Predictive mechanisms and object representations used in object manipulation

J. Randall Flanagan[1], Kyle Merritt[1] and Roland S. Johansson[2]

[1] Department of Psychology and Centre for Neuroscience Studies, Queen's University, Kingston, Ontario, K7L 3N6, Canada

[2] Physiology Section, Department of Integrative Medical Biology, Umeå University, SE-901 87 Umeå, Sweden

Summary

Skilled object manipulation requires the ability to estimate, in advance, the motor commands needed to achieve desired sensory outcomes and the ability to predict the sensory consequences of the motor commands. Because the mapping between motor commands and sensory outcomes depends on the physical properties of grasped objects, the motor system may store and access internal models of objects in order to estimate motor commands and predict sensory consequences. In this chapter, we outline evidence for internal models and discuss their role in object manipulation tasks. We also consider the relationship between internal models of objects employed by the sensorimotor system and representations of the same objects used by the perceptual system to make judgments about objects.

Although we have designed computers that can beat grand masters at chess, we have yet to design robots that can manipulate chess pieces with anything like the dexterity of a 5 year old child. What makes humans so good at object manipulation in comparison to robots? There is no question that the anatomy of the human hand is well adapted for manipulation. On the sensory side, the hand is richly endowed with tactile sensors that provide exquisitely precise information about mechanical interactions between the skin and objects. On the motor side, the numerous kinematic degrees of freedom of the hand enables it to grasp objects of all shapes and sizes. These sensory and motor capabilities provide the building blocks; however, it is the way in which manual tasks are organized and controlled by the nervous system that enables flexible and dexterous object manipulation. Skilled object manipulation requires the ability to generate motor commands tailored to the goals of the task and the physical properties of the manipulated objects. This involves both feedforward control, based on prediction, and feedback control that is shaped to the demands of the task. This chapter will focus on predictive mechanisms in the control of object manipulation tasks and on memory representations that support such prediction.

Prediction and internal models

Skilled object manipulation requires the ability to estimate, in advance, the motor commands needed to achieve desired sensory outcomes. For example, when lifting objects people scale the rate at which they increase vertical load force to the expected weight of the object and often begin to attenuate the increase in load force prior to lift-off (Johansson and Westling 1988a). This ensures that objects are lifted smoothly and quickly regardless of their weight. In addition, when using a precision grip with the tips of the thumb and index finger on either side of the object, people scale horizontal grip forces to both the predicted load force and the expected friction between the digits and object (Johansson and Westling 1984). This ensures that grip

forces are large enough to prevent slip but not so large as to cause fatigue or damage to the hand or object.

Skilled object manipulation also requires the ability to predict the sensory consequences of motor commands. By comparing predicted and actual sensory feedback, the motor system can monitor the progress of the task, adjust motor commands if a mismatch occurs so that the goals of the task can be achieved, and update predictive mechanisms so as to reduce future mismatches. A key feature of object manipulation tasks is that they are composed of a series of actions or phases that are often bounded by mechanical events that represent sub-goals of the task. 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. For example, the task of picking up and replacing an object on a tabletop involves three mechanical events: contact between the digits and object at the end of the reach phase, the breaking of contact between the object and table top at the end of the load phase, and contact between the object and table top at the end of the replacement phase.

Although sensory feedback may be continuously predicted and monitored throughout all action phases, tactile signals associated with mechanical contact events play an essential role in the control of object manipulation tasks. For example, when the fingertip contacts an object, ensembles of tactile afferents provide rich information about the timing, magnitude, direction, and spatial distribution of forces, the shape of the contact site, and the friction between the skin and the object (Johansson and Westling 1984; Jenmalm and Johansson 1997; Goodwin et al. 1998; Jenmalm et al. 1998, 2000; Birznieks et al. 2001; Johansson and Birznieks 2004). Thus, tactile signals not only confirm successful completion of the current action phase, they also provide critical information for controlling subsequent phases. By comparing actual and predicted sen-

sory feedback associated with contact events, the motor system can detect mismatches and respond intelligently. For example, when lifting an object, the motor system predicts the time at which it will receive tactile signals indicating that the object has lifted off the surface. If an object is lighter than expected, lift-off will occur before the predicted time and the resulting sensory mismatch will trigger a decrease in load force and grip force. Conversely, if the object is heavier than expected, lift-off will not occur at the expected time and the resulting mismatch will trigger and increase in grip force and load force (Johansson and Westling 1987; 1988a).

When moving a hand-held object, the mapping between motor commands and sensory outcomes depends on the dynamics of the object; i.e., the relationship between forces applied to the object and its motion. Therefore, in order to accurately predict the sensory consequences of our actions, we need to take the dynamics of the object in account. In other words, the motor system must have an internal representation, or internal model, the captures the mechanical behaviour of the object. For example, to accurately predict the time of lift-off when lifting an object, the motor system must know the weight of the object. Similarly, if we lift and replace an object, attached to a table top by a spring, we need to know the stiffness of the spring to accurately predict the time of contact as the object is replaced. With information about intended arm motor commands (i.e., efference copy) and an estimate of the current state of the arm and object, an internal model of the object can be used to predict or simulate the consequences of actual motor commands (Kawato 1999; Wolpert and Ghahramani 2000; Flanagan et al. 2006).

