Hand Movements

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GLOSSARY

grasp stability control The control of grip forces such that they are adequate to prevent accidental slips but not so large as to cause unnecessary fatigue or damage to the object or hand.

haptic perception Perception through the hand based on tactile and somatosensory information.

internal models Neural circuits that mimic the behavior of the motor system and environment and capture the mapping between motor outputs and sensory inputs.

precision grip The grip formed when grasping an object with the distal tips of digits. Usually refers to grasping with the tips of the thumb and index finger on either side of an object.

sensorimotor control The use of both predicted and unexpected sensory information in the control of action.

The human hand and the brain are close partners in two important and closely interconnected functions: exploration of the physical world and reshaping of parts of this world through manipulation. The highly versatile functions of the human hand depend on both its anatomical structure and the neural machinery that supports the hand. This article focuses on the sensorimotor control of hand movements in object manipulation–a hallmark of skilled manual action. The article also examines relationships between the two main functions of the hand–object perception and object manipulation.

I. THE ACTING AND PERCEIVING HAND

Many of our cultural and technological achievements that mark us as human depend on skilled use of the hand. We use of our hands to gesture and communicate, make and use tools, write, paint, play music, and make love. Thus, the human hand is a powerful tool through which the human brain interacts with the world. We use our hands both to perceive the world within our reach (haptic perception) and to act on this world. These two functions of the hand, which are largely accomplished by touching and manipulating objects in our environment, are intimately related in terms of sensorimotor control. Haptic perception requires specific hand movements that are tailored to the kinds of information the perceiver wishes to extract. For example, to obtain information about the texture of an object, people rub their fingertips across the object's surface, and to obtain information about shape they trace the contour of the object with their fingertips. Conversely, in object manipulation sensory and perceptual information is critical for precise motor control of the hands. The fact that individuals with numbed digits have great difficulty handling small objects even with full vision illustrates the importance of somatosensory information from the fingertips.

To control both the exploratory and manipulatory functions of the hand, the brain must obtain accurate descriptions of various mechanical events that take place when objects are brought into contact with the hand. Mechanoreceptive (tactile) sensors in the glabrous skin of the volar aspect of the hand play an essential role in providing such information. The density of mechanoreceptors increases in the distal direction of the hand and is exquisitely high in the fingertips. As a perceptual organ, the hand has several advantages over the eyes. The hand can effectively "see around corners," allowing us to explore all sides of an object, and it can directly appreciate object properties such as weight, compliance, and slipperiness.

The numerous skeletal and muscular degrees of freedom of the hand, orchestrated by highly developed neural control systems, provide for tremendous dexterity that allows for both delicate exploration and versatile manipulation of objects. With approximately 30 dedicated muscles and approximately the same number of kinematic degrees of freedom, the hand can take on all variety of shapes and functions, serving as a hammer one moment and a powerful vice or a delicate pair of tweezers the next. The utility of hand movements is further enhanced by our ability to amplify the functions of the hand by using tools.

Different primates have very different hand movement capacities, with humans demonstrating the greatest dexterity. For example, true opposition between the thumb and index finger is only observed in humans, the great apes, and Old World monkeys. New World monkeys can manage pseudo-opposition, but prosimians are only capable of crude grasping. It seems improbable that the tremendous dexterity of the human hand can be explained solely by differences in anatomical factors given that the structural anatomy of the hands of different primates seems similar. This is not to say, however, that anatomical differences do not contribute. For example, the human thumb is much longer, relative to the index finger, than the chimpanzee thumb. This allows humans to grasp small objects precisely between the distal pads of the thumb. Similarly, the greater independence of finger movements in humans compared to monkeys arises, in part, from differences in the passive biomechanical connections among tendons. Humans have more individuated muscles and tendons with which to control the digits.

In addition to structural factors, a major contributor to differences in hand movement capacity among primates, and between primates and lower mammals, is the neural machinery underlying hand movement. Compared to lower mammals, primates have evolved extensive cerebral cortical systems for controlling the hand and the corticospinal pathways have taken on an increasingly dominant role in controlling movement. Moreover, in primates the corticospinal tracts include direct connections between neurons in cortical motor areas and spinal motorneurons. Through these corticomotoneuronal connections, the cerebral cortex possesses monosynaptic control over motorneurons whose axons connect, in particular, with the hand muscles. In effect, these direct connections have moved the hand "closer" to the cerebral cortex. Furthermore, through cortical motor areas the corticospinal tracts provide rapid access to the hand from most other cortical areas and from subcortical structures, including the cerebellum and the basal ganglia, tightly involved in motor control.

The development of cortical systems for controlling the hand in primates parallels the evolution of the arm from a prop for balance and locomotion (in four-legged mammals) to a free and dexterous tool for sensing and acting on objects in the environment. The denser neuronal substrate for hand control provides more flexibility in the patterning of muscle activation and supports the ability to perform independent finger movements. Interestingly, across primates, there is a linkage between the number of corticomotoneuronal connections and manual dexterity in terms of performing tasks that require independent finger movements. Although there are many advantages in terms of control, the reliance on cortical control comes at a cost. Lesions to the motor cortex or corticospinal pathways due, for example, to cerebral vascular accident can be particularly devastating in humans.

The importance of the cortical involvement in fine fingertip control can be further appreciated by considering parallels between the ontogenetic development of central neural pathways and that of hand function. The efficacy of the corticomotoneuronal system can be probed using transcranial magnetic stimulation (TMS) of the brain. TMS applied over the hand area of the motor cortex activates muscles of the contralateral hand. During development the latency of this activation, and the stimulation strength required to elicit a response, decreases as the corticomotoneuronal connections are established. The conduction delays in these motor pathways, as well as in the somatosensory pathways conveying signals from the sensors of the hand, rapidly decrease during the first 2 years after birth and thereafter remain constant at adult values. Responses within the adult latency range appear during the age range in which young children demonstrate important improvements in their ability to grasp objects using the tips of the index finger and thumb. Similar parallels between hand function and corticomoto neurone (CM) system development have been demonstrated in monkeys using various electrophysiological and anatomical techniques.

II. SENSORIMOTOR CONTROL OF HAND MOVEMENTS IN OBJECT MANIPULATION

To understand and appreciate how the brain controls movements of the hand, it is best to study the natural behavior of the hand in everyday manipulatory tasks. During the past 20 years, the sensorimotor control of the hand in precision manipulation task has been investigated in great detail. In this section, we review what has been learned about the sensorimotor control of natural hand movements when grasping and manipulating objects with the fingertips.

The remarkable manipulative skills of the human hand are the result of neither rapid sensorimotor processes nor fast or powerful effector mechanisms. Rather, the secret lies in the way manual tasks are organized and controlled by the nervous system. Successful manipulation requires the selection of motor commands tailored to the manipulative intent, the task at hand, and the relevant physical properties of the manipulated object. For instance, most tasks require that we stabilize the object within our grasp as we move the object or use it as a tool. To prevent slips and accidental loss of the object we must apply adequately large forces normal to the grip surfaces (*grip forces*) in relation to destabilizing forces tangential to the grip surfaces (*load forces*) (Fig. 1). At the same time, excessive grip forces must be avoided because they cause unnecessary fatigue and may crush fragile objects or injure the hand. Hence, the term grasp stability entails prevention of accidental slips as well as excessive fingertip forces.

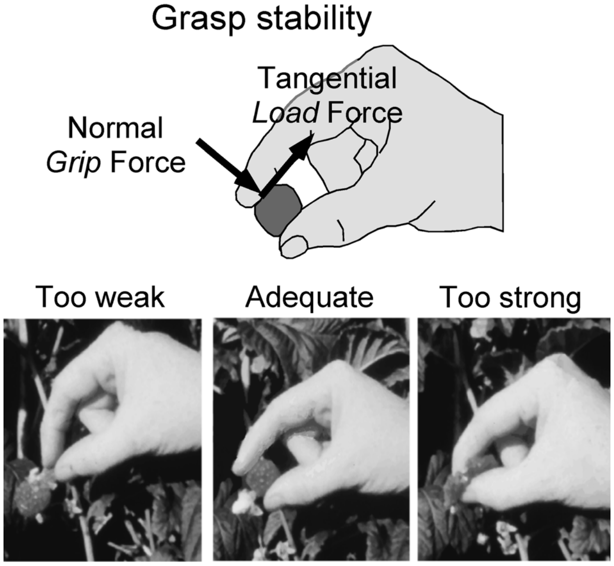

Figure 1 When manipulating objects grasped with a precision grip, we must carefully control the balance between grip force, normal to the contact surfaces, and load force tangential to the grasp surfaces. If grip force is too weak for a given load force, we risk having the object slip from our grasp. If grip force is too strong, we may crush the object or damage our hand and we waste energy.

