Sensorimotor Control of Manipulation

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Contact Events and Action Goals in Manipulation Tasks

Most natural object manipulation tasks involve a series of actions or phases that accomplish specific goals (or task subgoals) typically associated with mechanical contact events. For example, consider the task of lifting, holding, and replacing a box on a tabletop. This task involves a series of action phases separated by contact events involving either the making and breaking of contact (Figure 1(a)). Thus, the goal of the initial reach phase is marked by the digits contacting the box, and the goal of the subsequent load phase (during which increasing vertical load forces and horizontal grip forces are applied under isometric conditions) is marked by the breaking of contact between the object in hand and the support surface. These and subsequent contact events give rise to discrete sensory signals from one or more sensory modalities. For example, when the box is replaced on the table, the contact between the box and surface gives rise to discrete tactile and auditory signals and, if the box is in the field of view, visual signals as well. It is likely that such contact events also give rise to discrete signals in proprioceptive systems. Thus, in general, contact events can be associated with distinct signals in multiple sensory modalities, each providing a neural signature of the event. These signals provide information about not only the timing of the event but also the characteristics of the mechanical interaction (e.g., direction and amplitude of contact forces). Thus, a given object-manipulation task can be represented as a sensory plan wherein a sequence of sensory goals is specified. The implementation of such a plan requires the selection and execution of a corresponding sequence of basic actions, or action-phase controllers, to achieve the sensory goals. To be accurate, each of these controllers requires information about the initial configuration of the motor system and objects in the environment, as well as their mechanical properties. This state information (multimodal) is used for feed-forward or predictive adaptation of motor output of the controllers with reference to attainment of their sensory goals.

The implemented action-phase controllers also generate predictions about the sensory consequences of the motor output, which are compared with the actual sensory signals (Figure 1a)). Contact events, which denote completion of action goals, represent critical sensorimotor control points in this respect because they give rise to discrete and distinct sensory signals in one or more modalities. By comparing predicted and actual sensory feedback, the brain can monitor the progression of the task and, if a mismatch occurs because of misleading initial state information or a faulty action-phase controller, launch corrective actions (Figure 1(a)). This use of sensory information as well as the characteristics of the corrective actions are highly task- and phase-specific and are presumably learned with the learning of the underlying action-phase controller. Moreover, mismatches can lead to an updating of the memory representations of object properties that can be subsequently used for predictive control later in the task and in other tasks with the same object, thus reducing future prediction errors.

Although we have emphasized that manipulation tasks can be divided into a sequence of action phases, it is important to note that sensory predictions generated in one action phase are used in the next. Specifically, sensory predictions about the terminal state of the motor system and environment of one action phase also provide initial state information for the subsequent action-phase controller. This information can be used to parameterize the next action phase in advance, which allows a smooth transition between the component actions of the task. In the absence of such anticipatory control, delays between phases would occur because the brain would have to rely on peripheral afferent signals to obtain this state information. Such a process would be time consuming due to long time delays in sensorimotor control loops associated with receptor transduction and encoding, neural conduction, central processing, and muscle activation. For example, it takes approximately 100 ms before signals from tactile sensors in the digits can bring about a significant change in fingertip actions. Even longer delays, in excess of 200 ms, are usually required to transform visual events into purposeful fingertip actions. Because of these long time delays in sensorimotor control loops operating on the hand, anticipatory control policies govern the swift and smooth transitions characteristic of dexterous manipulation.

Vision provides critical information for predictive control of task kinematics. In addition to locating objects in the environment, vision is used for identifying contact sites that are both stable and advantageous for various actions that we want to perform with the grasped object. For example, when we pick