The control of grip force in manipulation tasks may also be based on predictive mechanisms that make use of internal models of object dynamics (Johansson and Westling 1988a; Flanagan and Wing 1997). When lifting and moving familiar objects with the grip axis normal to the plane of object motion, grip force is adjusted in phase with, and thus anticipates, movement-

dependent modulations in force and torques acting tangential to the grasp surfaces (Flanagan and Wing 1993, 1995; Flanagan and Tresilian 1994; Blakemore et al. 1998; Goodwin et al. 1998; Wing and Lederman 1998). Moreover, people can learn to generate anticipatory grip force adjustments for a variety of loads that depend on different kinematic parameters of the movement (Flanagan and Wing 1997; Flanagan et al. 2003). Because the mapping between arm motor commands and load force depends on object dynamics, the motor system can not rely on a set mapping between arm and grip force motor commands to modulate grip force in phase with load force. Instead, we have argued that motor system predicts load force (and hence the required grip force) using an internal model of the dynamics of the object (Flanagan and Wing 1997; Wolpert and Flanagan 2001; Flanagan et al. 2003). Our ability to independently modulate arm movement motor commands and grip force motor commands has been nicely demonstrated by Danion and colleagues who showed that predictive adjustments in grip force are sensitive to loads applied to the object but not to equivalent loads applied to the arm (Danion 2004; Descoins et al. 2006). Because the transformation from arm motor commands to fingertip load forces depends on both arm and object dynamics, accurate prediction of load forces acting the fingertips when moving a grasped object requires knowledge of arm dynamics in addition to knowledge of object dynamics. Thus, grip force can be used to examine the structure of internal models of arm dynamics in addition to object dynamics (Flanagan and Lolley, 2001).

The term forward model refers to an internal model that is used to predict the consequences of motor commands whereas the term inverse model refers to an internal model that is used to estimate the motor commands required to achieve desired sensory outcomes. Shadmehr and Mussa-Ivaldi (1994) examined the acquisition of inverse models of object dynamics using a task in which participants moved a handle attached to a robotic device that could generate com-

plex movement-dependent loads (or force-fields). Although the force-field initially perturbed the trajectory of the hand, participants adapted such that they could move the handle directly to targets in much the same way as they did before the force-field was turned on. Importantly, when the force-field was turned off following adaptation, hand trajectories were again perturbed. This indicates that participants did not simply stiffen the limb to compensate for the force-field but, instead, learned an inverse model of the dynamics of the handle (Shadmehr and Mussa-Ivaldi 1994). Note that after-effects are not observed following adaptation if the object in hand is released but are seen if participants re-grasp the object (Lackner and DiZio 2005; Corthos et al. 2006). This indicates that internal models can be recruited and de-recruited when grasping and releasing objects. Indeed, the fact that people can seamlessly lift myriad familiar objects shows that we can rapidly recruit and de-recruit appropriate internal models as we grasp and release objects.

As noted above, anticipatory adjustments in grip force could be generated using a forward model of the object to predict the load forces resulting from arm motor commands. However, it is also possible that grip forces could be generated using an inverse model. If one assumes that motion planning involves specifying a desired object trajectory, an inverse model could be used to transform the desired trajectory into the load forces required to move the object and hence the grip forces required to stabilize the object. However, studies showing the people can accurately predict grip forces even when they are unable to control the movement of the objects (Flanagan et al. 2003; see also Flanagan and Lolley 2001) suggest that grip forces are likely predicted based on an forward model of the object. In any case, what is clear is that knowledge of object dynamics is crucial for the accurate prediction of required grip forces in manipulation tasks.

It is important to emphasize that internal models of objects, as defined by most researchers in the field, are not necessarily complete or veridical representations of the actual dynamics of the object. Indeed, most studies examining how people adapt to unusual and novel loads applied to the hand or arm have shown that learning is action and context specific (e.g., Wang and Sainburg 2004; Nozaki et al. 2006). For example, studies examining adaptation of reaching movements to novel 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 when adapting to novel and unusual loads, people do not learn the full dynamics of the object mapping motion to applied force. Instead, they appear to 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 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.

In contrast to the unusual and novel loads often employed in studies of motor learning, the loads experienced in most natural manipulation tasks are familiar. For example, many of the objects we lift and move on a daily basis are standard inertial loads where the applied force varies with acceleration. When lifting familiar objects, the motor system does not have to learn a new class of dynamics; rather the challenge is to predict the load parameters. Thus, when lifting objects with inertial loads, the motor system generally attempts to predict the mass (or weight) of the object. People are very good at using information about object size and shape, obtained through vision or touch, to predict the weight (Johansson and Westling 1988a; Gordon et al. 1991a; 1991b; Mon-Williams and Murray 2000) and weight distribution (Wing and Lederman

1988; Salimi et al. 2003; Jenmalm et al. 1998; Johansson et al. 1999) of objects. Although we know of no experiments that have examined the control of fingertip forces when lifting similar objects composed of different materials, it seems likely that people also use visual (and perhaps haptic) information about object material to estimate weight. Gordon and colleagues (1993) have shown that people predictively scale their fingertip forces for familiar objects of varying size, shape, and material (e.g., a glass candle holder versus a box of crisp bread) and it is possible that they may be using information about material, in addition to object identify, to predict object weight. Although visual (and haptic) information about object size and shape often leads to good predictions about weight and weight distribution, such prediction is based on correlations and can be erroneous. Ultimately, it is not until the object is lifted, and tactile feedback received, that the weight and weight distribution of the objects can be determined. Similarly, the friction between the digits and the contact surfaces can only be accurately determined from tactile feedback arising when the digits contact the object.