When grasping and manipulating objects, the forces needed to ensure grasp stability depend on the physical properties of the object. Object properties such as weight, slipperiness, shape, and weight distribution all impose constraints on the fingertip forces (including their magnitudes, directions, and points of application) required for stability. Thus, a basic question for understanding the control in manipulation is how do people adapt their fingertip forces to the constraints imposed by various object properties. Although visual information about object properties may be helpful in terms of force selection, ultimately people adapt to such constraints by using sensory information provided by digital mechanoreceptors. Individuals with impaired digital sensibility have great difficulty performing manipulation tasks even under visual guidance. For instance, they often drop objects, may easily crush fragile objects, and have difficulties in dressing themselves because they cannot complete such apparently simple tasks as buttoning a shirt. Thus, it is clear that critical sensorimotor control processes required for manipulation are lost with impaired digital tactile sensibility.

The control of grip and load forces in object manipulation involves subtle interplay between two types of control: reactive control based on sensory feedback and predictive or feedforward control. These two control mechanisms are closely linked. On the one hand, reactive control mechanisms are invoked when errors arise between actual sensory feedback and the expected sensory feedback predicted from feedforward mechanisms. On the other hand, errors in sensory prediction are not only used for feedback control but also used to update feedforward mechanisms to reduce future prediction errors. In the following sections, we consider these two control processes in detail.

A. Feedback Control based on Digital Sensors

One way to use digital sensors to adjust the force output would be to engage these sensors in feedback loops. However, such loops imply large time delays. These time delays arise from impulse conduction time in peripheral nerves, conduction and processing time in the central nervous system, and the inherent sluggishness of muscles. In humans, these factors sum to at least 100 msec for the generation of a significant force response. Consequently, closed-loop feedback is not effective for rapid movement involving frequencies above 1 Hz. In natural manipulation tasks, movement frequency components up to 5 Hz can be observed. Thus, feedback control alone cannot support control of grip force for grasp stability in these movements.

Despite these control limitations, feedback control is essential in certain types of manipulative tasks. For example, feedback control is required in reactive tasks in which we restrain "active" objects that generate unpredictable load forces tangential to the grip surfaces. Examples of tasks in which we must deal with active objects are holding a dog's leash, restraining a child by holding his or her arm, or operating power tools. Consider the situation depicted in Fig. 2A

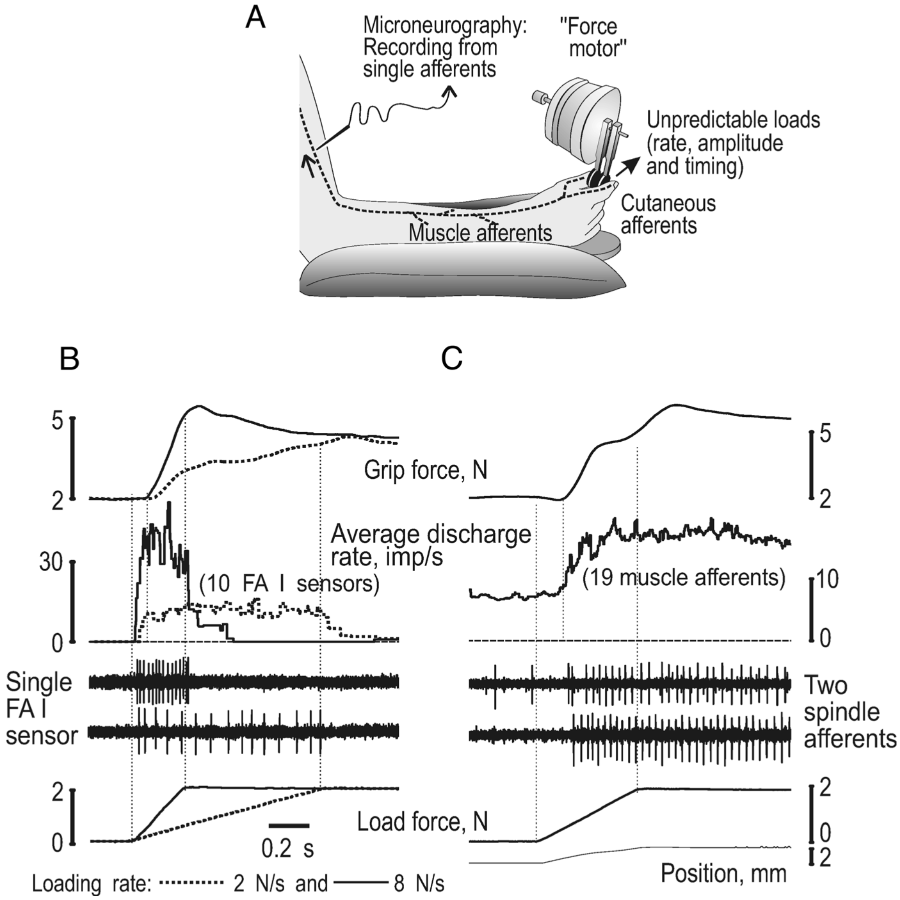

Figure 2 Peripheral afferent and reactive grip force responses to unpredictable loading of the precision grip by a pulling force. (A) The subject grasped the manipulandum with the tips of the thumb and index finger contacting parallel grip surfaces 25 mm apart. The force motor could deliver load forces pulled away from or pushed toward the hand. The grip and load forces, normal and tangential to the grip surfaces, respectively, and the position of the manipulandum were recorded. Afferent activity was recorded from the median nerve, with percutaneously inserted tungsten needle electrodes impaling the nerve about 10 cm proximal to the elbow. (B) Grip responses and average discharge rate of 10 FA I sensors to 2 N pulling loads delivered to the receptor-bearing digit at 2 N/sec (dashed lines) and 8 N/sec (solid lines). The two traces of single unit recordings are examples of responses in a single FA I sensor during load trials at 8 N/sec (upper trace) and 2 N/sec (lower trace). (C) Grip response and average discharge rate of 19 muscle afferents located in the long flexor muscles of the index, middle, or ring finger to 2.0 N pulling loads delivered at 4 N/sec. The single unit recordings are examples of responses in two different muscle spindle afferents. (B and C) The averages of forces and discharge rates are synchronized to the onset of the loading ramp; discharge rate represents average instantaneous frequency (adapted with permission from Macefield, V. G., Häger-Ross, C., and Johansson, R. S., *Exp. Brain Res.* **108,** 155–171, 1996; and Macefield, V. G., and Johansson, R. S., *Exp. Brain Res.* **108,** 172–184, 1996. Copyright © 1996 by Springer-Verlag).

in which an individual grasps an object attached to a force motor using a precision grip with the tips of the thumb and index finger on opposing vertical surfaces. The motor is used to generate increasing load forces (tangential to the grip surfaces) that are unpredictable in terms of onset time, amplitude, and direction (loading and unloading). To prevent the object from slipping, people automatically respond to increases in tangential load by increasing grip force normal to the grip surfaces in parallel with the load force changes (see load and grip force signals in Figs. 2B and 2C). When the load stops increasing, the grip force also stops increasing and may decrease slightly. Importantly, the changes in grip force lag behind the load force changes because they are reactively generated. A reactive grip response is initiated after a delay of approximately 100 msec but this varies with the load force rate. Because of this time lag, the object will slip from grasp unless the background grip force prior to a load increase is strong enough to meet the initial load increase. Indeed, following slips and trials with a high rate of load force increases, people learn to increase the initial background grip force as an adaptation to the expected range of loadings.