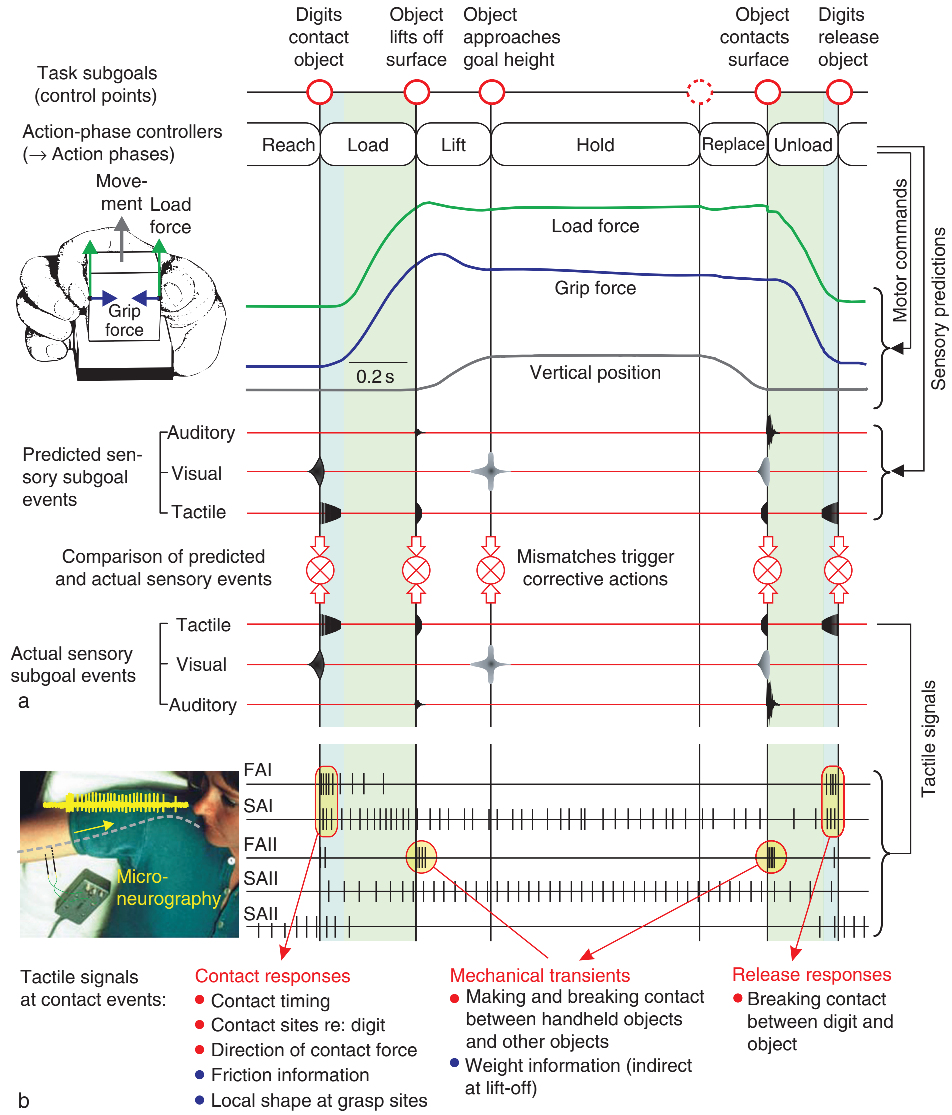

Figure 1 A person grasps and lifts an instrumented test object from a table, holds it in the air, and then replaces it, using the precision grip: (a) contact events and subgoals; (b) signals in the four types of tactile afferents from the glabrous skin of the human hand. In (a), the contact events shown at the top define the subgoals of the task (i.e., goals of each action phase). Sequentially implemented action-phase controllers generate motor commands that bring about the required action phases. After digits contact the object, the grip force increases in parallel with the tangential (load) force applied during isometric conditions to the object to overcome gravity. When the load force overcomes the force of gravity, the object lifts off. After the object is replaced such that it contacts the support surface, the load and grip forces decline in parallel until the object is released. In conjunction with generating motor command, the action-phase controllers predict internally the sensory consequences of these commands in one or more modalities (predicted sensory subgoal events), whereas the actual sensory consequences are signaled in one or more modalities (actual sensory subgoal events). For example, when the object is replaced on the surface, the contact event gives rise to tactile, visual, and auditory sensory events. By comparing predicted and actual sensory events, the sensorimotor system can monitor task progression and detect mismatches used to bring about corrective actions tailored to the action phase (see also **Figures 5, 6(b),** and **6(c)**). The predicted sensory events from each action phase can be used to provide initial state estimates for the next phase (not illustrated). In (b), signals in the four types of tactile afferents are recorded with the technique of microneurography during the lifting trial. At four points corresponding to subgoal events, tactile afferents show distinct burst discharges: (1) contact responses preferentially in FAI and SAI afferents when the object is first contacted, (2) burst responses in the FAII afferents related to the mechanical transients at lift-off and (3) when the object contacts the support surface, and (4) responses primarily in FAI afferents when the object is released. In addition to these event-related responses, SAII afferents and many SAI afferents show ongoing impulse activity when forces are applied to the object. Some spontaneously active SAII units are unloaded during the lift and cease firing. FA, fast-adapting; SA, slow-adapting. Data from Johansson RS and Westling G (1991) Afferent signals during manipulative tasks in man. In: Franzen O and Westman J (eds.) *Somatosensory Mechanisms*, pp. 25–48. London: Macmillan.

up a hammer to drive in a nail, we probably use different grasp sites than when we pick it up to give it to another person. Furthermore, visual cues about the identity, size, and shape of an object provide cues about its mechanical properties that are useful for predicting the forces required for successful manipulation. Visual cues related to object weight and mass distribution can be used to predict magnitudes of required fingertip forces and visual cues about the shape of grasp surfaces can be used to predict stable fingertip force directions. However, vision is of limited utility when objects are out of sight or partially occluded.

The use of vision in manipulation relies on learned associations between visual cues and their mechanical meaning. Such associations are grounded in movement–effect relationships evaluated through signals in sensors that transmit veridical information about mechanical interactions between the body and objects in the environment. The tactile modality directly provides information about mechanical interactions between our hands and objects and plays a pivotal role in the learning, planning, and control of dexterous object manipulation tasks. Relatively little is known about the contribution of proprioceptive signals in manipulation. Like vision, proprioception can provide only indirect information about mechanics. For example, signals related to muscle length, joint angle, and muscle force do not directly code the contact state between the hands and objects.

The importance of tactile afferent signals in manipulations is most apparent in people with impaired digital sensibility. Such individuals have great difficulty with routine tasks even under visual guidance. For example, they often drop objects, may easily crush fragile objects, and have tremendous difficulties with everyday activities such as buttoning a shirt or picking up a match. In humans, the density of tactile innervation is highest in body surface areas that typically contact objects including the palmar surfaces of the hands, the soles of the feet, and the tongue and lips. Approximately 2000 tactile afferents innervate each fingertip and some 10 000 afferent neurons innervate the remaining glabrous skin on the palmar surface of the hand. Microneurography studies in humans have shown that there are four types of tactile afferents that encode different aspects of the deformations of the soft tissues when the hands interact with objects (**Figure 2**). Overall, these sensors have evolved for extracting, rapidly and with high spatiotemporal fidelity, features of dynamic mechanical events that occur on top of the low-frequency and often large forces typically present when holding and transporting handheld objects. These dynamic tactile signals code the contact events that mark the attainment of subgoals in manipulation tasks (**Figure 1(b)**).

In the remainder of this article, we describe a series of experimental results from manipulation tasks that illustrate and further develop the general principles just described.

Predictions and Control Points in the Tactile Modality

The first action phase in most manipulation tasks is to bring the hand to the object in order to grasp it. The goal of this reach phase it to place the fingertips on the object in locations that will allow the development of a stable grasp in the context of the actions that will be performed with the object. In many manipulation tasks, it is important that the fingertips contact the object at around the same time and that the fingertip force vectors sum to zero. This is particularly important when grasping a light object that might otherwise be displaced or rotated when initially contacted. The contacts between the fingertips and object represent control points for goal completion of the reach phase. In some cases, these contact events may be visible and can be encoded visually. However, in many instances, the contact sites of at least some of the digits are out of view (as when digits contact the back side of an object). In contrast, tactile signals encode reliably and robustly all contact events (**Figure 1(b)**).

For each digit, contact responses in ensembles of afferents convey information about contact timing, the contact location on the digit, and the direction of contact force. Ensembles of tactile afferents also encode the frictional status of the contact and the shape of the contact surface, which are critical parameters in the control of object manipulation. All of these contact parameters are represented by signals in ensembles of tactile afferents that encode the patterns of stresses and strains distributed throughout the viscoelastic fingertip. Fast-adapting type I (FAI) afferents provide the most well-defined contact responses; however, slow-adapting type I (SAI) and fast-adapting type II (FAII) tactile afferents may also respond dynamically at the moment of contact. Tactile information associated with discrete mechanical fingertip events (including contact events) can lead to appropriate changes in motor output (i.e., fingertip forces) within 100 ms or less. Traditionally, it has been posited that tactile information is coded by the firing rates of tactile afferents. However, such a mechanism would be too slow to account for the rapid use of tactile information in manipulation. That is, to estimate firing rates at least two impulses in a given neuron are

