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R S Johansson, Umeå University, Umeå, Sweden

J R Flanagan, Queen's University, Kingston, ON, Canada

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Glossary

action-phase controller Represents a sensorimotor control policy for reaching a subgoal of an overall action plan by using sensory information and predictions in a specific way, each. As such, it is conceptually related to the notion of internal models in motor control that involve neural circuits that mimic the behavior of the motor system and environment and capture the mapping between motor outputs and sensory inputs (Wolpert, D. M. *et al.*, 2001).

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* Refers to the ability to experience the environment through active exploration, typically with our hands, as when palpating an object to gauge its shape and material properties. *microneurography* A method using metal microelectrodes to investigate directly neural signals in efferent and afferent peripheral nerves *in situ* in conscious human subjects, able to participate in sophisticated and cooperative experimental tests. Tungsten microelectrodes with an epoxy resininsulated shaft having diameter of about 200 μ m, a tip diameter of about 5 μ m, and an impedance around 500 k Ω measured at 1 kHz are generally used for recording action potentials in single axons. For an early review detailing this technique see Vallbo, Å. B. *et al.* (1979).

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 points Contact events that denote completion of action goals and give rise to discrete and distinct sensory signals in one or more sensory modalities.

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

tactile Refers to signals conveyed to the brain by low-threshold mechanoreceptive afferent neurons that innervate the skin and subcutaneous tissues in glabrous skin areas and oral mucosa, i.e., body areas used primarily for object interactions.

6.05.1 Organization of Object Manipulation Tasks

Most natural object manipulation tasks involve a series of actions or phases where each phase accomplishes a specific goal or subgoal of the overall task. Distinct mechanical contact events typically signify goal attainments. 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 that involve either the making or the breaking of contact (Figure 1(a)) (Johansson, R. S. and Westling, G., 1984a). 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 forces are applied under isometric conditions to overcome object weight, is marked by the breaking of contact between the object in hand and the support surface. These and subsequent contact events give rise to distinct and discrete sensory signals in the tactile modality and, in many cases, other modalities (Figure 1(a)). These sensory signals not only provide information about the timing of the events but also about the characteristics of the mechanical interaction. Thus, a given object manipulation task can be represented as a sensory plan specifying a sequence of sensory goals in one or more sensory modalities (Flanagan, J. R. et al., 2006). 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 (Figure 1(a)).

The task of each action-phase controller is to generate motor commands that will lead to the successful attainment of the sensory goal. When possible, the controller uses knowledge of object properties, combined with information about the current state of the system (including the motor apparatus and objects in the environment), to predictively tailor motor commands to the task at hand. For example, during the load phase of lifting, people normally scale the rate of change of force output to the predicted weight of the object. At the same time, the controller generates predictions about the sensory consequences of the motor output, including sensory signals associated with contact events. By comparing predicted and actual sensory feedback, task progression can be monitored (Figure 1(a)). If a mismatch occurs, the brain can launch learned task- and phasespecific corrective actions (or smart reflexes) that are part and parcel of the controller (Figure 1(a)). If the mismatch is due to erroneous predictions about object properties, memory representations related to these properties can be updated so as to improve predictive control in subsequent phases of the task and in other tasks with the same object.

Predictions about the terminal sensory state of each action phase provide initial state information for the next action-phase controller. In the absence of such predictions, this state information would have to be obtained by a peripheral afferent signal at the start of each phase. This would prevent smooth transitions between action phases because of substantial time delays in sensorimotor control loops. Due to delays associated with receptor transduction and encoding, afferent and efferent neural conduction, central processing, and muscle activation, it takes approximately 100 ms before signals from tactile sensors in the digits can bring about meaningful adjustments of fingertip actions. Even longer delays, in excess of 200 ms, are usually required to transform visual events into purposeful fingertip actions. Anticipatory control policies support dexterous object manipulation by avoiding these long time delays.

6.05.2 Sensory Systems Supporting Object Manipulation

In addition to multiple motor systems (arm, hand, postural), most natural object manipulation tasks engage multiple sensory systems. Vision can provide important information for planning and controlling task kinematics. For example, vision is used to locate target objects and to identify contact sites that are both stable and advantageous for actions we want to perform with the grasped object. Furthermore, visual cues about the identity, size, and shape of an object can be used for predictively adapting fingertip forces. For example, visual cues related to object weight and mass distribution can be used to predict force magnitudes and visual cues about shape to predict stable force directions. However, vision is of limited utility when objects are out of sight or partially occluded and for assessing contact sites for digits contacting the backside of objects. Furthermore, vision only proindirect information about mechanical vides interactions that is based on statistical correlations learned through experience. Similarly, proprioception can only provide indirect information about contact 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, and the sensitivity of nondigital