Figure 2A also shows signals, recorded using the technique of microneurography, from single nerve fibers of the median nerve that supply cutaneous, muscle, and joint sensors. Experiments with cutaneous anesthesia have demonstrated that reactive fingertip force responses are driven primarily by digital cutaneous inputs. Signals from fast adapting (FA I) cutaneous afferents seem most important, but slowly adapting cutaneous afferents may also contribute. As illustrated in Fig. 2B, the intensity of the cutaneous afferent responses is scaled by the rate of load force increase, and the afferent responses commence before the onset of the grip response. Furthermore, the size and duration of the grip force increase is scaled with the intensity and duration of the afferent response. This scaling is an attractive feature for feedback-based control.

Whereas cutaneous afferents contribute to the initiation and initial scaling of grip force responses, afferents from intrinsic and extrinsic hand muscles and interphalangeal joints do not respond to load increases early enough to allow them to contribute to the initiation of these grip responses. The muscle afferents respond reliably after the onset of the reactive grip force response and their discharge rates are related to changes in force output and, hence, to muscle activity (Fig. 2C). Thus, these muscle afferents are primarily concerned with events in the muscle itself rather than functioning as exteroceptors sensing mechanical events at the fingertips.

B. Feedforward Control Processes

Almost everyone will recall having fallen victim to an older sibling, cousin, or friend who passed us an empty box while pretending it was very heavy. When we took the box, our arms flailed upwards. This trick demonstrates that when we interact with objects, we anticipate the forces required to complete the task. Although it may occasionally result in large movement errors, anticipatory or feedforward control is essential for skilled object manipulation. Feedback control is important when our predictions are erroneous or, as in reactive tasks, when predictions are unavailable. However, because of the long time delays, feedback control cannot support the swift and skilled coordination of fingertip forces observed in most manipulation tasks that involve ordinary "passive" objects. Instead, the brain relies on feedforward control mechanisms that take advantage of the stable and predictable physical properties of these objects. These mechanisms parametrically adapt force motor commands to the relevant physical properties of the target object.

Figure 3 illustrates parametric anticipatory adjustments of motor output to object weight, friction between the object and skin, and shape of the contact surface. The task is to lift a test object from a support surface, hold it in air for a couple of seconds, and then replace it. To accomplish this task, the vertical load force increases until liftoff occurs, stays constant during the hold phase, and then starts to decrease when the object contacts the support surface during replacement. When lifting objects of different weight (Fig. 3A), people scale the rate of increase of both grip force and load force to object weight such that lighter and heavier objects tend to be lifted in about the same amount of time. The scaling occurs prior to liftoff–before sensory information about object weight becomes available–and is therefore predictive. To deal with changes in friction, the motor system adjusts the balance between grip force and load force. As shown in Fig. 3B, when lifting equally weighted objects of varying slipperiness, people scale the rate of increase of grip force while keeping the rate of change of load force constant. Thus, the ratio of these force rates is a controlled parameter that is set to the current frictional conditions. A similar scaling of the grip-to-load force ratio is observed when object shape is varied. A larger

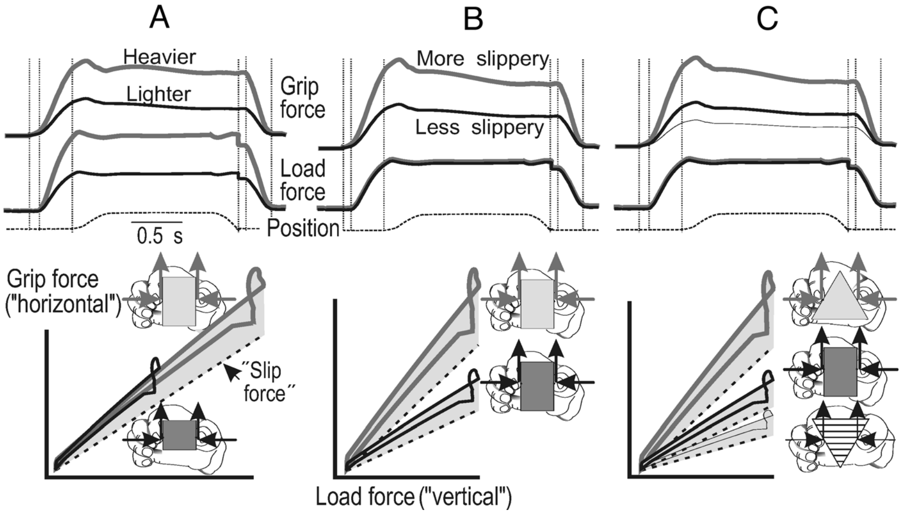

Figure 3 Feedforward adjustments of motor output to object weight (A), frictional conditions (B), and object shape (C) in a task in which a test object is lifted with a precision grip, held in air, and then replaced. The top graphs show horizontal grip force, vertical load force, and the vertical position of the object as a function of time for two superimposed trials. The bottom graphs show the relation between load force and grip force for the same trials. The dashed line indicates the minimum grip-to-load force ratio required to prevent slip. The gray area represents the safety margin against slip. After contact with the object (left most vertical line, top), grip force increases by a short period while the grip is established. A command is then released for simultaneous increases in grip and load force (second vertical line). This increase continues until the load force overcomes the force of gravity and the object lifts off (third vertical line). After replacement of the object and table contact occurs (fourth line), there is a short delay before the two forces decline in parallel (fifth line) until the object is released (sixth line). (adapted with permission from Johansson, R. S., and Westling, G., *Exp. Brain Res.* **56,** 550–564, 1984 by Springer-Verlag; Johansson, R. S., and Westling, G., *Exp. Brain Res.* **71,** 59–71, 1988. Copyright © 1988 by Springer-Verlag; and Jenmalm, P., and Johansson, R. S., *J. Neurosci.* **17,** 4486–4499, 1997 Copyright © 1997 by the Society for Neuroscience).

ratio is used when the grip surfaces are tapered upward compared to downward (Fig. 3C).

In each example shown in Fig. 3, grip force increases and decreases in phase with (and thus predicts) changes in vertical load force. This parallel coordination of grip force and load force ensures grasp stability. The grip force at any given load force is controlled such that it exceeds the corresponding minimum grip force, required to prevent slip, by a small safety margin (gray areas in the bottom of Fig. 3). This minimum grip force depends on the weight of the object, the friction between the object and skin, and the shape (e.g., angle) of the contact surfaces.

This parallel coordination of grip force and load force is a general feedforward control strategy and is not specific to any particular task or grip configuration. Parallel force coordination is observed when grasping with two or more digits of the same hand or both hands, when grasping with the palms of both hands, and even when gripping objects with the teeth. Moreover, it does not matter whether the object is moved by the arm or, for example, by the legs as when jumping with the object in hand. Importantly, the parallel coordination of grip and anticipatory load force is not restricted to common inertial loads. People also adjust grip force in parallel with load force when pushing or pulling against immovable objects and when moving objects subjected to elastic and viscous loads. Fig. 4 illustrates parallel coordination of grip and load forces under varying load conditions. People alternately pushed and pulled an object instrumented for force sensors and attached to a simple robot that could simulate various types of opposing loads acting tangential to the grasp surfaces (Fig. 4A). Figures 4B and 4C show kinematic and force records obtained under three different load conditions: an acceleration-dependent inertial load, a velocity-dependent viscous load, and an elastic load that largely depended on position but also contained viscous and inertial components. In all three cases, the grip force normal to the grasp surfaces changes in parallel with the magnitude of the load force tangential to the grasp surface. Importantly, the relationship between arm movement motor commands and the load experienced at the fingertips depends on the type of load being moved. Thus, to adjust grip force in parallel with load