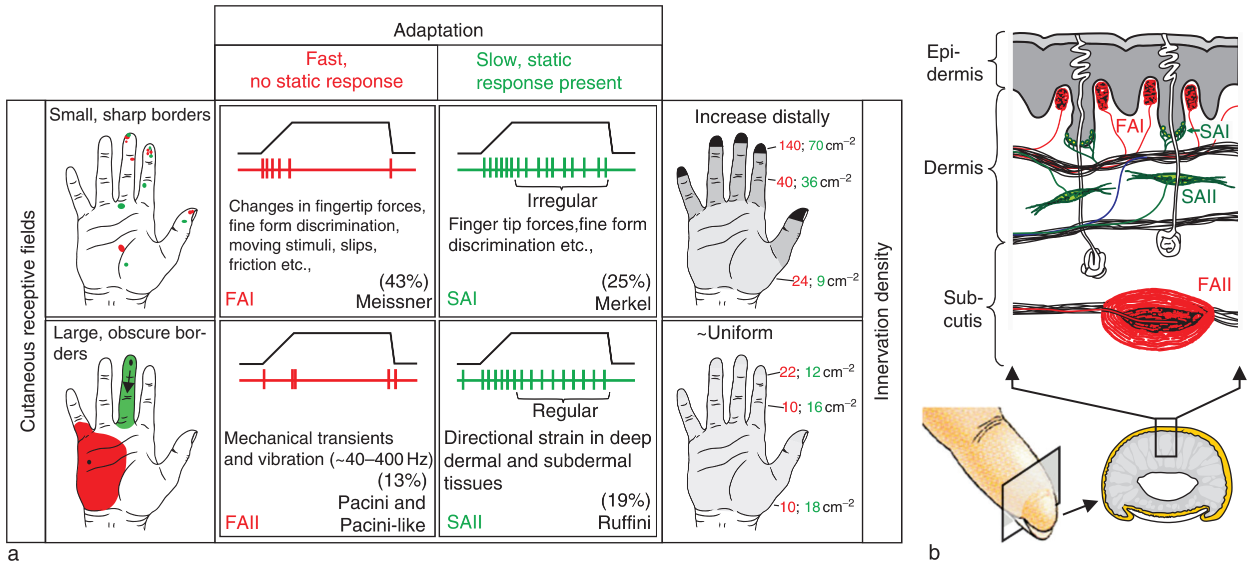

Figure 2 Types of tactile (mechanoreceptive) sensors in the glabrous skin of the inside of the human hand: (a) functional properties; (b) nerve endings in the fingertip. In (a), the middle graphs schematically show the impulse discharge (lower traces) to perpendicular ramp indentations of the skin (upper traces) for each sensor type. Two types (FA) show fast adaptation to maintained tissue deformation (i.e., they only respond to deformation changes). Two types adapt slowly (SA); that is, in addition to being dynamically sensitive (particularly the SAIs) they show an ongoing response related to the strength of maintained tissue deformation. The type I sensors (FAI and SAI) have small and well-defined coetaneous receptive fields (typically 10 mm^2) when defined by light, pointed stimuli (patches in the left drawing of the hand represent the fields of 15 different sensors). The density of these sensors increase in the distal direction of the hand and is especially high in the very tips of the digits (see the right drawing of the hand; the numbers indicate the innervation density as the number of afferents per square centimeter of skin area for the fingertips, fingers, and palm). In contrast, the FAII and SAII sensors show lower and approximately uniform densities over the hand and their receptive fields are larger and less well defined (left drawing of the hand). The FAIIs are especially responsive to mechanical transients that propagate though the tissues, whereas the SAIIs sense strain in the dermal and subdermal fibrous tissues, often with a remote origin. Sensors with encoding properties akin to the type II sensors of the hand are found in virtually all fibrous tissue in the body. The relative frequency of occurrence in the glabrous skin and the probable morphological correlate are indicated for each type of sensor. In (b), the organized nerve terminals corresponding to the four types of tactile sensors are shown for the fingertip. FA, fast-adapting; SA, slow-adapting. Data from Johansson RS and Vallbo ÅB (1983) Tactile sensory coding in the glabrous skin of the human hand. *Trends in Neuroscience* 6: 27–31.

required and reliable estimates generally require that neural responses are averaged over a substantial time window and over several trials. Recently it has been proposed that the relative timing of first spikes in ensembles of tactile afferents (temporal codes) encode tactile information for use in manipulation tasks. Neural recordings in humans indicate that such a mechanism would provide information about tactile events more rapidly than rate coding and fast enough to account for the use of tactile signals in natural manipulation.

Sensory Predictions That Support Grasp Stability

After contact is established between the object and the hand, practically all manipulation tasks require the application of forces tangential to the contacted surfaces (load forces). For example, to lift an object with the digits at the side, vertical load forces must be applied to overcome the weight of the object (Figure 1(a)). In many cases, twist forces (torques) tangential to the grasped surfaces are also applied. For example, if we lift a bar from one end, in addition to the vertical load force we need to apply tangential torque to prevent the bar from rotating as we lift it. These tangential loads destabilize the grasp, and to prevent the object from slipping (either linearly or rotationally) we need to apply forces normal to the surface (grip forces) to create stabilizing frictional forces.

When manipulating objects, grip forces are controlled to increase and decrease in phase with increases and decreases in the tangential loads with no time delay (Figures 1(a) and 3). This anticipatory modulation of grip force with movement-dependent changes in load force generates grip forces that are greater than the minimum required to prevent slip while at the same time not excessive. This coordination of grip and load forces is not innate but develops during ontogeny and is gradually refined until approximately 8 years of age. The coupling between grip force and load force supports grasp stability in a wide variety of maneuvers that we perform with objects. For example, it is observed at the level of

