans desired trajectories remains contentious (Kawato 1999; Todorov and Jordan 2002; Scott 2004; Todorov 2004) and it is possible that equilibrium-point control could be combined with knowledge about dynamics (i.e., an internal model) to generate movement (Flanagan et al. 1995). Over the last few decades, the idea that the sensorimotor system makes use of internal models has served as an important starting point for a great deal of innovative research aimed at understanding how such models are learned and represented, and how they might be implemented in the brain (for reviews see Wolpert and Ghahramani 2000; Shadmehr et al. 2010; see also Imamizu, this volume).

Distinct Object Representations in Action and Perception

As discussed earlier, the ability to predict accurately the weights of objects we interact with is essential for skilled manipulation. However, weight predictions are not just used in the control of action; they also influence our perception of weight. There is strong evidence that weight judgments are biased by expected weight, such that an object will be judged to be relatively heavy or light if it is heavier or lighter than expected, respectively (Ross 1969; Ellis and Lederman 1998; Flanagan et al. 2008). This bias is revealed by weight illusions, including the size–weight illusion (Charpentier 1891), in which the smaller of two equally weighted and otherwise similar objects is judged to be heavier; and the material–weight illusion (Wolfe 1898; Seashore 1899), in which an object that appears to be a dense material is judged to be lighter than an equally weighted and otherwise similar object that appears made of a less dense material. The fact that expectations about weight that bias weight judgments can be acquired through experience is well illustrated by the "golf ball" illusion (Ellis and Lederman 1998), in which experienced golfers (but not nongolfers) judge a golf ball to be lighter than a practice golf ball doctored to be equal in weight to a real golf ball.

The size–weight illusion is the most powerful and robust of the weight illusions, and this is presumably because, for a given family of objects, size is generally a very strong predictor of weight. This illusion, first described well over 100 years ago (Charpentier 1891; Murray et al. 1999), is experienced by almost all healthy people (Ross 1969; Davis and Roberts 1976), including children as young as 2 years of age (Robinson 1964; Pick and Pick 1967), and is not weakened when participants are verbally informed that the objects are equally weighted (Flourney 1894; Nyssen and Bourdon 1955; Flanagan and Beltzner 2000). The size–weight illusion is present when only visual cues about size are available, as when lifting viewed objects by strings, but is most powerful when haptic cues about object size are available, as when the hand grasps the objects directly (Ellis and Lederman 1993).

Experiments in which participants lift objects of varying size and weight have shown that predictions about weight, used in action, are independent of predictions about weight used when judging weight (Flanagan and Beltzner 2000; Flanagan et al. 2001; Grandy and Westwood 2006; Chang et al. 2007). In our first study (Flanagan and Beltzner 2000), we asked participants to repeatedly lift a small cube and an equally weighted large cube in alternation for a total of 40 lifts. Although participants initially scaled lifting force to object size, they quickly adapted the lifting force to the true weights of the cubes after about ten lifts. After 40 lifts, we assessed the strength of the illusion and found that the illusion did not differ from that observed in a control group who had not performed the repeated lifts. Thus, despite the fact that the sensorimotor system learned the true weights of the two cubes, at the perceptual level, participants still expected the large cube to be heavier than the small cube and therefore judged the large cube to be lighter than the small cube. This result also ruled out the hypothesis that the size–weight illusion arises from a mismatch between actual and expected sensory feedback related to lifting (Ross 1969; Granit 1972; Davis and Roberts 1976).

More recently we have shown that, in fact, the size–weight illusion can be altered by experience (Flanagan et al. 2008). We constructed a set of 12 blocks, consisting of four shapes and three sizes (Fig. 2.3A), whose weights varied inversely with volume (see circular cylinders in Figure 2.3B; the other shapes had the same sizes and weights). All blocks had the same color and texture. Participants gained experience with these size–weight inverted objects by repeatedly lifting and replacing them (in a random order), moving them from the tabletop to one of four force sensors or vice versa (Fig. 2.3A). Thus, in one-half of the lifts, we could measure the vertical load force participants applied to the object prior to lift-off. Three groups of participants performed lifts. Participants in Group 1 performed 1,050 lifts in a single session. Participants in Group 2 performed 1,200 lifts a day for 3 successive days and 120 lifts on day 4 and participants in Group 3 performed 240 lifts a day for 11 days. In all three groups, the size–weight illusion was tested once all lifts had been completed. We also tested the illusion in a control group of participants who never lifted the inverted size–weight objects.