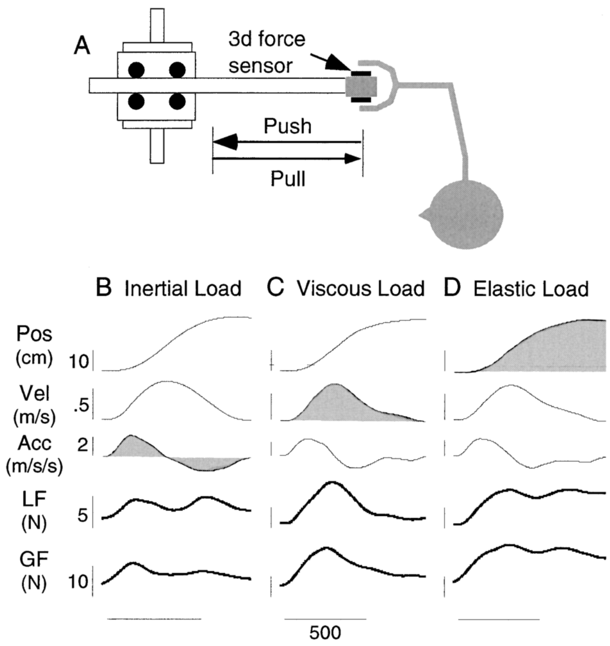

Figure 4 Kinematic and force records from one subject under the three load conditions. Shaded regions indicate the primary kinematic variable on which load depended. Under all three load conditions, grip force (GF) is adjusted in parallel with fluctuations in load force (LF), with the resultant load tangential to the grasp surface. The dashed vertical lines indicate movement onset (modified with permission from Flanagan, J. R., and Wing, A. M., *J. Neurosci.* **17,** 1519–1528, 1997. Copyright © 1997 by the Society for Neuroscience).

force under the different load conditions, people had to alter the mapping between the motor command driving arm movement and that driving the grip force.

In most everyday tasks, destabilizing loads acting on the grasp include not only linear load forces but also torques tangential to the grasped surfaces. Such torsional loads occur whenever we tilt an object around a grip axis that does not intersect the vertical line through the object's center of mass. In addition, torque loads arise in many natural manipulatory tasks due to changes in the orientation of the grip axis with respect to gravity. For example, this occurs when we hold a book flat by gripping it between the fingers beneath and the thumb above (vertical grip axis) and then rotate it by a pronation movement to put it in a bookshelf (horizontal grip axis). Because we rarely take a book such that the grip axis passes through its center of mass, a torque will develop in relation to the grasp. Importantly, the sensorimotor programs for object manipulation account for torsional loads by predicting the consequences of object rotation both when we rotate objects around the grip axis and when we rotate the grip axis in the field of gravity. Rotational slips are prevented by automatic increases in grip force that parallel increases in tangential torque. The sensorimotor programs thus model the effect of the total load in terms of linear forces, tangential torques, and their combination.

C. Internal Models underlying Predictive Force Control

As illustrated in Fig. 3A, with objects of different weight, people use different rates of force increase prior to liftoff. Since there is no sensory information available about object weight until liftoff, this behavior indicates that people predict the final force requirements. Likewise, with objects of different friction (Fig. 3B) and shape (Fig. 3C), the force output is tailored to the properties of the object from the start of the initial force attack, well before sensory information from the digits obtained after contact with the object could have exerted any influence. Thus, in all three cases, the motor controller operates in a feedforward fashion and uses motor command parameters determined by internal models that capture the physical properties of the object. Figure 4 further illustrates that such internal models also capture dynamic properties of objects. The question arises as to how such models are selected and updated for different objects and after changes in object properties.

1. Prediction based on Object Shape

Figures 5A and 5B show three consecutive trials taken from a series of lifts in which the angle of the grasped surfaces was changed between trials in a pseudorandom order. The sequence is 30°, −30°, and −30° and thus includes a transition from an upward tapered object (30°) to a downward tapered object (−30°). In the trials preceding this sequence, a 30° object was lifted. First consider the trials in which vision of the objects is available (Fig. 5A). When the shape of the object is changed, the grip force is adjusted from the very start of the lift in anticipation of the lower grip force required to lift the object. In particular, grip force is now increased more slowly before sensory feedback from the digits could have influenced the motor output. The predictive adjustment in grip force observed in the first trial after the switch in object shape is very accurate. Indeed, no further adjustment is

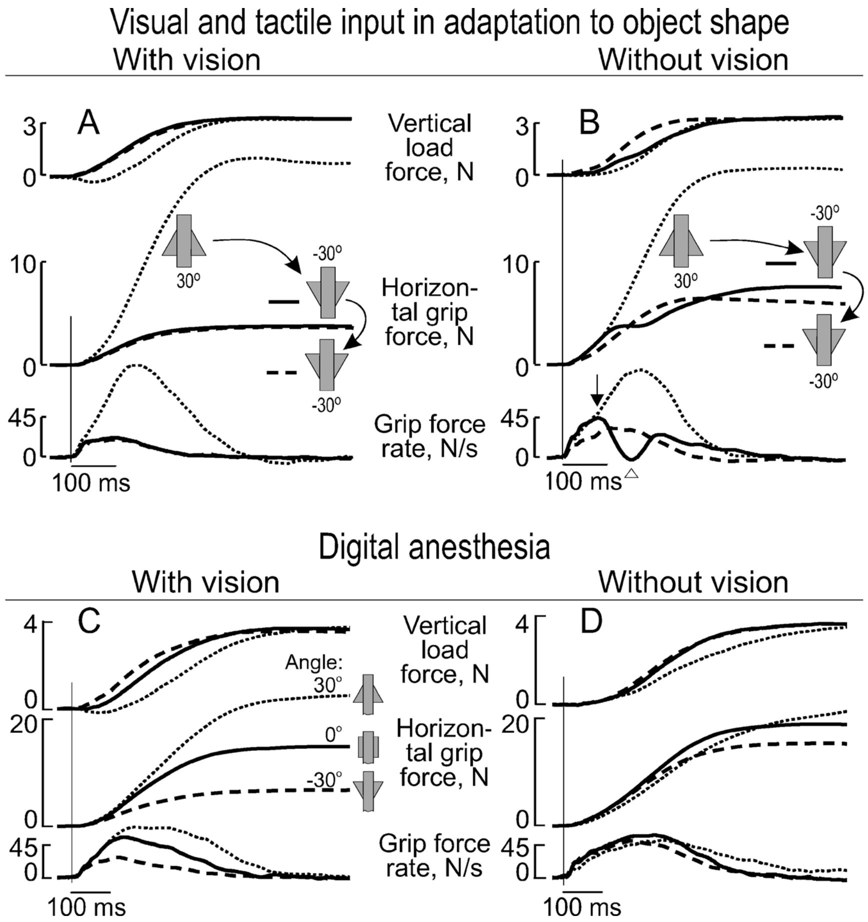

Figure 5 (A and B) Force adjustments to changes in surface angle during lift series in which surface angle was unpredictably varied between lift trials. Vertical load force, horizontal grip force, and grip force rate shown as a function of time for trials with (A) and without (B) vision and with normal digital sensibility. The dotted curves are from the last trial before the switch with the 30° object. The solid curves show the next trial with the −30° object. These curves illustrate adjustments to the smaller angle. The dashed lines show the following trial again with the −30° object. The downward arrow in B indicates the point in time when the new surface angle was expressed in terms of motor output. (C and D) Adaptation to surface shape during digital anesthesia with (C) and without (D) vision. Vertical load force, horizontal grip force, and grip force rate as a function of time for trials with 30° (dotted lines) 0° (solid lines and −30°, (dashed lines) surface angle (modified with permission from Jenmalm, P., and Johansson, R. S., *J. Neurosci.* **17,** 4486–4499, 1997. Copyright © 1997 by the Society of Neuroscience).

observed on the second trial after the change when information about shape has been obtained through tactile sensory signals. These results demonstrate that visual geometric cues can be used to efficiently specify the force coordination for object shape in a feedforward manner. These cues are used to parametrically adapt the finger force coordination to object shape in anticipation of the upcoming force requirements.

When vision of the object is not available, a very different pattern of force output is obtained. On the first trial after the switch to the −30° object, grip force develops initially according to the force requirements in the previous trial. This indicates that memory of the previous surface angle determines the default force coordination in a feedforward manner. However, about 100 msec after the digits contacted the object, the grip force was modified and tuned appropriately for the actual surface angle (see first trial with the −30° in Fig. 5B). This amount of time is required to translate tactile information into motor commands, a process that likely involves supraspinal processing. By the second trial after the switch, the force output is appropriately adapted to the −30° surface angle from the onset of force application. Thus, an internal model related to object shape determines the force coordination in a feedforward fashion and tactile sensory information obtained at initial contact with the object mediates an updating of this model to changes in object shape. Furthermore, a single trial is enough to update the relevant internal model.