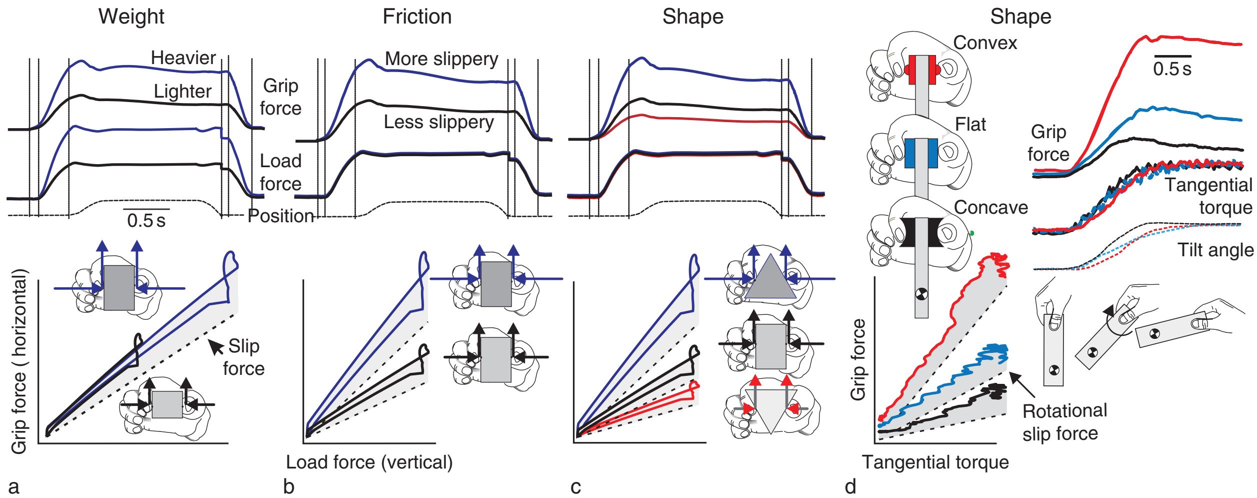

Figure 3 Parametric adjustments of motor output: (a) to change in object weight; (b) to change in friction between the object and skin; (c) to change in shape of the contact surface during object lifting; (d) to change in shape of the contact surface during object tilting change in tilt. In (a–c), the subject lifts an instrumented test object from a table, holds it in the air, and then replaces it, using a precision grip. Upper graphs show the horizontally oriented grip force, the vertically oriented load force (lift force), and the object's vertical position as a function of time for superimposed trials, indicated by differently colored curves. The lower graphs show the grip force as a function of the load for the same trials. The dashed lines indicate the minimum grip force to prevent slips and the safety margin against slips is indicated by hatching. In (a), with weight variations, the parallel change in grip and lift forces coordinated by the action-phase controllers ensures grasp stability when lifting objects of different weights. In (b), the balance between grip force and load force is adjusted to deal with changes in friction. In (c), a similar scaling of the grip-to-load force ratio is observed when object shape is varied. In either instance, the coordination of grip and load force ensures an adequate safety margin against slips. In (d), an already lifted object is tilted by 65° around the grip axis, which causes tangential torques at the grasp surfaces. Three superimposed trials are shown, one for each of the following surface curvatures: spherically convex with a radius of 5 mm, flat, and spherically concave with a radius of 20 mm. The top traces show the grip force, tangential torque, and tilt angle against time. Note the parallel change in grip force and the tangential load and the higher grip force with the greater surface convexity. The bottom graph emphasizes this adjustment by plotting the grip force against tangential torque load for the corresponding data. The shading indicates a similar safety margin against rotational slips irrespective of curvature. (a) Based on data from Johansson RS and Westling G (1988) Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Experimental Brain Research* 71: 59–71. (b) Data from Johansson RS and 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. (c) Data from Jenmalm P and Johansson RS (1997) Visual and somatosensory information about object shape control manipulative fingertip forces. *Journal of Neuroscience* 17: 4486–4499. (d) Data from Goodwin AW, Jenmalm P, and 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.

individual digits when people use two or more digits of the same or both hands to manipulate objects, when grasping and moving objects held between the palms, and when load forces on a handheld object are generated by jumping up and down. Likewise, it applies to bimanual coordination when the hands have different and complementary roles, such as when we use one hand to add things into, or remove things from, a receptacle held by the other hand. Coupling between grip and load forces also operates when we move objects with different complex dynamics (combinations of inertial, elastic, and viscous loads), even though this involves altering the mapping between motor commands that generate load forces and those that generate grip forces.

The control of grasp stability requires that the balance between the grip and load forces be adapted to the properties of contacted surfaces. The friction between digit and object surface determines the minimum ratio between grip force and load force required to prevent slip, and people parametrically adapt the balance between grip and load forces for different frictional conditions, using greater grip forces with more slippery surfaces. This is achieved by varying the ratio between the grip force change and load force change (Figure 3(b)). In the same vein, people parametrically scale the balance between the grip and load forces to the shape of the contacted surface. For example, the greater the curvature of a spherically curved grasp surface, the larger the grip force required to generate a given tangential torque (Figure 3(d)). Similarly, when people lift tapered objects, a greater grip-to-load force ratio is required when the grip surfaces are tapered upward as compared to downward (Figure 3(c)). These parametric adaptations to contact surface friction and shape typically result in grip forces that exceed the minimum required to prevent slips by a safety margin of 10–40% of the applied grip force (gray areas in the force coordination plots of Figure 3).

When manipulating objects, people control their fingertip forces based on predictions of surface properties. Vision can, under favorable conditions, provide accurate information about object shape that can be used for predictive parameterization of fingertip forces. In contrast, it appears that vision is unhelpful in predicting the friction of an object, in part because friction depends not only on the object surface but also on sweating rate and the greasiness and wetness of the skin (Figure 4(a)). Instead, predictions of frictional conditions are based on the memory of previous haptic experiences with the same or similar objects, whereas a default prediction, perhaps based on some average, appears to be used in novel situations. The critical role of tactile afferents in the control of grasp stability is clearly illustrated by the fact that people with digital sensory impairments fail to adapt grip-to-load force ratios to object surface properties and, instead, consistently use large grip forces (cf. Figures 4(b) and 4(c)).

Information about surface friction and shape is rapidly extracted during initial contact between the fingertip and object surface by signals in ensembles of tactile afferents (Figure 4(d)). Thus, the initial contact event