Figure 2.3C shows load force and load force rate records from two trials in which one of the small, heavy objects was lifted. In initial trials, participants typically underestimated the weight of the small objects, and several increases in load force, associated with distinct peaks in load force rate, were required to achieve lift-off (*gray vertical lines*). However, in later trials in the same session, participants accurately predicted the weight of the small objects such that lift-off occurred after a single, rapid increase in load force. To quantify lift performance, we determined the load force at the time of the first peak in load force rate (LF_1; see gray circles in Figure 2.3C), focusing on trials with the small and mid-sized objects for which we could accurately measure the initial peak in load force rate. For each participant and object size, we computed the median value of LF_1 for each successive block of five lifts from a force sensor (collapsing across object shape). Figure 2.3D shows LF_1 as a function of trial block for Group 2; the first eight blocks and last four blocks on day 1 and the first four blocks on day 2 are shown. The horizontal gray lines are included as visual references, and the dashed line shows an exponential fit to the day 1 data. For the small, heavy objects, LF_1 increased substantially over the first eight blocks (i.e., 40 lifts of a small object from a force sensor and ~240 lifts in total) and had almost fully adapted by the 15th block. Moreover, participants retained this adaptation on day 2. When initially lifting the mid-sized, mid-weighted objects, participants' estimates of object weight were quite accurate, and modest changes in LF_1 occurred across trial blocks. Similar learning of the applied load force was seen in all three experimental groups. That is, all groups of participants fully adapted their lifting forces to the true weights of the objects on day 1 and retained this adaptation if lifting on subsequent days.

To test the size–weight illusion, we used a small and a large cube equal in volume to the small and large inverted objects, respectively, and both equal in weight to the mid-sized inverted objects (Fig. 2.3B). These cubes had the same color and texture as the size–weight inverted objects. Based on the absolute magnitude estimation procedure, in which participants lifted each cube and assigned numbers corresponding to their weights, we quantified the strength and direction of the illusion. A positive score of 100 indicates that the small object was judged 100% heavier than the large objects; a negative score of 50 indicates that the large object was judged 50% heavier than the small object. Figure 2.3E shows the strength of the illusion measured for the Groups 1–3 and the controls. On average, the control participants judged the small cube to be 141% heavier than the large cube. Participants in Group 1 also judged the small object to be heavier than the large objects, but the strength of the illusion was attenuated relative to the controls. Participants in Group 2 did not judge the cubes to be