Sensors in the digits are thus used to update the force coordination for object shape when visual cues are unavailable or misleading. When digital sensibility is removed by local anesthesia, leaving neither visual nor somatosensory cues about shape, the adaptation in force output is severely impaired (Fig. 5D). Although grip force and load force still change in parallel, force output is no longer updated following contact. People adapt to the loss of both visual and tactile sensory cues about shape by applying strong grip forces regardless of surface angle. When vision is available during digital anesthesia, people are able to adapt their forces to object shape with only minor impairments (Fig. 5C). Thus, visual geometric cues can be used effectively for feedforward control even in the absence of somatosensory cues about shape.

The curvature of the grasp surfaces is another aspect of object shape. Surprisingly, the curvature of spherically curved symmetrical grasp surfaces has little effect on grip force requirements for grasp stability under linear force loads. However, it becomes acute in tasks involving torsional loads. The relationship between the grip force and tangential torque is parametrically scaled by surface curvature: For a given torque load, people increase grip force when curvature increases. As with linear force loads, this scaling of grip force is directly related to the minimum grip force required to prevent slip. Under torsional loads, people maintain a small but adequate safety margin against rotational slip. As with surface angle, visual information about surface curvature can be used for feedforward control of force. Likewise, people use cues provided by tactile afferents to adapt force once finger contact is established.

2. Prediction based on Object Weight

When we manipulate familiar or common objects that we can identify either visually or haptically, we are extremely adept at selecting fingertip forces that are appropriately scaled to the weight of the object. That is, during the very first lift of a common object, before sensory information related to weight becomes available at liftoff, the force development is tailored to the weight of the object. This indicates that we can use visual and haptic cues to select internal models that we have acquired for familiar objects and can use these models to parametrically adjust our force output to object weight. For "families" of familiar objects that vary in size (e.g., screwdrivers, cups, soda cans, and loafs of bread), we can exploit size–weight associations, in addition to object identity, to scale our force output in a feedforward fashion. However, as we have all experienced, our force output may sometimes be erroneous. Such situations can be created experimentally by unexpectedly changing the weight of a repeatedly lifted object without changing its visual appearance. In such cases, the lifting movement may be either jerky or slow. For example, if the object is lighter than expected from previous lifting trials, the load force and grip force drives will be too strong when the load force overcomes the force of gravity and liftoff takes place. Although somatosensory afferent events, evoked by the unexpectedly early liftoff, trigger an abrupt termination of the force drive, this occurs too late (due to control loop delays) to avoid an excessively high lift. Burst responses in FA II (Pacinian) afferents, which show an exquisite sensitivity to mechanical transients, most quickly and reliably signal the moment of liftoff. Conversely, if the object is heavier than expected, people will initially increase load force to a level that is not sufficient to produce liftoff and no sensory event will be evoked to confirm liftoff (Fig. 6A, solid curves). Importantly, this *absence* of a sensory event at the expected liftoff causes the release of a new set of motor commands. These generate a slow, discontinuous force increase until terminated by a neural event at the true liftoff (Fig. 6A, afferent response during the 800-g lift following the 400-g lift). Taken together, these observations indicate that control actions are taken as soon there is a mismatch between an expected sensory event and the actual sensory input. Thus, the absence of an expected sensory event may be as efficient as the occurrence of an unexpected sensory event in triggering compensatory motor commands. Moreover, this mismatch theory implies that somatosensory signals that represent the moment of liftoff are mandatory for the control of the force output whether or not the weight of the object is correctly anticipated. Finally, once an error occurs, the internal model of the object is updated to capture the new weight. In natural situations, this generally occurs in a single trial. As shown in Fig. 6A, in the trial after the switch trials when the weight of the object was unexpectedly increased from 400 to 800 g, the forces were correctly scaled for the greater weight (dashed curves)

3. Prediction based on Friction

Whereas people use visual information about object size and shape to scale fingertip forces, there is no

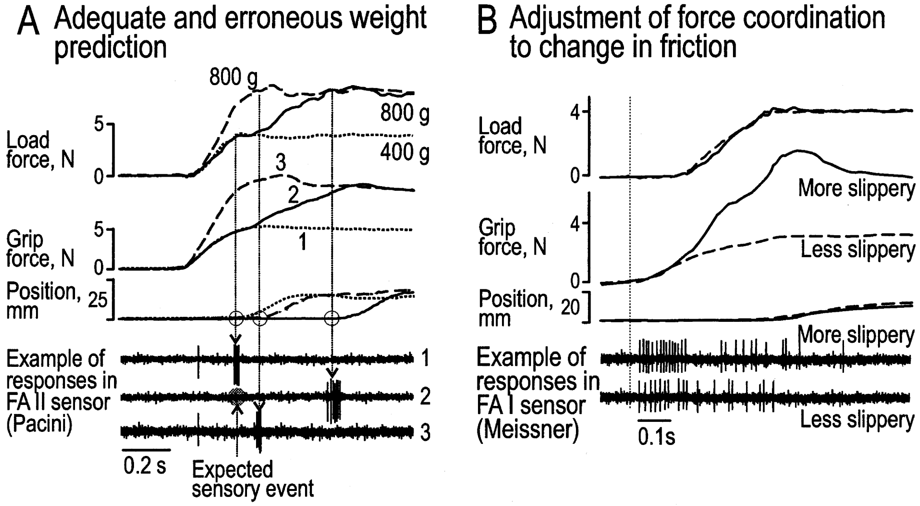

Figure 6 Single unit tactile afferent responses and adjustments in force to changes to object weight (A) and to the frictional condition between the object and the digits (B). Data are from single lift trials (A) Three successive trials in which the subject lifted a 400-g object. (dotted curves), an 800-g object (solid curves), and then the 800-g object again (dashed curves). The forces exerted in the first lift are adequately programmed because the subject had previously lifted the 400-g object. The forces are erroneously programmed in first lift of the 800-g object because they are tailored for the lighter 400-g object lifted in the previous trial. The vertical lines with arrowheads pointing downward indicate the moment of liftoff for each trial and they indicate the evoked sensory events exemplified by signals in a single FA II afferent. The absence of burst responses in FA II afferents at the expected point in time for the erroneously programmed 800-g trial is used to initiate a new control mode. This involves slow, discontinuous, and parallel increases in grip force and load force until terminated by sensory input signaling liftoff. (B) The influence of friction on force output and initial contact responses in a FA I unit. Two trials are superimposed, one with less slippery sandpaper (dashed lines) and a subsequent trial with more slippery silk (solid lines). The sandpaper trial was preceded by a trial with sandpaper and therefore the force coordination is initially set for the higher friction. The vertical line indicates initial touch (modified with permission from Johansson, R. S., and Westling, G., *Exp. Brain Res.* **66,** 141–154, 1987. Copyright © 1987 by Springer-Verlag; and from *Curr. Opin. Neurobiol.* Johansson, R. S., and Cole, K. J., **2,** 815–823, Copyright © 1992, with permission from Elsevier Science).

evidence that they use visual cues to control the balance of grip and load force for friction. However, tactile receptors in the fingertips are of crucial importance. The most important adjustment after a change in friction takes place shortly after the initial contact with the object and can be observed about 100 msec after contact (Fig. 6B). Prior to this force adjustment, there are burst responses in tactile afferents of different types but most reliably in the population of FA I (Meissner) afferents. The initial contact responses in subpopulations of excited FA I afferents are markedly influenced by the surface material as exemplified in Fig. 6B with a single afferent. The adjustment of force coordination to a change in frictional condition is based on the detection of a mismatch between the actual and an expected sensory event. This adjustment involves either an increase in the grip-to-load force ratio if the surface is more slippery than expected (as shown in Fig. 6B) or a decrease in the ratio of the surface if less slippery than expected. The adjustment also includes an updating of the internal model so as to capture the new frictional conditions between the object and the skin for predictive control of the grip-to-load force ratio in further interactions with the object. However, sometimes these initial adjustments to frictional changes are inadequate and an accidental slip occurs at a later point, often at one digit only. Burst responses in dynamically sensitive tactile afferents to such slip events promptly trigger an automatic upgrading of the grip-to-load force ratio to a higher maintained level. This restores the grip force safety margin during subsequent manipulation by updating the internal model controlling the balance between grip and load force.