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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) The contact events shown at the top define 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 between the object and the surface 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 Figures 7 and 8). The predicted sensory events from each action phase can be used to provide initial state estimates for the next phase (not illustrated). (b) Schematic illustration of signals in four types of tactile afferents innervating the human fingertips as recorded from the median nerve at the level of the upper arm using the technique of microneurography. At four points corresponding to subgoal events of the task, tactile afferents show distinct burst discharges: (1) contact responses preferentially in fast-adapting type I (FA-I) and slowly adapting type I (SA-I) afferents when the object is first contacted, (2) responses in the fast-adapting type II (FA-II) afferents related to the mechanical transients at liftoff, and (3) when objects contact the support surface, and (4) responses primarily in FA-I afferents when the object is released (goal of the unloading phase). In addition to these event-related responses, slowly adapting type II (SA-II) afferents and many SA-I afferents show ongoing impulse activity when forces are applied to the object. Some spontaneously active SA-II units are unloaded during the lift and cease firing. (a) Compiled from data presented in Westling, G. and Johansson, R. S. 1987. Responses in glabrous skin mechanoreceptors during precision grip in humans. Exp. Brain Res. 66, 128–140. (b) From Vallbo, Å. B. and Hagbarth, K.-E. 1968. Activity from skin mechanoreceptors recorded percutaneously in awake human subjects. Exp. Neurol. 21, 270-289.

mechanoreceptive afferents (e.g., musculotendinous afferents) to fingertip events is very low in comparison to that of tactile sensors (*cf.* Macefield, V. G. and Johansson, R. S., 1996; Macefield, V. G. *et al.*, 1996; see also Häger-Ross, C. and Johansson, R. S., 1996).

Conversely, the tactile sensors directly provide information about mechanical interactions and thus play a pivotal role in the control of dexterous manipulation. The importance of tactile afferent signals in manipulation tasks is most apparent in people with impaired digital sensibility who 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. About 2000 tactile afferents innervate each fingertip and some 10000 afferent neurons innervate the remaining glabrous skin on the volar surface of the digits and the palm. As discussed below, these afferents provide various types of contact information critical for the control of the hands in dexterous object manipulation (see also Figure 1(b)). Because tactile information in object manipulation is used in control processes that generally operate automatically, transiently, and quickly, traditional studies of tactile sensory mechanisms, where perceptual (declarative) phenomena are examined in psychophysical experiments, provide limited information about the function of these mechanisms in manipulation.

6.05.2.1 Tactile Sensory Innervation of the Human Hand

Microneurography recordings of signals in single peripheral neurons in humans have shown that four different types of tactile afferents supply the inside of the hand (Johansson, R. S. and Vallbo, Å. B., 1983; Vallbo, A. B. and Johansson, R. S., 1984). Figure 2 summarizes characteristic features of these four types of afferents. Two types, termed fast-adapting type I (FA-I) and fast-adapting type II (FA-II) afferents, respond only during dynamic phases of tissue deformation. The other two types, called slowly adapting type I (SA-I) and slowly adapting type II (SA-II) afferents, respond to sustained skin deformation with a graded sustained discharge.

The type I afferents (FA-I and SA-I) terminate in end organs located at the dermal–epidermal margin. If delineated by weak point indentations of the skin, both types have small and well-defined cutaneous receptive fields ($\sim 10 \text{ mm}^2$), which in humans comprise multiple (\sim 4–17) highly sensitive zones corresponding to individual terminal branches of the afferent axon (Johansson, R. S., 1978; Phillips, J. R. et al., 1992). The receptive fields of both types exhibit enhanced representations of spatial discontinuities with comparable spatial resolution when tested with edge contours indenting the skin (Johansson, R. S. et al., 1982b) and embossed dots scanned over the receptive field (Phillips, J. R. et al., 1992). Their density in the skin increases stepwise in the distal direction of the hand (Figure 2(a)) and is especially high in the very tips of the digits where there are \sim 140 FA-I afferents and \sim 70 SA-I afferents per square centimeter of skin area (Figure 2). Hence, these afferents can transmit detailed spatial information about mechanical fingertip events, including the location and distribution of contact events. The FA-I and SA-I afferents provide complementary temporal information, with the SA-Is encoding static tissue deformations and deformation changes of lower frequencies (Johansson, R. S. et al., 1982a). Accordingly, intraneural microstimulation of FA-I afferents typically evokes subjective sensations akin to wobbling, fluttering, or tapping feelings that are sharply delimited on the skin surface whereas stimulation of SA-I afferents typically evokes sensations of light pressure located more diffusely slightly below the skin surface (Vallbo, A. B. et al., 1984; Torebjörk, H. E. et al., 1987).