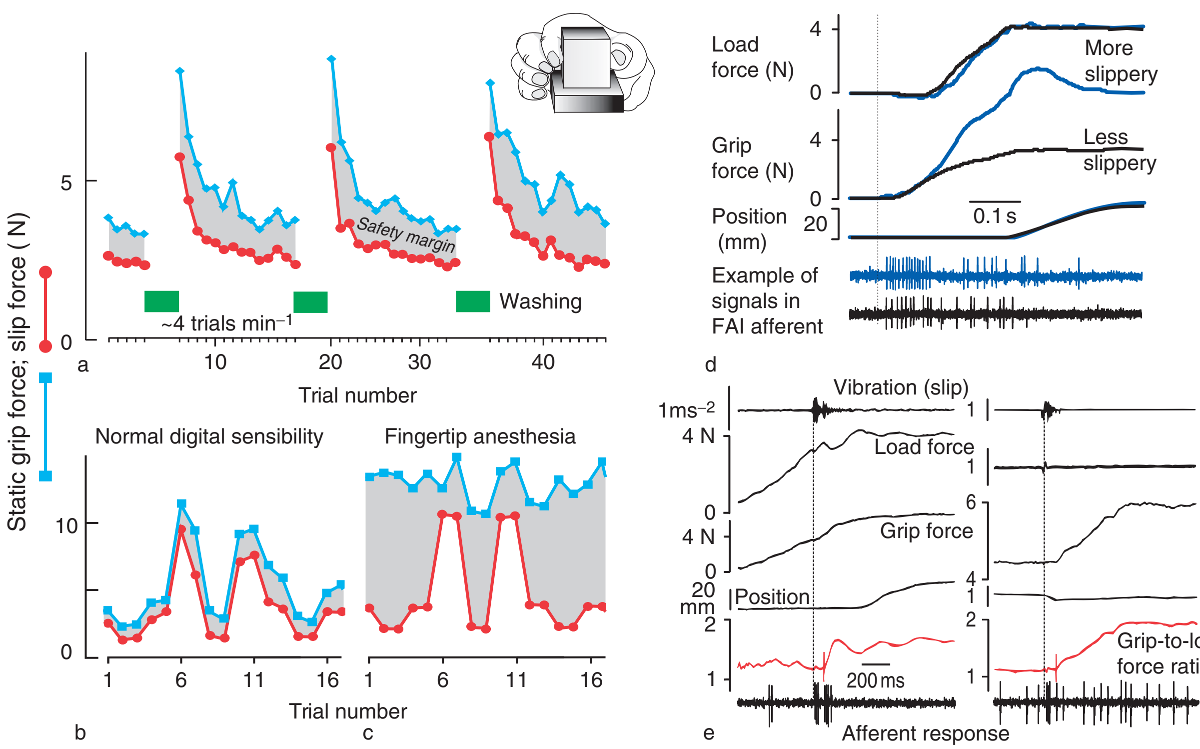

Figure 4 Adjustment of hand grip force to frictional changes in everyday situations: (a) static grip force before and after washing the hand; (b) with changes in object surface structure with normal digital sensibility; (c) with changes in object surface structure with anesthetized fingertips; (d) with friction; (e) in response to accidental slippage. In (a), the static grip force when holding an object in air using a precision grip (diamonds) and the corresponding minimum grip forces to prevent slips (slip force (dots)) are shown before and after the subject's hand was washed (with soap and water) and dried (towel); there were 48 consecutive lifts with suede as surface structure (single subject, weight constant at 400 g). In (b–c), the corresponding grip force data is shown during frictional changes between lifts caused by changing the surface structure among fine-grain sandpaper, suede, and smooth rayon. In (d), the influence of friction on force output and initial contact responses in a fast-adapting type I (FAI) afferent are shown. Two trials are superimposed, one with less slippery sandpaper (black lines) and a subsequent trial with more slippery silk (blue 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. In (e), examples are shown of afferent slip responses and the upgrading of the grip-to-load force ratio elicited by small slip events occurring at only one of the digits engaged. Vertical dotted lines indicate the onset of the slips as revealed by vibrations in the object (acceleration signal); short vertical lines indicate the onset of the slip-triggered upgrading of the force ratio. The new higher and stable ratio restores the safety margin, preventing future slips. On the left, slip during the load phase is shown; the middle burst is the afferent slip response, whereas the third burst represents dynamic responses to the force changes following the slips. On the right, slip during the static phase is shown. (a) Based on data from Johansson RS and Westling G (1984) Influences of cutaneous sensory input on the motor coordination during precision manipulation. In: von Euler C, Franzen O, Lindblom U, and Ottoson D (eds.) *Somatosensory Mechanisms,* pp. 249–260. London: Macmillan. (b–c) From Johansson RS and Westling G (1991) Afferent signals during manipulative tasks in man. In: Franzen O and Westman J (eds.) *Somatosensory Mechanisms,* pp. 25–48. London: Macmillan. (d–e) Based on data from Johansson RS and Westling G (1987) Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. *Experimental Brain Research* 66: 141–154.

represents a critical control point in the manipulation task at which predicted and actual sensory feedback related to surface properties can be compared. Mismatches between predicted and actual contact responses – primarily provided by ensembles of FAI afferents – lead to an updating of the grip–load force coordination approximately 100 ms after contact. Figure 5 illustrates such updating when people repeatedly lift objects with tapered grasp surfaces without vision of the object. The tapering was changed between trials in a pseudorandom order. In all trials, the initial increase in grip force was determined by the tapering (and hence force requirements) in the previous trial. This indicates that knowledge about the status of the object, obtained in previous trials, specifies the force coordination. When the tapering was changed, the grip force output is modified approximately 100 ms after the digits contacted the object and tuned for the actual object properties (Figure 5(a)). By the second trial after the change, the force coordination is appropriately adapted right from the onset of force application. Thus, when a prediction error occurs, tactile information obtained at initial contact with the object rapidly initiates a corrective action accompanied with an updating of the representation of the object used to control forces in future interactions with the object. As previously indicated, people with digital sensory impairments fail to adapt grip-to-load force ratios to object surface properties (cf. Figure 4(c)).

Under favorable conditions, visual cues about object shape can influence the initial contact forces used in lifting in a feed-forward manner. For example, in sequential lifting trials with tapered contact surfaces, a change from upward to downward tapering results in a slower increase in grip force right from the beginning of the force application (Figure 5(b)). Similarly, with a change from downward to upward tapering surfaces, the grip force is adjusted from the very start of the lift in anticipation of the higher grip force required to lift the object. Hence, visual cues about object geometry can provide state information for anticipatory parametric adaptation of component actions of the manipulation task. Once the object is contacted, tactile signals also provides state information about object shape that can override visual predictions if necessary.

Occasionally, the updating of frictional and shape representations that typically occurs at initial contact is

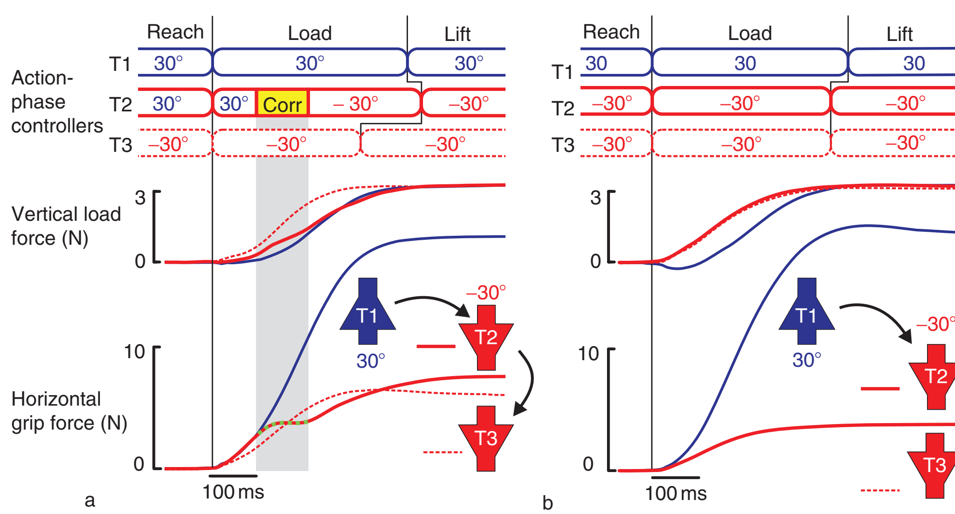

Figure 5 Adaptation of fingertip forces to changes in object shape; vertical load force and horizontal grip force shown as a function of time for trials from a lift series in which surface angle was unpredictably varied between lifts: (a) without vision of the contacted surfaces; (b) with vision of the contacted surfaces. The blue curves refer to the last trial with the 30° object before the switch (T1; upward tapered grasp surfaces). (This trial was preceded by a trial with a 30° object.) The solid red curves show the next trial (T2) performed with the –30° object (downward tapered grasp surfaces). These curves thus illustrate adjustments to the smaller angle. The yellow dashed segment in the grip force curve in (a) indicates the epoch of the corrective action elicited by the new surface angle. The thin red dashed curves show the following trial, again with the –30° object. The top diagram represents the status of the sequentially implemented action-phase controllers. In T1, they are parameterized for the 30° object throughout. In T2, without vision of the contacted surfaces (a), a corrective action (Corr) is triggered approximately 100 ms after contact based on a mismatch between predicted and actual tactile information obtained at contact related to object shape. This action is interspersed during the loading phase and involves a change in the ratio between the grip force change and load force change, which, in turn, change the balance between grip and load forces to better suit the –30° object for the remainder of the trial (see also **Figure 3(c)**). In T3, the controllers remain updated to the –30° object. With vision of the contacted surfaces (b), visual cues about object geometry provide state information for anticipatory parametric adaptation of the motor output after the change in tapering (T2), and no corrective action is triggered. Data from Jenmalm P and Johansson RS (1997) Visual and somatosensory information about object shape control manipulative fingertip forces. *Journal of Neuroscience* 17: 4486–4499.

inadequate and may result in an accidental slip later in the task. For example, when an object is held in air after being lifted, such a slip usually results in a transitory and partial unloading at one digit, and this increases the loads on the other digits engaged (Figure 4(e)). These transient load shifts are signaled by tactile afferents and trigger a corrective action that increases the grip-to-load force ratio at all digits for the remainder of the task. The nature of the corrective action triggered by slips depends on the phase of the task. Slips during the load phase in lifting lead to a slowing down of the increase in load force, whereas slips during the hold phase lead to an increase in grip force. Hence, different action-phase controllers are associated with different smart reflexes that support grasp stability and help achieve the current subgoal of the task.