In summary, skilled manipulation involves two major types of control processes: *anticipatory parameter control* and *discrete event, sensory-driven control.* Anticipatory parameter control refers to the use of visual and somatosensory inputs, in conjunction with internal models, to tailor finger tip forces for the properties of the object to be manipulated prior to the execution of the motor commands. For familiar objects, visual and haptic information can be used to identify and select the appropriate internal model that is used to parametrically adapt motor commands, prior to their execution, in anticipation of the upcoming force requirements. People may also use geometric information (e.g., size and shape) for anticipatory control, relying on internal forward models capturing relationships between geometry and force requirements. There is ample evidence that the motor system makes use of internal models of limb mechanics, environmental objects, and task properties to adapt motor commands.

Discrete event, sensory-driven control refers to the use of somatosensory information to acquire, maintain, and update internal models related to object properties. This type of control is based on the comparison of actual somatosensory inflow and the predicted somatosensory inflow—an internal sensory signal referred to as corollary discharge. (The somatosensory input provided by tactile signals in the digital nerves is obviously critical in the control of skillful manipulation.) Thus, when we lift an object, we generate both efferent motor commands to accomplish the task and this internal sensory signal. Together, these are referred to as the sensorimotor program. Predicted sensory outcomes are produced by an internal forward model in conjunction with a copy of the motor command (referred to as an efference copy). Disturbances in task execution due to erroneous parameter specification of the sensorimotor program give rise to a mismatch between predicted and actual sensory input. For example, discrete somatosensory events may occur when not expected or may not occur when they are expected (Fig. 6A). Detection of such a mismatch triggers preprogrammed patterns of corrective responses along with an updating of the relevant internal models used to predict sensory events and estimate the motor commands required. This updating typically takes place within a single trial. With respect to friction and aspects of object shape, the updating primarily occurs during the initial contact with the object. In trials erroneously programmed for object weight and mass distribution, the updating takes place when the object starts to move (e.g., at liftoff in a lifting task).

III. ONTOGENETIC DEVELOPMENT OF SENSORIMOTOR CONTROL IN MANIPULATION

The ability to grasp using a precision grip involving the tips of the thumb and index finger first emerges in humans at approximately 8–10 months of age. However, fully mature patterns of grasping, lifting, and holding objects are not observed until about 8 years of age. During this period, there is gradual improvement in grasping behavior as well as qualitative improvements in the capacity to produce independent finger movements. These changes parallel the gradual maturation of the ascending and descending neural pathways that link the hand with the cerebral cortex. These observations strongly suggest that the control of the skilled precision lifting and manipulation relies to a large extent on cerebral processes.

As noted previously, when adults lift objects, they increase grip force and load force in phase such that the two forces increase and decrease together. As a consequence, a linear relationship between these forces is observed (Figs. 3B, 3C and 7B). The motor system adapts the slope of this relationship to factors such as the frictional conditions and the shape of the contact surfaces but robustly maintains this force synergy (Figs. 3B and 3C). However, before 18 months of age, children do not exhibit such parallel control of grip and load forces (Fig. 7). Instead, they tend to increase grip force in advance of the load force in a sequential fashion. The transition from sequential force coordination to the mature parallel coordination is not completed until several years later. Young children also produce comparably slow increases in fingertip force before liftoff and these increases are discontinuous, featuring multiple peaks in force rate (Fig. 7A). In contrast, adults smoothly increase grip force and load force with a single peak in force rate. The discontinuous or start-and-stop force increases observed in young children suggest that they employ a feedback control strategy rather than feedforward control. That is, they continue to increase force in small increments until liftoff occurs. It is not until they receive somatosensory information that liftoff has occurred that they stop these increases. This feedback strategy is similar to that observed when adults underestimate the weight of an object and then have to increase force again until liftoff occurs (Fig. 6B, solid lines). These observations suggest that young children may not have the cognitive resources for accurate feedforward control.

In addition, very young children appear to be relatively inefficient at integrating sensory information into sensorimotor programs. In precision lifting, people start to increase grip force and load force soon after the digits contact the object. Signals from tactile afferents related to object contact trigger the next phase of the lift. In very young children, there is a

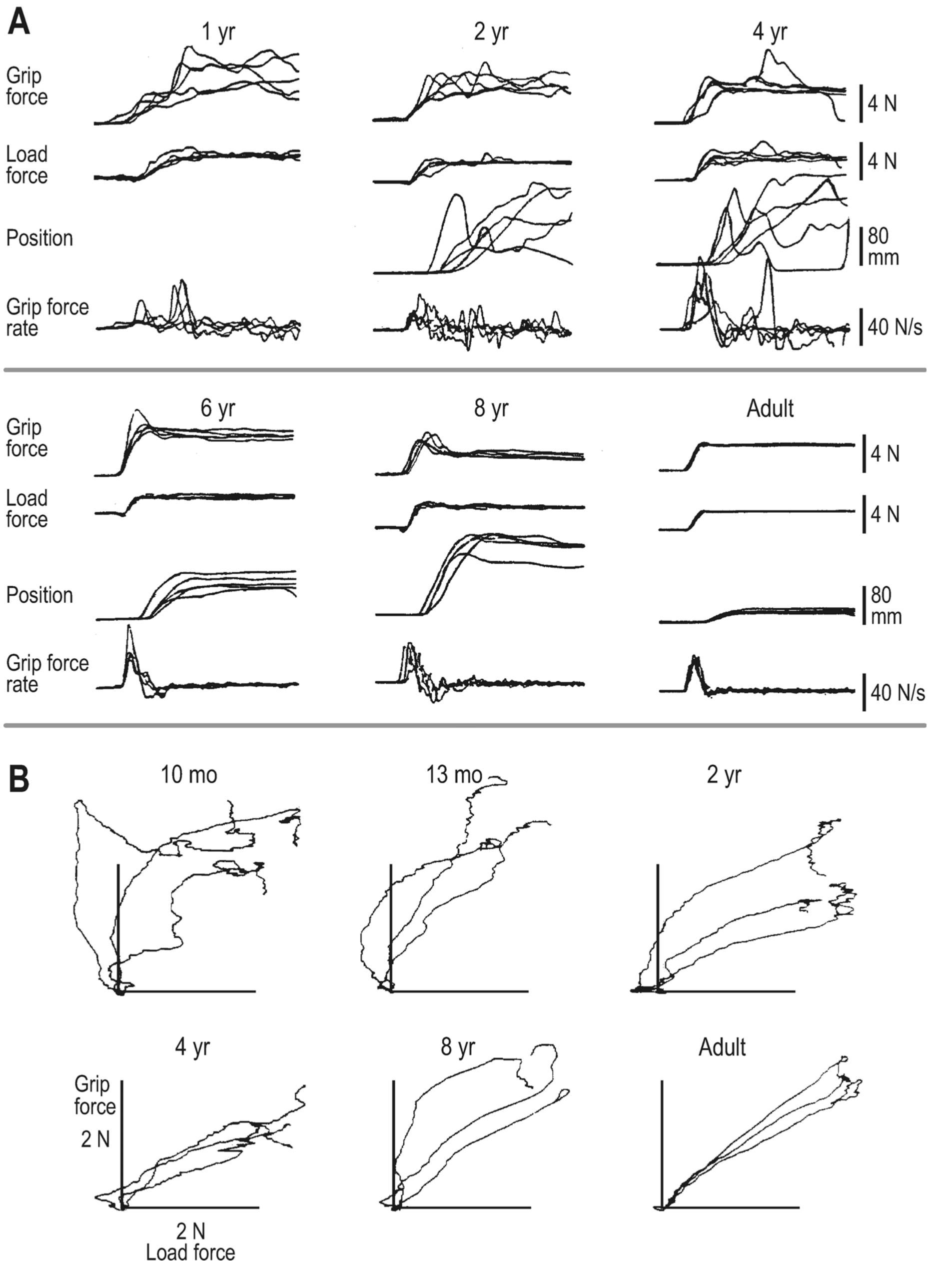

Figure 7 Ontogenetic development of the coordination of grip and load forces during precision lifting. (A) Grip force, load force, and grip force rate as a function of time during several consecutive trials (superimposed) for individual children of various ages and an adult. Note the large variability and excessive grip forces used by young children compared to the adults. (B) Relationship between grip force and load force during the initial parts of lifting trials by children of various ages and an adult. Note the nonparallel increase in grip and load forces for young children compared to adults. (A and B) Surface material and object's weight are constant (adapted with permission from Forssberg, H., Eliasson, A. C., Kinoshita, H., Johansson, R. S., and Westling, G., *Exp. Brain Res.* **85,** 451–457, 1991. Copyright © 1991 by Springer-Verlag).

relatively long delay between initial contact and the onset of increases in grip and load force. This long delay indicates immature control of hand closure and inefficient triggering of the motor commands by cutaneous afferents. The decrease in this delay during subsequent years parallels a maturation of cutaneous reflexes of the hand as assessed by electrophysiological methods.