The predominance of FA-I afferents in the hand, and especially in the fingertips, indicates the premium placed on extracting with high-fidelity spatiotemporal features of dynamic mechanical events. Such events occur when objects are contacted and are often superimposed on low-frequency and large forces typically present when holding and maneuvering objects, including tools. Indeed, there is a predominance of FA-I afferents (or afferents similar to FA-Is) on other body areas used for accurate object interactions, such as the lips, the tip of the tongue (Trulsson, M. and Essick, G. K., 1997), and the sole of the foot (Kennedy, P. M. and Inglis, J. T., 2002). In contrast, hairy skin areas have no Meissner corpuscles (i.e., no FA-I sensors) and a predominance of slowly adapting sensors (Nordin, M. and Hagbarth, K. E., 1989; Edin, B. B. and Abbs, J. H., 1991; Edin, B. B. et al., 1995; Vallbo, A. B. et al., 1995).

The type II afferents (FA-II and SA-II) innervate the hand with a lower and more uniform density compared to the type I afferents. Their cutaneous receptive fields are an order of magnitude larger (Johansson, R. S., 1978), presumably partly because they terminate in the deeper dermal and subdermal



Figure 2 Types of tactile (mechanoreceptive) sensors in the glabrous skin of the inside of the human hand. (a) Graphs schematically show the impulse discharge (lower traces) to perpendicular ramp indentations of the skin (upper traces) for each sensor type. Two types (fast-adapting type I (FA-I) and fast-adapting type II (FA-II)) show fast adaptation to maintained tissue deformation, i.e., they only respond to deformation changes. These afferents were originally termed RA (rapidly adapting) and PC (Pacinian). Two types adapt slowly (slowly adapting type I (SA-I) and slowly adapting type II (SA-II)), that is, they show an ongoing response related to the strength of maintained tissue deformation. The type I sensors (FA-I and SA-I) have small and well-defined cutaneous receptive fields (typically 10 mm²) when defined by light pointed stimuli (patches in the drawing of the hand represents the fields of 15 different sensors). The density of these sensors increases stepwise in the proximo-distal direction of the hand, with one step from the palm to the main parts of the digits and one at the border between the proximal to the distal half of the distal phalanx (see the rightmost drawing of the hand where the number of afferents per square centimeter of skin area is indicated for the fingertips, fingers, and palm, respectively). In contrast, the fast-adapting type II (FA-II) and SA-II sensors show lower and about uniform densities over the hand and their receptive fields are larger and less well defined. The FA-IIs are especially responsive to mechanical transients that propagate through the tissues whereas the SA-IIs sense strain in the dermal and subdermal fibrous tissues, often with a remote origin. The relative frequency of occurrence in the glabrous skin and the probable morphological correlate are indicated for each type of sensor. (b) Diagrammatic vertical section of a fingertip showing the organized nerve terminals corresponding to the four types of tactile sensors. Compiled from data reviewed in Johansson, R. S. and Vallbo, A. B. 1983. Tactile sensory coding in the glabrous skin of the human hand. Trends Neurosci. 6, 27-31 and in Vallbo, A. B. and Johansson, R. S. 1984. Properties of cutaneous mechanoreceptors in the human hand related to touch sensation. Hum. Neurobiol. 3, 3-14.

tissues (Figure 2(b)). The FA-II afferents efficiently encode transient mechanical events containing high frequencies (~40-400 Hz) because of high-pass filtering properties of their end organs (Pacinian and Pacinian-like corpuscles) (Loewenstein, W. R. and Skalak, R., 1966). Such events arise in manipulation tasks when handheld objects form and break contacts with other objects and give rise to traveling waves in the tissues that can excite FA-II afferents located remotely from the contact areas. For example, it has been estimated that some 500-1000 FA-II afferents respond at liftoff and at support contact when objects are lifted and replaced, as illustrated in Figure 1 (Westling, G. and Johansson, R. S., 1987). The SA-II afferents sense directional strain in deep dermal and subdermal tissues (Johansson, R. S., 1978), including shear strain generated by forces tangential to the skin in object manipulation tasks (Westling, G. and Johansson, R. S., 1987). The fact that afferents with functional and structural properties akin to the type II afferents of the hand terminate in all fibrous tissues in the body, e.g., interosseous membranes, muscle fascias, and joint capsules and ligaments, suggests that they constitute a general mechanoreceptive system that supports proprioceptive in addition to tactile function.