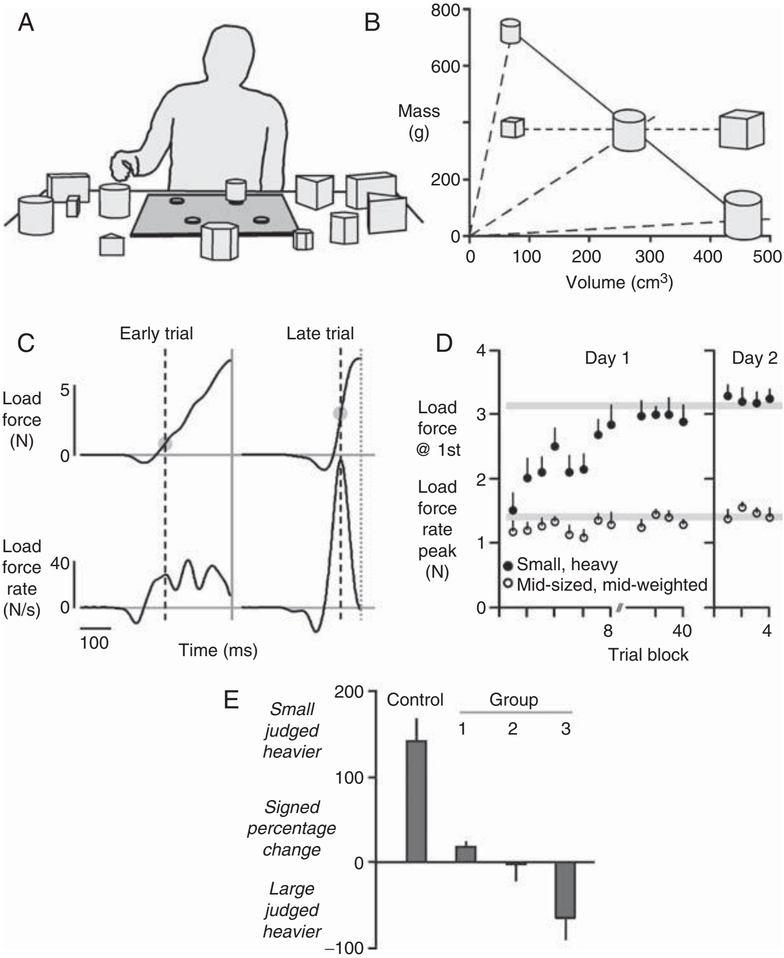

Figure 2.3 Adaptation of lifting forces and weight judgments to size-weight inverted objects. **A**: While seated, participants lifted the objects from the tabletop and placed them on to one of four force sensors or vice versa. All objects were covered with a thin sheet of balsa wood and painted green. A data projector, located above the participant, provided instructions about which object to place on a given force sensor and which object to remove from a given force sensor. **B**: Relation between volume and size for the size-weight inverted objects (circular cylinders given as the example) and for the small and large equally weighted cubes. **C**: Individual load force and load force rate records from an early and a late trial in which a small, heavy object was lifted. The black dashed vertical lines mark the time of the initial peak in load force rate and the gray dotted vertical lines mark the time of lift-off. **D**: Load force at the time of the initial peak in load force rate for the small and mid-sized objects as a function of trial block and day. Each point represents the average across participants and the height of each vertical bar represents 1 SE. **E**: The height of each bar represents the strength and direction of the size–weight illusion, measured as the signed percentage change score, across participants and the height of each error bar represents 1 SE. Modified from Flanagan, J.R., J.P. Bittner, and R.S. Johansson. 2008. Experience can change distinct size-weight priors engaged in lifting objects and judging their weights. *Current Biology* 18: 1742–47, with permission of the publisher.

significantly different in weight and thus did not experience the illusion. Finally, participants in Group 3 exhibited an inversion of the illusion when tested after 11 days of lifting. These results provide support for the dual proposition that (1) people perceive object weight relative to expected weight, generated from learned size–weight maps associated with families of objects, and that (2) experience can alter these expectations.

The fact that participants in all three groups fully adapted their lift forces to the inverted size–weight objects and yet exhibited striking differences in the strength and direction of the size–weight illusion supports the claim (Flanagan and Beltzner 2000) that sensorimotor predictions about weight used in lifting are independent of predictions about weight that influence weight judgments. This finding can be related to the idea, proposed by Goodale and Milner and their colleagues (e.g., Goodale et al. 1991; Culham et al. 2003; Goodale and Westwood 2004), that the control of action and the formation of perceptual judgments rely on neural mechanisms that use and represent sensory information in different ways. Perhaps the even broader point is that the way in which sensory information is processed depends on the demands of the task, rather than on whether the task is perceptual or motor per se (Smeets and Brenner 2006).

Note that expectations about object weight, used when judging weights, are distinct from verbal or cognitive reports about weight. In the standard size–weight illusion, subjects judge the small object to be heavier because they expect the small object to be lighter, and this expectation biases weight perception. If the illusion is tested a second time, the subject will still judge the smaller object to be heavier (and still expect it to be lighter) even though they just said it was heavier. Thus, it is clear that the previous judgment does not alter the expectation of weight underlying the size–weight illusion. Indeed, if expectations were based on the previous report, then the illusion would flip every time it was tested!

The different adaptation rates observed for lifting forces and the size–weight illusion suggest that distinct, adaptive size–weight maps (or priors) underlie the weight predictions used when lifting objects and predictions about weight used when judging their weights. We have suggested that size–weight priors used when judging the weights of familiar objects are resistant to change because they are based on well-established and stable correlations between size and weight that apply to families of objects (Flanagan et al. 2008). For weight perception, this resistance is important. If size–weight priors engaged when judging weight were modified quickly, people would effectively lose their ability to recognize and tag objects as being relatively heavy or light and to communicate this information to others. Conversely, because the sensorimotor system must deal with specific objects, the weights of which may, or may not, be well predicted from visual cues, it is critical that size–weight priors used when lifting objects adapt quickly.

We have argued that, with extensive experience lifting the size–weight inverted objects, people adapt their size–weight priors for these objects such that they learn a single inverted size–weight map for these objects (Flanagan et al. 2008). However, it is also possible that participants in our study learned separate size–weight maps for the small, mid-sized, and large objects. We are currently carrying out experiments to test this alternative account. Regardless of how these experiments pan out, the main conclusion still stands. That is, our results indicate that the brain maintains two distinct representations involved in predicting the weights of objects: a slowly adapting representation that supports weight perception, and a rapidly adapting one that supports manipulatory actions. Importantly, these representations are associated with families of objects, rather than individual objects, and allow generalization across objects within these families (Cole 2008; Flanagan et al. 2008). Similar representations likely encode the dynamics of objects with more complex dynamics in addition to simple inertial loads (Ingram et al. 2010).

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