When prediction of object physical properties based on visual or haptic cues goes awry, reflex-mediated corrections of force output are observed (see above). At the same time, memory representations are updated such that, if the object is lifted a second time, prediction improves. Johansson and Westling (1984) coined the term sensorimotor memory to refer to knowledge of object properties gained from previous lifts. In the absence of useful visual cues, sensorimotor memory typically dominates fingertip force control after a single lift. For example, when repeatedly lifting a test object, the weight of which is occasionally and unexpected altered, people update their force output within a single trial following a weight change (Johansson and Westling 1988a). In the presence of misleading visual cues, several trials may be required before sensorimotor memory dominates (Gordon et al. 1991c; Flanagan and Beltzner 2000; Grandy and West-

wood 2006). Sensorimotor memory is closely related to notion of an internal model. In a study using objects with misleading size cues about weight, we have shown that sensorimotor memory for weight can be long lasting (Flanagan et al. 2001). In particular, participants who lifted a small high density cube and a large low density cube several times on one day exhibited accurate prediction of required fingertip forces when lifting the same objects a day later. Such persistent sensorimotor memory is tantamount to an internal model.

The idea that sensorimotor memories, or internal models, encode object mechanical properties has been challenged by Quaney and colleagues (2003). These authors showed that pinching a force transducer before lifting an object influences the grip force used during the lift. Based on this observation they argued that sensorimotor memory is based on recent fingertip actions rather than object properties. However, Cole and colleagues (2006) recently demonstrated that this finding does not extend to load force; the generation of vertical load forces at the fingertips prior to lifting an object does not influence load force development during the lift. Cole and coworkers suggested that separate memory representations may be used for grip and load force control (see also Quaney et al. 2005). Because the load force required to lift the object depends solely on the physical properties of the object (i.e., object weight), we suggest that an internal model of the object is used to control load force. In contrast, grip force depends not only on weight but is also influenced by the frictional conditions at the contact surfaces and the grip safety margin selected by the individual to guard against slip. Given that grip force depends on factors that are independent of the object (e.g., the dryness of the skin), it seems reasonable that the control of grip force may involve memory mechanisms that are distinct from the internal model of the object and that can be influenced by actions, involving the fingertips, on other objects.

To test the idea that people might remember motor commands or actions rather than object properties, we conducted an experiment in which we asked participants to lift an object, instrumented with force sensors (Figure 1A), to different heights within a prescribed time period (Merritt and Flanagan 2004). The object was attached to a manipulandum that could simulate different loads including an inertial and a viscous load. For each load, participants first lifted the object 20 times to a target height of 7 cm and then lifted the object another 20 times to a target height of 14 cm. In all lifts, participants were asked to lift the object to the target within a 200 ms time window. Figure 1B show kinematic and forces records for three lifts of the inertial (or mass) load performed by a representative participant. The solid black, solid gray, and dashed black curves illustrate the last 7 cm lift, the first 14 cm lift, and the second 14 cm lift. Note that reasonably good generalization was observed in the first lift to the 14 cm target as the participant increased both grip and load force. In all three lifts, grip force was modulated in phase with load force indicating good prediction of the load. Figure 1C shows corresponding records for three lifts with the viscous load performed by another representative participant. Although this load is somewhat unusual, the participant adapted well to the load. Specifically, in the last lift to the 7 cm target, the participant accurately and smoothly reached the target and grip force was modulated in phase with velocity dependent load force. When first lifting the viscous load to the 14 cm target, the object undershot the target. However, partial generalization of learning was observed in that the participant appropriately increased both grip force and load force and continued to modulate grip force in-phase with load force. These results indicate that when lifting both familiar and novel loads, participants acquire knowledge of dynamics that is linked to the object. (Note that it is not clear how memory representations based on motor commands could support generalization across lifts of varying height and speed that require different motor commands.)

Neural Basis of Anticipatory Grip Force Adjustments

Recently, Pilon and colleagues (2007) have argued that the modulation of grip force with changes in load force, observed in many manipulation tasks, results from biomechanical rather than neural mechanisms. Specifically, these authors suggested that once an object is grasped, tangential load forces compress and move the finger pads and that this leads to changes in grip force that are proportional to the load force. Although this idea may seem attractive in terms of simplifying grip force control, there is an abundance of evidence demonstrating that anticipatory grip forces result from neural control processes and that load and grip forces are not, in fact, mechanically coupled as assumed (but not tested) by Pilon and coworkers. In this section of the chapter, we will describe some of this evidence.