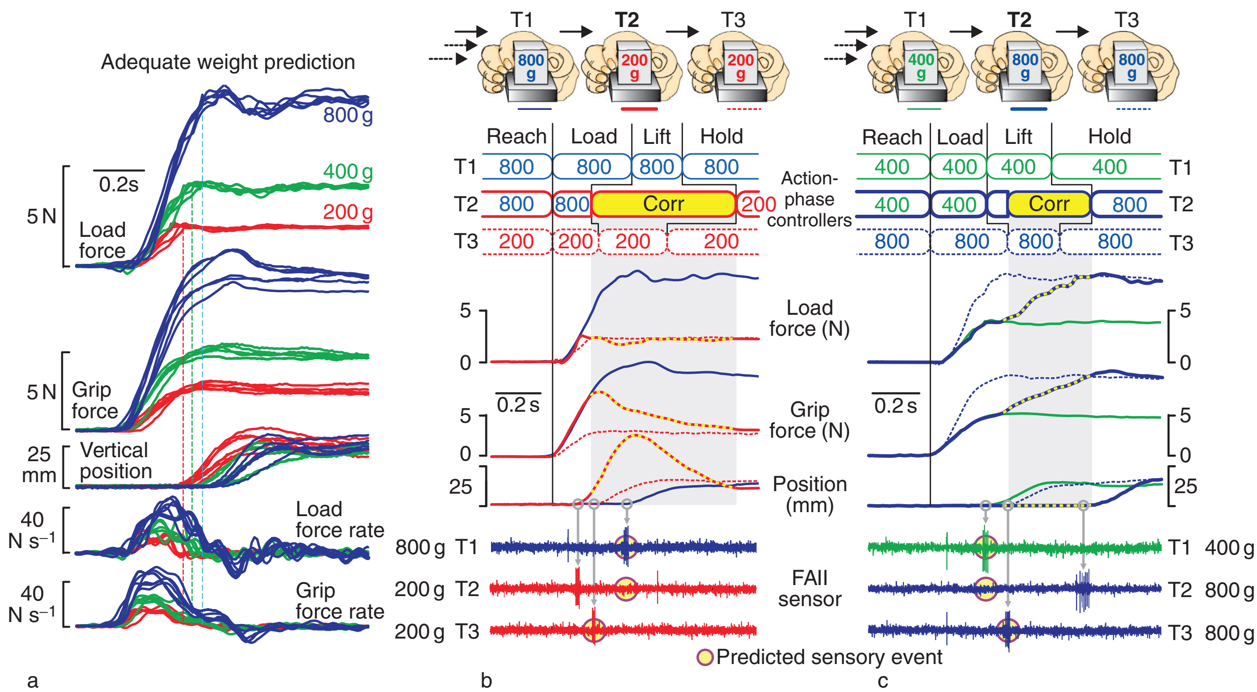

Figure 6 Adaptation of motor output to object weight: (a) fingertip forces and object movement during the initial part of adequately programmed lifts with three objects of different weights (data from 24 single trials superimposed; single subject); (b) single-unit tactile afferent responses and adjustments in force to unexpected decrease in object weight (trials between lifts from 800 to 200 g); (c) second experiment showing single-unit tactile afferent responses and adjustments in force to unexpected increase in object weight (trials from 400 to 800 g). In (b–c), the data from the single-lift trials are aligned on initial touch (vertical line). Gray circles and vertical lines indicate the moment of lift-off for each trial and the arrowheads point to the actual sensory events generated by the lift-off in a fast-adapting type II (FAII) afferent. The circles behind the nerve traces indicate the corresponding predicted sensory events. In (b), three successive trials (T1–T3) are shown in which the subject lifted an 800 g object (blue curves), a 200 g object (red solid curves), and then the 200 g object again (red dashed curves). The forces exerted in the first lift are adequately programmed because the subject had previously lifted the 800 g object. The forces are erroneously programmed in the first lift of the 200 g object (T2) because they are tailored for the heavier 800 g object lifted in the previous trial. The sensory information about the start of movement occurs earlier than expected for the erroneously programmed 200 g object trial (cf. the actual and predicted sensory events) and initiates a corrective action (yellow dashed red curves). The strong force drive of the ongoing load phase is terminated but still results in an overshoot in position due to the reflex delay, and corrective motor command is launched that brings the object back to the intended position. In (c), the participant performed an adequately programmed lift with a 400 g weight (T1, green curves), followed by a lift with an 800 g object erroneously programmed for the lighter 400 g weight lifted in the previous trial (T2, blue solid curves) and then a lift with the 800 g object again (T3, blue dashed curves). The absence of burst responses in FAII afferents at the predicted point for the erroneously programmed 800 g object trial (cf. the actual and predicted sensory events) elicits a corrective action (yellow dashed blue curves). This involves abortion of the lift-phase command followed by triggering of a second load-phase command that involves a slow, discontinuous, and parallel increase in grip and load forces until terminated by sensory input signaling lift-off. The top diagrams in (b) and (c) represent the status of the sequentially implemented action-phase controllers. In T1, they are parameterized for the 800 g (b) and 400 g (c) weight throughout. In T2, a corrective action (Corr) is triggered approximately 100 ms after the occurrence of the mismatch between predicted and actual sensory information related to object lift-off. This action involves abortion of the operation of the current action-phase controller and the implementation of action patterns that allow the task to continue. The corrective action is linked to an updating of the subsequently implemented controllers for the new weight. In T3, the controllers remain updated to this weight. Elements compiled from Johansson RS (1996) Sensory control of dexterous manipulation in humans. In Wing AM, Haggard P, and Flanagan JR (eds.) *Hand and Brain: The Neurophysiology and Psychology of Hand Movements*, pp. 381–414. San Diego: Academic Press.