During the latter part of the second year, children begin to use sensorimotor memory, obtained from previous lifts, for scaling forces in anticipation of object weight. However, adult-like lifting performance with precise control of the load force for smooth object acceleration does not appear until 6–8 years of age. At about 3 years of age, children start to use vision for weight estimation through size–weight associations for classes of related objects. Thus, additional cognitive development is apparently required before the necessary associative size–weight mapping can take place. Unlike adults, once children begin to use visual size cues, they are unable to suppress adequately their influence when the cues are misleading (i.e., in situations in which weight and size do not reliably covary). This observation is consistent with the view that vision has a particularly strong influence on motor coordination in children. Thus, the context-related selective suppression of visual cues appears to require even further cognitive development.

Young children display a limited capacity to adapt the ratio of grip force and load force to frictional conditions. These children use unnecessarily high grip forces in trials with high friction (or low slipperiness) and their behavior is reminiscent of that of adults with impaired digital sensibility. This increased grip force may be a strategy to compensate for immature tactile control of precision grip because overgripping will prevent slips when handling slippery objects. Nevertheless, even the youngest children (1–2 years) show some capacity to adjust grip force to friction if the frictional conditions are kept constant over several consecutive precision grip lifts. The need for repetitive lifts suggests a poor capacity to form sensorimotor memory related to friction and/or to use this memory to control force output. Older children require fewer lifts to update effectively their force coordination to new frictional conditions, and adults require only one lift.

IV. DISSOCIATIONS AND INTERACTIONS BETWEEN PERCEPTION AND ACTION

An important concept in neuroscience is the idea that sensory information is processed in multiple pathways for different uses. For example, in the visual system, there is strong evidence that neural systems that process visual information for use in guiding action are at least partly distinct from neural systems involved in processing visual information for perception and cognitive reasoning. Similarly, there is evidence that sensory information obtained from the hand can have differential effects on action and perception. Here, we discuss evidence for a dissociation between perception and action related to hand movement. However, first we discuss how manipulatory actions can influence perception.

A. Influences of Action on Weight Perception

Because haptic perception of objects generally involves manipulation, the question arises as to whether the perception of particular object properties is influenced by other object properties or by the way in which the object is handled. For example, does the perceived weight of an object depend on the angle of its contact surfaces or the friction between the object and the digits, both of which influence the grip force required to lift the object? Here, one question is whether the grip forces in lifting influence weight perception even though the grip forces are not directly involved in overcoming the force of gravity. For example, does the greater effort required to lift a slippery object give rise to the perception of it being heavier than a less slippery object of the same weight?

More than 150 years ago, Ernst Heinrich Weber observed that the ability to discriminate weight is better when the weights are actively lifted by the hand than when they are supported by a passive hand. This observation suggests that a sense of effort, associated with voluntary muscular exertion, contributes to the perception of weight. Although afferent signals contribute to weight perception, at least under some conditions there is ample evidence that effort, defined as the level of central or efferent drive, contributes to weight perception. The idea is that when we generate motor commands to lift an object, a copy of the commands (efference copy) generates an internal sensation (corollary discharge) that influences perceived weight. The centrally generated sensation is referred to as the sense of effort.

Figure 8A shows the results of an experiment in which people were asked to compare the weights of a reference object and a series of randomly presented test objects of varying weight both heavier and lighter than the weight of the reference. The test objects had the same size and shape as the reference object, and the objects were lifted using a precision grip with the tips of the index fingers on either side. In one condition, the reference object was covered in less slippery sandpaper and the test objects were covered in more slippery satin (Fig. 8, solid circles and solid curve), whereas in a second condition the reference object was covered in satin and the test objects were cover in sandpaper

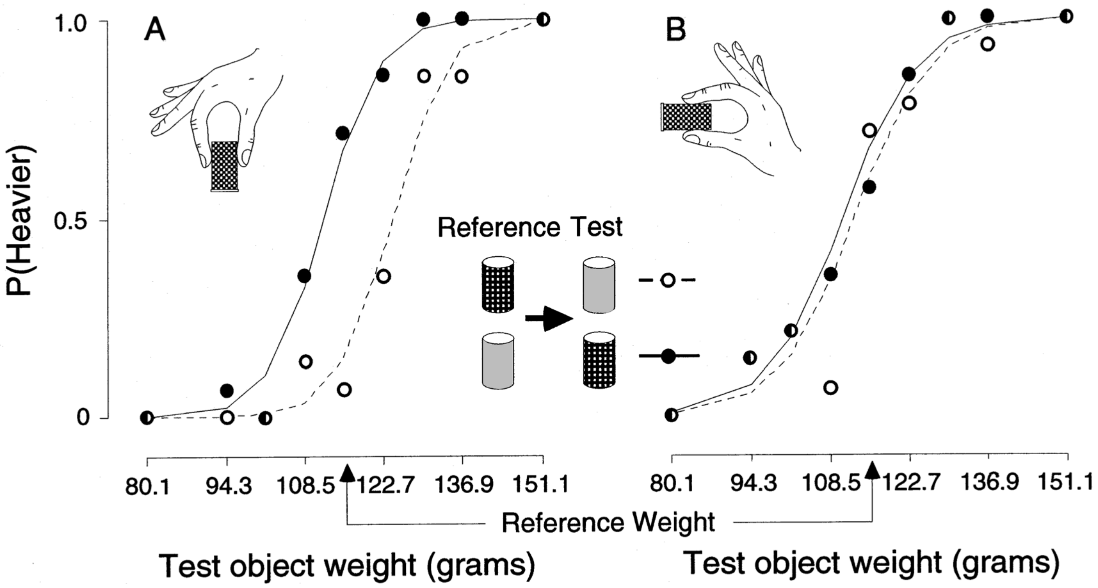

Figure 8 Probability (n=14) of responding that the test canister is lighter than the previously lifted reference canister as a function of the test canister weight. In different experiments, the canisters were lifted with either a vertical (A) or horizontal (B) precision grip. Open circles and dashed lines code the condition in which the test canister was covered in less slippery satin, and the closed circles and solid lines code the condition in which the test canister was covered in less slippery sandpaper. The triangles indicate the reference weight (modified with permission from Flanagan, J. R., Wing, A. M., Allison, S., and Spencely, A., *Perception Psychophys.* **57,** 282–290, 1995).

(Fig. 8, open circles and dashed curve). Figure 8A shows the probability of judging the test object to be heavier than the reference as a function of the weight of the test object. In both conditions, when the test object is much heavier (151.1 g) than the reference (115.6 g) the test object is always judged to be heavier. Conversely, when the test object is much lighter (80.1 g), it is never judged to be heavier. However, in between these extremes, the probability of judging the test object to be heavier is greater when the test object is covered in slippery satin. (Note that there is a general tendency to judge the second of two successively lifted weights, in this case the test object, to be heavier.) This indicates that when lifting with the fingertips on the sides of the object, a more slippery object is judged heavier than an equally weighted object that is less slippery. One interpretation of the results shown in Fig. 8A is that humans judge the more slippery object to be heavier because the grip force used in lifting is greater. When people hold the reference and test objects with a horizontal grip (Fig. 8B), in which surface slipperiness has little influence on the required grip force, there is no effect of surface slipperiness on weight perception.