Clear decoupling between changes in grip force and changes in load force can be observed in precision grip lifting when object weight is unexpectedly decreased (Johansson and Westling 1988a). When a participant expects to lift an 800 gram object but actually lifts a 200 gram weight, the object lifts off earlier than expected. Due to biomechanical factors (e.g., muscle shortening), there is a rapid cessation of load force increase at the moment of lift-off (see Figure 2 from Johansson and Westling 1988a). However, grip force continues to increases for some 100 ms after lift-off. (After 100 ms, grip force starts to decrease due to a reflex-mediated mechanism triggered by the earlier than expected lift-off.) For the first 100 ms after lift-off, the grip force profile is indistinguishable from the profile observed when the participant both expects and receives the 800 gram object. Thus, for a critical 100 ms window there is a strong dissociation between changes in grip force and changes in load force and grip force is unaffected by dramatic changes in load force. This result clearly demonstrates that load force and grip force are not me-

chanically coupled and shows that both anticipatory and reactive changes in grip force are achieved through neural control mechanisms.

Blakemore and colleagues (1998) have shown that when a participant holds an object to which a cyclical load force is externally applied, grip force is modulated but lags behind changes in load force by some 100 ms. This indicates that participants could not predict the external load and instead relied on reactive mechanisms to modulate grip force. This decoupling between grip and load changes provides another example where grip and load forces are not mechanically coupled. Pilon and colleagues (2007) cite the Blakemore study but argue that because participants employed high overall grip forces (around 10 N on average), the finger pads would not have moved much and that therefore grip force was not modulated in phase with load force. However, Flanagan and Wing (1995) showed that when moving an object in a cyclic fashion, grip force can vary between 10 and 25 N and still be modulated in phase with load force (see Figure 2 from Flanagan and Wing 1995). Thus, if it is true that the finger pads do not move when grip forces are large (i.e., around 10 N or higher), then the mechanical explanation for grip-load coupling posited by Pilon and colleagues can not explain the coupling observed by Flanagan and Wing (1995). (It also cannot explain the coupling observed when lifting heavy objects where large grip forces are observed (e.g., Johansson and Westling 1988)). Conversely, if the finger pads do move even with large grip forces, then the decoupling between grip and load force observed by Blakemore and colleagues demonstrates that finger pad motion does not lead to grip-load coupling.

Using a task similar to that one employed by Blakemore and colleagues (1998), Hermsdörfer and Blankenfeld (2008) observed that when the externally applied sinusoidal load force is suddenly and unexpectedly turned off (in catch trials), grip force continues to be modulated (in

the same way as in non-catch trials) for 100 ms. If the changes in grip force were due to mechanical interactions, this continued modulation would not be observed. Witney and colleagues (1999) examined the control of grip force in a bimanual task in which participants grasped the top and bottom of a virtual object with the left and right hand. Participants were instructed to pull up with the left and, at the same time, prevent the object from moving. This required the generation of equal and opposite load forces with the two hands as well as grip forces with both hands. On unexpected catch trials, the two objects could be "unlinked" so that no load force was delivered to the right hand when the participant pulled up with the left hand. In these catch trials, participants generated increases in grip force with the unloaded right hand that closely matched those produced in normal "linked" trials. This result indicates that the modulation of grip force (in both linked and unlinked trials) was not caused by mechanical coupling with load force.

Several studies have shown that grip force is modulated in anticipation of contact forces that occur when the hand-held object strikes another object (Johansson and Westling 1988b; Turrell et al. 1999; Delevoye-Turrell and Wing 2003). For example, when participants drop a ball into a cup held in a precision grip, they increase grip force shortly before the anticipated contact and grip force is scaled to the predicted contact force (Johansson and Westling 1988b). Obviously, these predictive changes in grip force are achieved by neural control mechanisms. Johansson and Westling (1988b) also examined reflex-mediated changes in grip force when the experimenter dropped the ball and the participant was unaware that the ball had been dropped. The sudden increase in load force due to contact resulted in very small mechanically induced changes in grip force that were orders of magnitude smaller than the subsequent reflex-induced increase in grip force observed when the mechanical effects of the perturbation are no longer present (see Johansson et al. 1992; Flanagan and Wing 1993; Cole and Abbs 1988 for similar results). In

other words, the load force at the fingertip did not result in significant mechanical changes in grip force.

We have shown that grip force is modulated in phase with changes in load force when participants grasp objects, such as a cup, by inserting their index finger and thumb inside and pushing outwards with the finger nails (Flanagan and Tresilian 1994). Thus, anticipatory coupling between grip force and load force is observed when the fingertip pads are not employed in gripping. Indeed, predictive coupling between normal and load forces is observed even when participants lift and move objects held between the teeth (unpublished observations from both the Johansson and Flanagan labs) or use the hand to push and pull on an object held between the teeth (Westberg et al. 2001; Figure 2). Figure 2 show results from an experiment in which participants held a bar between their teeth and hand and were instructed to either push the bar toward the mouth or pull it away from the mouth. As shown by the individual records shown in Figure 2B, these pushes and pulls created load forces acting at the teeth and participants modulated their bite force in anticipation of the load. Figure 2C shows averaged bite and load force traces for pushes. On average, bite force increased 44 ms ahead of load force and was therefore predictive. Clearly, motion of the finger pads cannot explain the anticipatory modulation of bite force with load force.