6.05.2.2 Deformational Properties of the Fingertips and Coding of Tactile Information in Ensembles of Afferents

Signals in ensembles of afferents from the entire distal phalanx can contribute to the encoding of tactile information in natural object manipulation tasks because the interaction between the fingertips and objects typically causes widespread distributions of complex stresses

and strains throughout the engaged fingertips, including in the skin (Birznieks, I. *et al.*, 2001; Jenmalm, P. *et al.*, 2003). Hence, afferents that terminate outside regions of direct contact with objects can be vigorously excited, including FA-I and SA-I afferents, and constitute a part of the population code (Figure 3(b)). This applies, for example, to the encoding of fingertip force direction. Firing rates of individual tactile afferents distributed over the fingertips are tuned broadly to a preferred direction of fingertip force and this preferred direction varies amongst afferents such that ensembles of afferents can encode force direction (Figure 3(c) and 3(d)) (Birznieks, I. *et al.*, 2001). Directional preferences of individual afferents of specific types could, for example, be combined in population models such as the vector model of direction proposed for neurons in the motor cortex (Georgopoulos, A. P. *et al.*, 1986) and for encoding the direction of tooth loads by periodontal mechanoreceptors (Trulsson, M. *et al.*, 1992). In a similar vein, it has been proposed that the centroid of the population response can encode the position of a stimulus on the skin surface (Goodwin, A. W. and Wheat, H. E., 2004).

Firing rates in ensembles of tactile afferents also encode shape of contacted surfaces. Most studies of neural encoding of shape have concerned fine form



Figure 3 (Continued)



Figure 3 Signals in human tactile afferents under stimulation conditions representative for object manipulation tasks: Encoding of direction of fingertip forces. (a) Superimposed on a 0.2 N normal force (Fn), force was applied to the fingertip in the normal direction only (N), together with tangential components in the proximal (P), ulnar (U), distal (D), or radial (R) directions. Each stimulus consisted of a force protraction phase (125 ms), a plateau phase (4 N force), and a retraction phase (125 ms) and was applied with a flat contact surface at a standard site on the fingertip that serves as a primary target for object contact in grasping and manipulation of small objects. (b) The centers of the circles mark the location of the centers of the receptive fields of 186 tactile afferents, and the area of the circles represents the number of impulses evoked during the protraction phase with stimuli in the normal direction only. Nearly all afferent responded; crosses indicate locations of sampled afferents that did not respond. Pink zone represents the area of contact at 4 N normal force. (c) Impulse ensembles exemplifying responses in a single highly responsive fast-adapting type I (FA-I), slowly adapting type I (SA-I), and slowly adapting type II (SA-II) afferent to repeated force stimuli (n = 5) applied in each force direction (P, U, D, R, and N). Traces above show the instantaneous discharge frequency averaged over the five trials. Top traces show the normal force component (F_n) superimposed for all trials. Circles on the finger indicate the location of the afferents' termination and the cross the primary site of stimulation. (d) Distributions of preferred direction of tangential force components for 68 SA-I, 53 FA-I, and 32 SA-II afferents from the fingertip shown as unit vectors (arrows) with reference to the primary site of stimulation. These afferents terminate at various locations on a terminal phalanx (cf. (b)). Preferred directions were estimated by vector summation of the mean firing rates during the force protraction phase (gray zone in (c)) obtained with different directions of the tangential force component. (e-g) Discrimination of force direction by FA-I and SA-I afferents based on the relative timing of first spikes and on first-interspike intervals. Impulse ensembles in (e) exemplify responses during the force protraction phase in two FA-I and two SA-I afferents to repeated force stimuli (n = 5) applied in each of five force directions (see (a)). Force direction influenced consistently the first-spike latencies of all of these afferents. (f and g) Top graph: Solid curves show the probability of correct discrimination of stimuli in each of the five force directions (coded by different colors) by afferents' recruitment sequence as a function of time during the force protraction phase; dashed curve shows the development of the normal force component (F_n). Horizontal line indicates the probability for one-half of the stimuli being discriminated correctly, i.e., with force direction a probability of 60% given that chance performance is 20% (i.e., five force directions). Thin dashed curves show the time-varying probability of correct discrimination based on first-interspike intervals. Bottom graph: Solid curves give the number of sampled afferents recruited as a function of time for stimuli in each force direction, i.e., cumulative distributions of first-spike latencies. Thin dashed curves show the corresponding data for the second spike. (a-d) Adapted from Birznieks, I., Jenmalm, P., Goodwin, A., and Johansson, R. 2001. Encoding of direction of fingertip forces by human tactile afferents. J. Neurosci. 21, 8222-8237 and (e-g) from Johansson, R. S. and Birznieks, I. 2004. First spikes in ensembles of human tactile afferents code complex spatial fingertip events. Nat. Neurosci. 7, 170-177.