Sensory Predictions Related to Object Motion

The successful lifting of an object requires that the forces developed during the load phase be predictively tuned to the weight of the object. People tend to lift objects of varying weight in about the same amount of time. To accomplish this, they scale the rate of increase of vertical load force, prior to lift off, to the expected weight of the object – increasing load force more rapidly for objects they expect to be heavy (Figure 6(a)). In addition, people predict the load force required for lift-off and, when lifting an object just off the surface, reduce the increase in load force rate so that it approaches zero at the expected lift-off time. When people lift to different heights – requiring different amount of object acceleration – load forces are likewise scaled predictively to achieve the desired acceleration and lift height. This ensures a smooth and critically damped lifting motion. Because no sensory information is available about weight until lift-off, this tuning of force output relies on estimates of weight. Such estimates are based on sensorimotor memory of the object derived from previous interactions with the object. Familiar objects can be identified visually (or by haptic exploration) for retrieval of weight estimates. Moreover, memory representations of familiar objects are organized into families or categories of objects in which the objects within a family can vary in size (e.g., cups, books, and loafs of bread). In such situations, people exploit size–weight associations when predicting the motor commands required to lift objects.

The fact that people rely on predictions related to object properties is clearly illustrated when people make erroneous predictions that result in pronounced performance errors. For example, when we lift up an object that is lighter than we expect, we typically make a jerky movement and lift the object higher than intended. A jerky movement occurs because the load phase is programmed for a heavier weight such that lift-off happens earlier than predicted and excessive lifting force is generated (Figure 6(b), T2). Conversely, an unexpected increase in weight results in a slow and hesitant load phase because the force drive is targeted for a lighter weight and additional increases in force are required to bring the object aloft (Figure 6(c), T2).

The expected lift-off represents a control point related to the goal of the load phase. Ensembles of FAII afferents, supplied by Pacinian corpuscles located in subcutaneous tissues, most quickly and reliably signal the outcome of the load phase by encoding both the timing and the dynamics of the lift-off event. Such afferents, which are distributed throughout fibrous tissues of the body, are particularly sensitive to transient mechanical events that propagate through handheld objects into the hand and arm. The transient events take place when contacts between handheld objects and surfaces are formed or broken and effectively excite these highly sensitive afferents. When lifting an object that is lighter than expected, the sensory events elicited by the lift-off occur before the predicted events that are part of the sensory plan (cf. predicted and actual neural events in Figure 6(b)). The mismatch triggers a learned corrective action that involves termination of the load phase force followed by corrective motor commands that bring the object back to the intended position. However, due to delays in sensorimotor control loops, this corrective action pattern kicks in too late to avoid an overshoot in the lifting movement (see position signal in Figure 6(b)). When lifting an object that is heavier than expected, the sensory event elicited by lift-off occurs neither before nor at the point predicted by the sensory plan (cf. predicted and actual neural events in Figure 6(c)). Hence, again there is a mismatch between actual and predicted sensory events. In this case, the corrective action triggered by the mismatch results in slow, probing increases in finger forces until terminated reactively by sensory events signaling lift-off. Thus, the sensorimotor system reacts to both the presence of an unpredicted event and the absence of a predicted sensory event. Significantly, in addition to triggering corrective actions, these sensory mismatches lead to an updating of memory representations related to object weight, which in turn improves predictive control in subsequent action phases and tasks that engage the same object. In natural situations, this updating generally occurs in a single trial (see Figures 6(b) and 6(c)). However, in the presence of misleading or confounding visual and haptic cues, or when people deal with objects with unusual dynamics (relating applied force to motion), updating may require repeated lifts or movements of the object.

When people transport and hold an object, knowledge about object weight, mass distribution, and surface properties remains critical for controlling action and maintaining grasp stability. When people replace the object on a surface, the sensory goal is to produce an afferent signature signifying contact. This contact event, which represents a sensorimotor control point, is signaled by FAII afferents that encode the timing and nature of the event (Figure 1(b)). The contact event is followed by an unloading phase where grip and load forces decrease in parallel. The sensory events related to the digits breaking contact with the surface of the object represent the goal of this phase. The coupled decrease in the load and grip forces ensures the maintenance of a grip-to-load force ratio that provides grasp stability even in this phase. The outcome of the unloading phase is distinctly signaled by release responses in ensembles of tactile afferents, especially FAI afferents (Figure 1(b)).

Predictions and Control Points in the Visual Modality

Because visual resolution is far better in and around the fovea, we use saccadic eye movements (fast jumps in the line of sight) to shift gaze to targets of interest. In addition to providing high-resolution visual information about target features, gaze fixations provide information about target location in space based on knowledge about the orientation of the eyes with reference to the head and to other body segments as well. Different types of visually supported tasks have characteristic patterns of eye movements that accompany them. In object manipulation, people direct their gaze to successive contact locations as they gain salience in the evolving task according to the demands of the implemented action plan. For example, when people pick up a bar, move the bar in hand to contact a target switch, and then replace the bar, gaze is successively directed to the grasp site on the bar, the target, and the landing surface where the bar is replaced (Figures 7(a) and 7(b)). Furthermore, people may direct fixations to points where contact must be avoided, including obstacles that must be circumnavigated with the hand (or object in hand). In familiar manipulation tasks, subjects almost never fixate their hand or objects being moved by the hand. An important role of foveal vision is to monitor contact events representing subgoals of the task.

The spatiotemporal coordination of gaze and hand movements emphasizes the segmentation of manipulation tasks into distinct action phases (Figure 7(c)). At the start of most action phases, congruent hand and eye movements are launched concurrently to the contact location representing the goal. Thus, both hand and eye movements are specified based on peripheral vision about the contact location (or on memorized landmark locations). Because eye movements are quick, gaze reaches the contact location well before the hand (or object in hand). This permits the use of foveal and parafoveal vision in monitoring the final approach of the hand to the contact location. Gaze typically remains at the contact location until around the time of goal completion (e.g., until the grasp is established, the target switch is released, or the bar is replaced in the target contact task) or remains at a location where a contact should be avoided until the time of the potential contact (e.g., when the tip of the bar passes closest to the obstacle in the target contact task). Thus, the gaze shift to the contact location associated with the next action phase occurs around