INSERT FIGURE 2 ABOUT HERE

Finally, Häger-Ross and colleagues (1996) examined the mechanical properties of the fingertips when subjected to load forces while gripping an object. These authors showed that grip force changes only slightly due to mechanics. Moreover, they found that grip force could increase or decrease depending on the direction of loading. Thus, fingertip mechanics simply cannot account for large grip force modulation observed during movement. All of the results de-

scribed above (as well as a number of other results that we have left out) clearly show that anticipatory grip force adjustments observed in manipulation tasks are based on predictive neural control mechanisms and cannot be explained by the mechanics of the fingertip pads. Indeed, these results rule out any mechanical explanation (e.g., based on finger tendons) for grip-load coupling.

Independent Object Representations in Action and Perception

When people lift a large object and a similar but smaller object of equal weight, they typically judge the smaller of the two objects to be substantially heavier. This size-weight illusion, first described well over 100 years ago (Charpentier 1981; Murray et al. 1999), is experienced by almost all healthy people (Davis and Roberts 1976; Ross 1969), 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 powerful when only visual cues about size are available, as when lifting viewed objects by strings, but is strongest when haptic cues about object size are available, as when the hand grasps the objects directly (Ellis and Lederman 1993).

Recently, we ruled out the hypothesis (Ross, 1969; Granit, 1972; Davis & Roberts, 1976) that the size-weight illusion arises from a mismatch between actual and expected sensory feedback related to lifting (Flanagan & Beltzner 2000). We asked participants to repeatedly lift a small cube and an equally weighed large cube, in alternation, for a total of 40 lifts (Figure 3A). As expected, when lifting the two cubes for the first time, participants generated erroneous predictions about object weight based on size. That is, they overestimated the fingertip forces required to lift the large object and underestimated the forces required to lift the small object. Fig-

ure 3B shows fingertip forces and force rates for the first lifts of the large and small cubes performed by a representative participant. During the first lift of the small cube, the initial rise in grip force and load force was too small and lift-off did not occur when expected. The resulting mismatch between expected and actual tactile feedback gave rise to a reflex-mediated increase in both grip and load force and lift-off then occurred. During the first lift of the large cube, overshoots of the grip and load forces were observed and lift-off occurs earlier than expected. In this case, the mismatch between expected and actual tactile feedback triggered a decrease in force output approximately 100 ms later.

Although participants were initially fooled by the misleading size cues, they adapted their force output to the true weights of the objects within 5-10 pairs of lifts. Figure 3C shows fingertip forces and force rates for the eighth lifts of the large and small cubes (lifts 15 and 16) performed by the same participant shown in Figure 3B. In these lifts, the force and force rate functions for the small and large cubes were very similar and lift-off occurred at about the same time for both cubes. Importantly, grip force and load force neither overshoot nor undershoot their final levels and no corrective adjustments in force were observed. Thus, the participant scaled their force output appropriately for the two cubes and also generated accurate sensory predictions about the timing of lift-off. This pattern of results, observed in all participants, indicates that the sensorimotor system acquired accurate representations of the weights of the two cubes (see also Westwood and Grandy 2006; Davidson and Wolpert 2004). Using two new groups of participants, we assessed the strength of the size-weight illusion after a single lift of each cube and after 20 lifts of each cube (Flanagan and Beltzner 2000). This involved asking participants to assign numbers corresponding to the weights of the two cubes after lifting them. We found that the strength of the illusion was as strong after 20 pairs of lifts as it was after the first lift.

Taken together, these results indicate that the brain maintains two independent representations of object weight: a perceptual representation that is influenced by the size of objects (as revealed by the size-weight illusion) and a sensorimotor representation that is not. The results indicate that the size-weight illusion does not arise from a mismatch between actual weight and the sensorimotor representation of weight. Instead, we suggest that the illusion stems from a mismatch between the actual weight of the object and the perceptual representation of object weight that continues to be influenced by object size even when the object is lifted a number of times and the sensorimotor representation of weight is updated (Flanagan and Beltzner 2000).

The finding that the brain maintains separate sensorimotor and perceptual representations for object weight can be related to the growing body of work demonstrating the sensory information is processed differently (and in different brain regions) depending on whether the information is used for the guidance of action or for perceptual tasks. For example, Goodale and his colleagues have provided evidence from behavioural, neuropsychological, and neuroimaging studies that visual information about object size, shape and orientation is processed in distinct neural pathways depending on whether the information is used to control grasping or make perceptual judgments about the objects (e.g., Goodale et al. 1991; Milner and Goodale 1995; Hu and Goodale 2000; Culham et al. 2003; Ganel and Goodale 2003).

We have suggested that the smaller of two equally weighted objects is judged to be heavier because it is heavier than would be expected based on size. Such expectations are based on the statistical relationship between size and weight learned through experience manipulating myriad objects. In addition to influencing perception, this statistical knowledge is extremely valuable in guiding our actions. Although motor commands based on such expectations will sometimes be inappropriate (as when lifting size-weight stimuli), they enable the motor system

to make good guesses most of the time. Our results (Flanagan and Beltzner 2000; Flanagan et al. 2001) show that when we encounter an object that is heavier or lighter than expected, the sensorimotor system can acquire a new (and long-lasting) representation of the object without affecting the perceptual representation. Presumably, the perceptual representation is unaffected because lifting one or two objects with abnormal density does not appreciably affect the learned correlation between size and weight. It is unclear what happens when the weight of a new object, but one that belongs to a given family or type of objects, closely matches the expected weight. In principle, if predictions based on the size and type of object are accurate, it would not be necessary to form a sensorimotor representation (or internal model) of that specific object. However, this question has not been investigated and more work needs to be done to understand the relationship between correlative knowledge about the properties of families of objects (e.g., how weight scales with size for a given object family) and knowledge about the properties of individual objects in the control of object manipulation tasks.