The results shown in Fig. 8A suggest that people fail to fully distinguish between the effort related to grip force and that related to load force when judging weights lifted with a precision grip. However, this overflow effect may only pertain to muscle actions that are functionally related. Support for this view comes from the observation that the perceived heaviness of a given weight, lifted by one digit, increases if a concurrent weight is lifted by any other digit of the same hand. When the foot or other hand lifts the concurrent weight, the perceived heaviness is not affected.

Although differences in grip force influence weight perception when these differences are determined by frictional conditions, grip force does not appear to influence perceived heaviness when it is manipulated by changing surface shape. When people compare the weights of triangular blocks lifted either on the angled or flat side, there is no effect of angle of perceived weight. It may be that when the grip force requirements strongly match those prescribed by visual cues, people suppress the effort related to grip force differences in evaluating weight. Recall that visual cues related to surface angle can be used effectively for feedforward force control but that there is no evidence that visual information related to frictional condition can be exploited for anticipatory force control.

B. Independent Sensorimotor and Perceptual Predictions of Weight

As discussed previously, people use visual information about object size and shape to estimate parametrically the impending force requirements in manipulation. Thus, people will increase grip and load force more rapidly when lifting a large object than a similar looking small object. This feedforward strategy takes advantage of the link between size and weight that normally pertains to a class or family of similar objects; for example, big cups should weigh more than small ones. However, it fails when this link is altered. In such a case, people must rely on reactive control mechanisms to correct for their erroneous prediction and on feedback mechanisms to tune the internal models used for predictive control. Such a situation arises in the classic size–weight illusion in which people are asked to compare the weights of two equally weighted objects of similar form but unequal size. This illusion, first documented more than 100 years ago, refers to the fact that people reliably judge the smaller of the two objects to be heavier when lifted, even after many lifting trials.

A leading theory of the size–weight illusion is that the illusion arises from a mismatch between predicted and actual sensory feedback. The idea is that when we lift the smaller object, the actual sensory feedback about liftoff will not occur when predicted and the object will thus be judged heavier. Conversely, the larger object, which is lighter than expected, will be judged heavier.

The sensory mismatch seems entirely plausible when one considers lifting the two equally weighting objects the very first time. Here, visual size cues will be misleading and we would expect people to use too much force for the larger object and too little force for the smaller object. However, we also know that people acquire sensorimotor memory related to object weight over repeated lifts. The question arises whether people will continue to misjudge the force required when repeatedly lifting large and small objects of equal weight. Figure 9 reveals the answer. People were asked to repeatedly lift a small and a large cube (Fig. 9A) in alternation. Predictably, when the two objects are lifted for the first time, the forces required for the large object are overestimated and the forces required for the small object are underestimated (Fig. 9B, left). Compensatory, reflex-mediated adjustments in force are triggered in either case. When lifting the small object, the initial increase in grip force and load force is too small and liftoff does not occur when expected. As a result, the forces increase again until liftoff is achieved. When lifting the large object, overshoots occur in the grip and load forces and liftoff occurs earlier than expected. The unexpected early liftoff

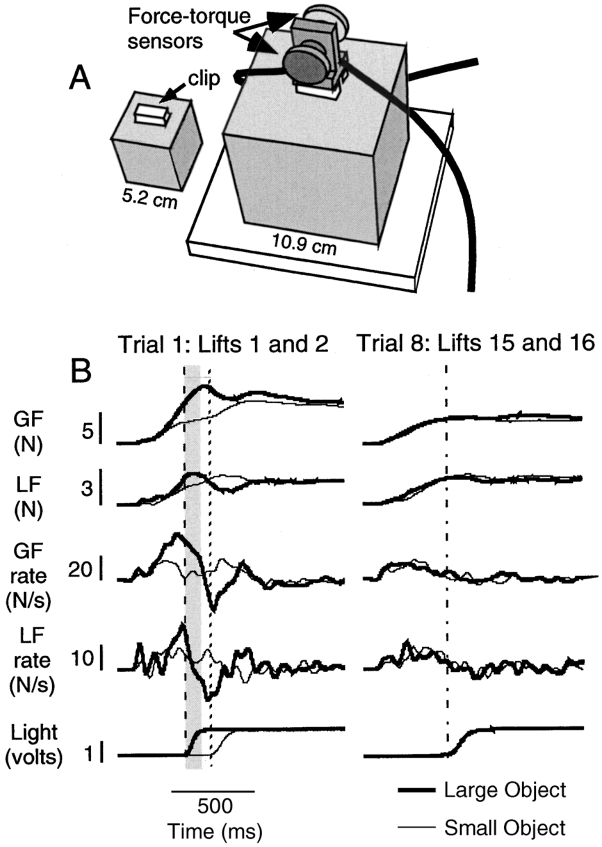

Figure 9 Independent sensorimotor and perceptual predictions of weight. (A) Drawing showing the relative sizes of two equally weighted cubes. Subjects lifted the cubes using a precision grip with the tips of the index finger and thumb on either side of a handle. The handle was attached by clips located on top and in the center of each object. The handle was instrumented with two sensors that measure the forces and torques applied by each digit. Plastic contact disks (3 cm in diameter) were mounted on each sensor and covered in medium-grain sandpaper. A light-sensitive diode embedded into the center of the lifting platform recorded liftoff. (B) Grip force (GF), load force (LF), grip and load force rates, and light-sensitive diode recorded in the first trial (lifts 1 and 2) and the eighth trial (lifts 15 and 16). The subjects lifted the large object (thick traces) and then the small object (thin traces) in each trial. In all trials, subjects grasped the object and increased grip and load force together until liftoff, signaled by the light diode, occurred. In the first trial, peak grip and load force rates were scaled to object size, whereas by the eighth trial the peak force rates were similar for the two objects and appropriately scaled to object weight. Although the subjects adapted their motor output to the true object weights, they still reported verbally that the small object was heavier (adapted with permission from Flanagan, J. R., and Beltzner, M. A., *Nature Neurosci.* **3,** 737–741, 2000).

triggers a decrease in force approximately 100 msec later. However, a very different pattern of force output is observed by the time the cubes are lifted for the eighth time (Fig. 9B, right). Now the force and force rate functions for the small and large cubes are very similar and liftoff occurs at about the same time for both cubes. In contrast to the initial lift trials, grip and load force neither overshoot nor undershoot their final levels, and no corrective adjustments in force are observed. These results illustrate that people adapted their force output, and thus their sensory predictions used for force control, to the actual object weights. Thus, sensorimotor memory about object weight, obtained from previous lifts and based on somatosensory information, comes to dominate visual size cues in terms of feedforward force control.

Although the motor system gradually adapts force output to the true, equal weights of the size–weight stimuli, the perceptual system that mediates awareness of object weight does not adapt. After lifting the two cubes 20 times each, people still reported that the small object was heavier. Moreover, the strength of the size–weight illusion—measured using magnitude estimation techniques—is equally strong. That people experience the size–weight illusion while accurately predicting the fingertip forces required for lifting clearly debunks the theory that the perceptual illusion is accounted for by a sensory mismatch. Instead, the results indicate that the illusion can be caused by high-level cognitive factors. Although the size–weight illusion occurs while there is no evidence of mismatch at the sensorimotor level, the mismatch theory may still operate at a purely perceptual level. For example, people may continue to make erroneous *perceptual* predictions about weight based specifically on visual size cues. A mismatch between these perceptual predictions and actual sensory feedback may give rise to the size-weight illusion. This implies separate comparison processes for perceptual and sensorimotor predictions.

The finding that people continue to experience the size–weight illusion even though they learn to make accurate sensorimotor predictions about object weight indicates that sensorimotor systems can operate independently of perceptual systems. This idea is supported by a growing body of research on visuomotor control showing that partly distinct neural pathways are used depending on whether the sensory information is used to control actions or make perceptual judgments.

See Also the Following Articles

Suggested Reading

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