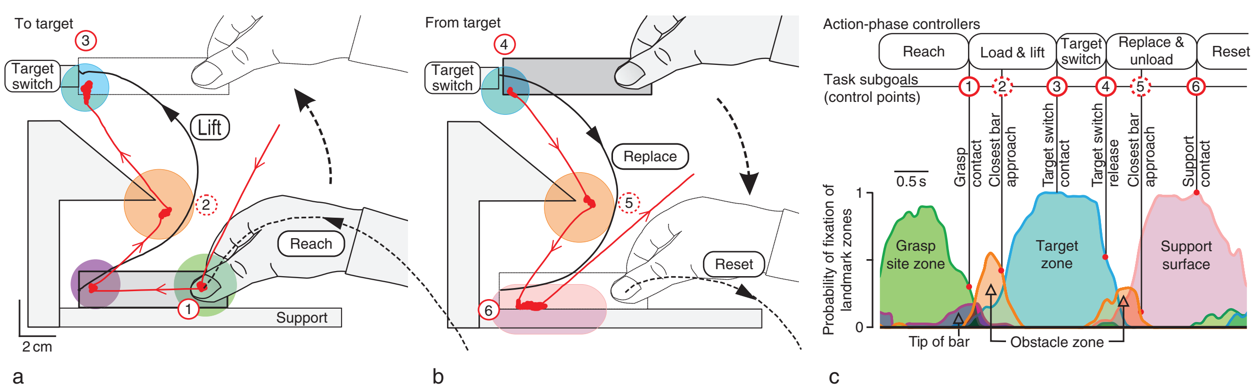

Figure 7 Predictions and control points in the visual modality, gaze, and hand movements for a target contact task: (a) a single trial in which the participant reached for and grasped a bar and moved it to press a target switch; (b) and then moved it from target contact and replaced it on the support surface; (c) spatiotemporal coordination of gaze and manipulatory actions shown as time-varying instantaneous probability of fixations within the landmark zones indicated in (a) and (b). In the task in (a–b), a triangular obstacle was located between the bar and target. Dashed black lines in (a–b) represent the path of the tip of the index finger during the reach for the bar and during the reset phase when the hand was transported away from the bar after it was replaced and released. The solid black lines represent the path of the tip of the bar. The red lines indicate the position of gaze; the thin segments with the arrowheads represent saccadic eye movements and the thick patches represent gaze fixations. The colored zones represent landmark zones that captured 90% of the fixations recorded during several trials by 10 participants; these zones are centered on the grasp site (green), tip of the bar (purple), protruding part of the obstacle (orange), target (blue), and support surface (pink). The plot in (c) is derived from data pooled across 10 participants, each performing four trials with the triangular obstacle. The red circles and vertical lines mark contact events demarcating phase transitions in the task, and the spatial locations of these events are schematically indicated by the location of the corresponding numbered circles in (a) and (b). The common time base has been normalized such that each phase of each trial has been scaled to the median duration of that phase. Data from Johansson RS, Westling G, Bäckström A, and Flanagan JR (2001) Eye-hand coordination during learning of a novel visuomotor task. *Journal of Neuroscience* 21: 6917–6932.

the predicted time of goal completion. In fact, in most cases, both gaze and hand movement commands are initiated in anticipation of goal completion and are not delayed until sensory feedback is obtained verifying goal completion. With the latter strategy, a smooth transition between successive phases of the manipulation task would not be possible because of the substantial time delays in sensorimotor control loops. In summary, contact events that demarcate action phases can be predicted and monitored in both the tactile modality and the visual modality.

Predictions in Action Observation

Although there is no question that tactile feedback related to control points is essential for skilled object manipulation, there are control points that do not give rise to tactile events. For example, when we drop a ball onto a surface, we typically direct our gaze to the predicted contact point between the ball and surface. Here, sensory feedback related to contact is available only through vision (and possibly audition). Thus, vision and the tactile system can play complementary roles in monitoring contact events. We have recently argued that, when observing an actor perform an object manipulation task, the observers – like the actor – predict and monitor contact events linked to the subgoals of the task. Although the observers cannot use tactile feedback to monitor contact events, they are free to move their gaze to monitor contact events via vision.

When people observe an actor performing a predictable block-stacking task, their gaze behavior is similar to the actor's gaze behavior. Specifically, the gaze of both the actor and observer predicts forthcoming contact sites (where blocks are grasped and replaced), and gaze is maintained at each contact site until around the time of goal completion (grasp contact and block landing). Even when observers do not know, in advance, which of two possible blocks the actor will grasp, they shift their gaze proactively to the correct target as soon as possible based on vision information. Taken together, these results indicate that observers implement a dynamic sensory representation of the task they are observing. Furthermore, these findings provide support for the hypothesis that observing and understanding the actions of another person involves a mechanism that maps the observed action on to sensorimotor representations in the observers' brain. In action observation, as in action, we argue that gaze is controlled, in part, for monitoring the consequences of action in central vision. By comparing actual and predicted visual feedback related to contact events, both observers and actors may be able to obtain valuable information about the outcomes of action and action plans that can be exploited by the sensorimotor system when learning, planning, and controlling future actions.

Sensory Control Policies during Learning

Although skilled behaviors involve learning to execute motor commands that fulfill sensory goals, little is known about possible changes in sensory control policies across learning stages. We have recently studied the learning of a novel visually guided object manipulation task in which participants had to discover how to move a cursor to successive targets presented on a screen by applying forces and torques to a rigid tool held between the two hands. As when people discover how to ride a bicycle, the learning proceeds in three stages. In the initial exploratory stage, participants attempt to discover the basic mapping rule relating motor and sensory signals by busily generating apparently uncontrolled cursor movements. In the skill acquisition stage that follows, control begins to emerge and performance improves rapidly. In the final skill refinement stage, performance continues to improve but gradually. During the exploratory stage, gaze reactively pursues the cursor via saccades directed to successive cursor locations, possibly allowing the learner to build a map between hand actions and gaze-related signals. As the learner starts to gain control over the cursor during the subsequent skill acquisition stage, gaze begins to predict forthcoming cursor positions. In the subsequent skill refinement phase, learners launch spatially and temporally congruent gaze and cursor movements directed to the target as in well-learned natural manipulations. These findings indicate that people adopt different sensorimotor schemas depending on the stage of learning and that learning to predict sensory consequences of motor commands precedes accurate control. It is not yet known how the use of other sensory modalities in manipulation may also depend on learning stage.

Conclusion

Dexterity in object manipulation depends on anticipatory control policies that rely on knowledge about movement–effect relationships when interacting with environmental objects. A sensory plan specifies the sequence of task subgoals in terms of sensory signals linked to contact events. This sensory representation of the task provides a scaffold for the selection and shaping of the action-phase controllers required for achieving sensory subgoals. Prediction of sensory states pertaining to the outcome of executed action phases allows for smooth phase transitions, in contrast to the stuttering transitions that would result if the brain relied on peripheral afferent information to confirm subgoal completion and to update state information before launching the next action phase. Tactile sensors signal information about both the timing and the physical nature of the discrete mechanical events that represent the outcomes of the action phases. Contact events in manipulation are also represented in the visual and auditory modalities and, presumably, the proprioceptive modality. When the brain successfully predicts the actual sensory signals at a given contact event, no corrective action is required and the task runs in a feed-forward fashion. When a prediction error arises, a learned corrective action, the nature of which depends on the task and its action phase, is generated and representations of object properties are updated. We suggest that contact events that represent sensorimotor control points are encoded in multiple sensory modalities and serve at least two critical functions. First, by comparing actual and predicted sensory events in multiple sensory modalities, the sensorimotor system can simultaneously monitor multiple aspects of task performance and, if prediction errors arise, respond to the pattern of errors observed in different modalities. Second, because contact events give rise to salient sensory signals from multiple modalities that are linked in time and space, they provide an opportunity for sensorimotor integration and intermodal alignment helpful for learning and upholding multimodal sensorimotor correlations that support prediction of purposeful motor commands.

See also: Cross-Modal Interactions Between Vision and Touch; Finger Movements: Control; Human Haptics; Posterior Parietal Cortex and Tool Usage and Hand Shape; Reaching and Grasping; Sensorimotor Integration: Models; Spatial Transformations for Eye–Hand Coordination; Tactile Coding in Peripheral Neural Populations; Tactile Texture.

Further Reading

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