References

Aglioti S, DeSouza JFX, Goodale MA (1995) Size-contrast illusions deceive the eye but not the hand. Current Biology 5:679-685.

Blakemore SJ, Goodbody SJ, Wolpert DM (1998) Predicting the consequences of our own actions: The role of context sensorimotor context estimation. Journal of Neuroscience 18:7511-7518.

Birznieks I, Jenmalm P, Goodwin AW, Johansson RS (2001) Encoding of direction of fingertip forces by human tactile afferents. Journal of Neuroscience 21:8222-8237.

Culham JC, Danckert SL, DeSouza JF, Gati JS, Memon RS, Goodale MA (2003) Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. Experimental Brain Research 153:180-9.

Charpentier A (1891). Analyse experimentale quelques elements de la sensation de poids [Experimental study of some aspects of weight perception]. Archives de Physiologie Normales et Pathologiques 3:122-135.

Cole KJ, Abbs JH (1988) Grip force adjustments evoked by load force perturbations of a grasped object. Journal of Neurophysiology 60:1513-1522.

Cole KJ, Potash M, Peterson C (2006) 'Sensorimotor' memory affects the lift and grip forces differently in a simple grip and lift task. Society for Neuroscience Abstracts, Poster 655.1.

Cothros N, Wong JD, Gribble PL (2006) Are there distinct neural representations of object and limb dynamics? Experimental Brain Research 173:689-697.

Danion F (2004) How dependent are grip force and arm actions during holding an object? Experimental Brain Research 158:109-119.

Davidson PR, Wolpert DM (2004) Internal models underlying grasp can be additively combined. Experimental Brain Research 155:334-340.

Davis CM, Roberts W (1976). Lifting movements in the size-weight illusion. Perception & Psychophysics 20:33-36.

Delevoye-Turrell YN, Wing AM (2003) Efficiency of grip force adjustments for impulsive loading during imposed and actively produced collisions. Quarterly Journal of Experimental Psychology 56A:1113–1128.

Descoins M, Danion F, Bootsma RJ: Predictive control of grip force when moving object with an elastic load applied on the arm. Experimental Brain Research 172:331-342.

Ellis RR, Lederman SJ (1993) The role of haptic versus visual volume cues in the size-weight illusion. Perception & Psychophysics 53:315-324.

Flanagan JR, Beltzner MA (2000) Independence of perceptual and sensorimotor predictions in the size-weight illusion. Nature Neuroscience 3:737-741.

Flanagan JR, Bowman MC, Johansson RS (2006) Control strategies in object manipulation tasks Current Opinion in Neurobiology 16:650-659.

Flanagan JR, King S, Wolpert DM, Johansson RS (2001) Sensorimotor prediction and memory in object manipulation. Canadian Journal of Experimental Psychology 55:89-97.

Flanagan JR, Lolley S (2001) The inertial anisotropy of the arm is accurately predicted during movement planning. Journal of Neuroscience 21:1361-1369.

Flanagan JR, Tresilian J (1994) Grip-load force coupling: a general control strategy for transporting objects. Journal of Experimental Psychology: Human Perception and Performance 20:944-957.

Flanagan JR, Vetter P, Johansson RS, Wolpert DM (2003) Prediction precedes control in motor learning. Current Biology 13:146-150.

Flanagan JR, Wing AM (1993) Modulation of grip force with load force during point-to-point arm movements. Experimental Brain Research 95:131-143.

Flanagan JR, Wing AM (1995) The stability of precision grip forces during cyclic arm movements with a hand-held load. Experimental Brain Research 105:455-464.

Flanagan JR, Wing AM (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 17:1519-1528.

Flourney T (1894) De l'influence de la perception visuelle des corps sur leur poids apparrent [The influence of visual perception on the apparent weight of objects]. L'Année Psychologique 1:198-208.

Ganel T, Goodale MA (2003) Visual control of action but not perception requires analytical processing of object shape. Nature 426:664-7.

Goodale MA, Milner AD, Jakobson LS, Carey DP (1991). A neurological dissociation between perceiving objects and grasping them. Nature 349:154-156.

Goodwin AW, Jenmalm P, Johansson RS (1998) Control of grip force when tilting objects: effect of curvature of grasped surfaces and applied tangential torque. Journal of Neuroscience 18:10724-10734.

Gordon AM, Forssberg H, Johansson RS, Westling G (1991a) Visual size cues in the programming of manipulative forces during precision grip. Experimental Brain Research 83:477-482.

Gordon AM, Forssberg H, Johansson RS, Westling G (1991b) The integration of haptically acquired size information in the programming of precision grip. Experimental Brain Research 83:483-488.

Gordon AM, Forssberg H, Johansson RS, Westling G (1991c) Integration of sensory information during the programming of precision grip: Comments on the contributions of size cues. Experimental Brain Research 85:226-229.

Gordon AM, Westling G, Cole KJ, Johansson RS (1993) Memory representations underlying motor commands used during manipulation of common and novel objects. Journal of Neurophysiology 69:1789-1796.

Grandy MS, Westwood DA (2006) Opposite perceptual and sensorimotor responses to a size-weight illusion. Journal of Neurophysiology 95:3887-3892.

Granit R (1972) Constant errors in the execution and appreciation of movement. Brain 95:451-460.

Häger-Ross C, Cole KJ, Johansson RS. (1996) Grip force responses to unanticipated object loading: load direction reveals body- and gravity-referenced intrinsic task variables. 110: 142-150.

Hermsdörfer J, Blankenfeld H (2008) Grip force control of predictable external loads. Experimental Brain Research, DOI 10.1007/s00221-007-1195-6.

Hu Y, Goodale MA (2000) Grasping after a delay shifts size-scaling from absolute to relative metrics. Journal of Cognitive Neuroscience 12:856-68.

Jenmalm P, Dahlstedt S, Johansson RS (2000) Visual and tactile information about object-curvature control fingertip forces and grasp kinematics in human dexterous manipulation. Journal of Neurophysiology 84:2984-2997.

Jenmalm P, Goodwin AW, Johansson RS (1998) Control of grasp stability when humans lift objects with different surface curvatures. Journal of Neurophysiology 79:1643-1652.

Jenmalm P, Johansson RS (1997) Visual and somatosensory information about object shape control manipulative fingertip forces. Journal of Neuroscience 17:4486-4499.

Johansson RS, Backlin JL, Burstedt MK (1999) Control of grasp stability during pronation and supination movements. Experimental Brain Research 128:20-30.

Johansson RS, Birznieks I (2004) First spikes in ensembles of human tactile afferents code complex spatial fingertip events. Nature Neuroscience 7:170-177.

Johansson RS, Häger C, Riso R (1992) Somatosensory control of precision grip during unpredictable pulling forces. II: Changes in load force rate. Experimental Brain Research 89: 192-203.

Johansson RS, Westling G (1984) Roles of glabrous skin receptors and sensorimotor memory in automatic-control of precision grip when lifting rougher or more slippery objects. Experimental Brain Research 56:550-564.

Johansson RS, Westling G (1987) Signals in tactile afferents from the fingers eliciting adaptive motor-responses during precision grip. Experimental Brain Research 66:141-154.

Johansson RS, Westling G (1988a) Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. Experimental Brain Research 71:59-71.

Johansson RS, Westling G (1988b) Programmed and triggered actions to rapid load changes during precision grip. Experimental Brain Research 71:72-86.

Kawato M (1999) Internal models for motor control and trajectory planning. Current Opinion In Neurobiology 9:718-727.

Lackner JR, DiZio P (2005) Motor control and learning in altered dynamic environments. Current Opinions in Neurobiology 15:653-659.

Mah CD, Mussa-Ivaldi FA (2003) Generalization of object manipulation skills learned without limb motion. Journal of Neuroscience 23:4821-4825.

Malfait N, Shiller DM, Ostry DJ (2002) Transfer of motor learning across arm configurations. Journal of Neuroscience 22:9656-9660.

Merritt K, Flanagan JR (2004) Internal models of object dynamics in skilled manipulation. Poster presented at the Seventh Annual Meeting For Health Sciences Research Trainees, Queen's University, May 2004.

Milner AD, Goodale MA (1995) The visual brain in action. Oxford University Press, Oxford.

Mon-Williams M, Murray AH (2000) The size of the visual size cue used for programming manipulative forces during precision grip. Experimental Brain Research 135:405-410.

Murray DJ, Ellis RR, Bandomir CA, Ross HE (1999). Charpentier (1891) on the Size-weight Illusion. Perception & Psychophysics 61:1681-1685.

Nozaki D, Kurtzer I, Scott SH (2006) Limited transfer of learning between unimanual and bimanual skills within the same limb. Nature Neuroscience 9:1364-1366.

Nyssen R, Bourdon J (1955) Contribution to the study of the size-weight illusion by the method of P. Koseleff. Acta Psychologia 11:467-74.

Pick HL, Pick AD (1967) A developmental and analytic study of the size-weight illusion. Journal of Experimental Child Psychology 5:362-371.

Pilon J-F, De Serres SJ, Feldman AG (2007) Threshold position control of arm movement with anticipatory increase in grip force. Experimental Brain Research 181:49-67.

Quaney BM, Nudo RJ, Cole KJ (2005) Can internal models of objects be utilized for different prehension tasks? Journal of Neurophysiology 93:2021-2027.

Quaney BM, Rotella DL, Peterson C, Cole KJ (2003) Sensorimotor memory for fingertip forces: evidence for a task-independent motor memory. Journal of Neuroscience 23:1981-1986.

Robinson HB (1964) An experimental examination of the size-weight illusion in young children. Child Development 35:91-107.

Ross HE (1969) When is a weight not illusory? Quarterly Journal of Experimental Psychology 21:346-355.

Salimi I, Frazier W, Reilmann R, Gordon AM (2003) Selective use of visual information signaling objects' center of mass for anticipatory control of manipulative fingertip forces. Experimental Brain Research 150:9-18.

Shadmehr R, Moussavi ZMK (2000) Spatial generalization from learning dynamics of reaching movements. Journal of Neuroscience 20:7807–7815.

Shadmehr R, Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning of a motor task. Journal of Neuroscience 14:3208-3224.

Turrell YN, Li F-X, Wing AM (1999) Grip force dynamicss in the approach to a collision. Experimental Brain Research 128:86-91.

Wang J, Sainburg RL (2004) Interlimb transfer of novel inertial dynamics is asymmetrical. Experimental Brain Research 92:349-360.

Westberg K-G, Trulsson M, Johansson RS (2001) Oro-manual force coordination in humans. Poster presented at the Neural Control of Movement meeting, March 25-31, 2001, Seville, Spain.

Wing AM, Lederman SJ (1998) Anticipating load torques produced by voluntary movements. Journal of Experimental Psychology: Human Perception and Performance 24:1571-1581.

Witney A, Goodbody SJ, & Wolpert. DM (1999) Predictive motor learning of temporal delays. Journal of Neurophysiology 82:2039-2048.

Wolpert DM, Flanagan JR (2001) Motor prediction. Current Biology 11:R729-R732.

Wolpert DM, Ghahramani Z: Computational principles of movement neuroscience. Nat Neurosci 2000, 3 Suppl:1212-1217.

Figure captions

Figure 1. Generalization of sensorimotor memory when lifting to different heights. A: Participants grasped and lifted an object instrumented with sensors that measured the forces applied by the tips of the index fingertip and thumb. The object was attached to the tip of a robot manipulandum that could simulate different loads. The contact surfaces mounted on each force sensor could freely spin so that the object could effectively rotate about the grip axis. In addition, the joint between the object and manipulandum allowed rotation of the object about any axis orthogonal to the grip axis. B and C: Kinematic and force records when lifting an inertial (B) and a viscous load (C) load. The solid black curves are from the last of 20 lifts to the initial 7 cm target and the solid gray curves are from the next trial that was the first lift to the 14 cm target. The dashed black curves represent the second lift to the 14 cm target. The gray boxes represent the 200 ms time window in which participants were instructed to lift the object to the target.

Figure 2. Predictive coupling between bite force and load force. A. The participant held a bar with the teeth and fingertips at either end and was instructed to use the hand to push and pull the bar while preventing it from moving with the teeth. In each trial a target load force was displayed on a monitor. Forces normal and tangential to the contact surfaces were recorded using 6-axis force-torque transducers built into the bar. The load force was defined as the magnitude of the vector sum of tangential forces at the teeth. B. Examples of single trial forces when the bar was pushed and pulled by the hand. The dashed line shows the target load force. C. Averaged bite force (solid trace) and load force (dashed trace) records for pushes. On average, bite force increased 44 ms ahead of the load force. Adapted from Westberg et al. 2001.

Figure 3. Sensorimotor adaptation when lifting size-weight stimuli. A: In alternate trials, participants lifted either a large or a small cube by grasping a handle, mounted on top of the cube, with the tips of the index finger and thumb on either side. The handle could be moved quickly between cubes and was instrumented with two force-torque sensors with circular contact surfaces (3 cm in diameter) covered in sandpaper. B and C: Grip force, load force, grip and load force rates, and the reading from a light sensitive diode signaling lift-off recorded in the first two lifts (B) and lifts 15 and 16 (C) performed by a representative participant. This participant lifted the large object (thick traces) and then the small object (thin traces) in each pair of lifts. The trials are temporally aligned to the time at which load force started to increase. The vertical dashed lines mark lift-off times. In the eighth trial, the lift-off times for the large and small cubes were indistinguishable. Adapted from Flanagan and Beltzner 2001.

Figures

A

Inertial Load

Viscous Load

B
Move
Window

C
Move
Window

14 cm
target

Object
Height
(cm)

7 cm
target

5

5

Object
Velocity
(cm/s)

50

50

Grip
Force
(N)

2

2

Load
Force
(N)

2

2

200
Time (ms)

200

Flanagan, Merritt, Johansson
Figure 1

A

Bite force

Tangential force

Push ⟷ Pull

Elastic

Grip force

Load force

B

Load direction:
Push towards mouth

25N

Bite force

0N

4N

Grip force

0N

0N

Load force

-4N

1 sec

Load direction:
Pull from mouth

25N

Bite force

0N

4N

Grip force

0N

0N

Load force

-4N

1 sec

C

Bite force
8N

Bite force

Load force

Load force
1N

0   0.5   1

Time, sec

Flanagan, Merritt, Johansson
Figure 2

A

5.2 cm

10.9 cm

B   Lifts 1 and 2   C   Lifts 15 and 16

Grip
Force
(N)   5

Load
Force
(N)   3

Grip
Force
Rate   20
(N/s)

Load
Force
Rate   10
(N/s)

Light
indicating   1
Lift-off
(volts)

500
Time (ms)

Large Object
Small Object

Flanagan, Merritt, Johansson
Figure 3