geometric features (e.g., Braille-like patterns and gratings), including markedly curved surfaces (radii $<\sim$ 5 mm, i.e., curvatures $>\sim$ 200 m⁻¹), gently stimulating the fingertips in monkeys (Johnson, K. O., 2001; Goodwin, A. W. and Wheat, H. E., 2004). Such stimuli primarily engage afferents that terminate in the area of contact. However, objects that humans grasp in most everyday situations (e.g., cups, knobs, handles,

pens, fruit) involve larger curvatures (curvatures $\leq \sim 200 \text{ m}^{-1}$), and the control of fingertip actions in dexterous object manipulations depends critically on tactile information about these gross geometrical features (Jenmalm, P. and Johansson, R. S., 1997; Jenmalm, P. *et al.*, 2000). Recent findings in humans suggest that, in contrast to the encoding of fine form shapes, encoding of gross shapes engages ensembles of afferents terminating over the entire terminal phalanx (Jenmalm, P. *et al.*, 2003). Shape changes robustly influence firing rates in the majority of responsive SA-I, SA-II, and FA-I afferents, including afferents that terminate at the sides and end of the fingertip. For each afferent type, roughly half

the afferents for which response intensity correlate with curvature showed a positive correlation and half a negative correlation (Figure 4(a) and 4(b)); afferents terminating at the sides and end of the fingertip tend to show negative correlations. Consequently, there is a curvature contrast signal within the populations of tactile afferents. This contrast signal may aid curvature recognition even though the overall discharge rates of afferent populations are influenced by various factors, e.g., the magnitude, direction, and rate of change of the contact force and changes in viscoelastic properties of the fingertip related to previous interactions with objects. Although the FA-I, SA-I, and SA-II afferents



Figure 4 (Continued)

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Figure 4 Signals in human tactile afferents under stimulation conditions representative for object manipulation tasks: Encoding of shape of spherically curved surfaces contacting the fingertips. (a) Impulse ensembles show responses to repeated stimuli (n = 5) of two single fast-adapting type I (FA-I), slowly adapting type I (SA-I), and slowly adapting type II (SA-II) afferents with forces applied in the normal direction with each of three surface curvatures 0, 100, and 200 m⁻¹ (force stimulation as in Figure 3(a)). Traces above show the instantaneous discharge frequency averaged over the five trials. Top traces show the normal force. Left and right panels for each afferent type represent afferents for which response intensity increased (positively correlated) and decreased (negatively correlated) with an increase in curvature. (b) Left and right panels show, for each type of afferent, afferents with responses positively and negatively correlated with surface curvature, respectively; response is represented as the mean number of impulses evoked during the protraction phase (gray zone in (a)) with each curvature. Solid circles on the fingertip indicate the location of the receptive field centers of the afferents and the cross the stimulation site; the side view of the fingertip includes afferents located on either side of the finger. (c) Interaction effects between curvature and force direction on afferent responses illustrated by responses in one SA-I afferent during stimulation with forces in five directions (see Figure 3(a)) with the flat (0 m⁻¹) and most curved (200 m⁻¹) surface. Force profiles shown for the normal force component and for the tangential force components (F_{d-p}, F_{r-u}); radial, distal, ulnar, and proximal refer to the direction of the tangential force component. Profiles of instantaneous discharge frequency show responses to the 0 and 200 m⁻¹ curvature; the center line indicates the mean instantaneous firing rates averaged over repeated stimuli (n = 5) and the thin lines represent the recorded maximum and minimum of the five rates. The dots on the fingertip indicate the afferents' receptive field center, the cross marks the stimulation site. (d-f) Discrimination of shape of stimulus surface by FA-I and SA-I afferents based on relative timing of the first spikes evoked in ensembles of tactile afferents and on the firstinterspike intervals. (d) Impulse ensembles illustrate the effect of shape of stimulus surface on first-spike latencies of two single FA-I and SA-I afferents during five normal force stimuli with the flat (0 m^{-1}) and the most curved surface (200 m⁻¹). Traces above show normal force (F_n) and traces below instantaneous discharge frequency averaged over the five trials. Surface influenced consistently the first-spike latencies of all of these afferents. (e and f) Solid curves in the top graph show the probability of correct discrimination of each shape (coded by different colors) based on afferents' recruitment sequence as a function of time during the force protraction phase. Thin horizontal line indicates the probability for one-half of the stimuli being discriminated correctly, i.e., a probability of 66.5% given that chance performance is 33.3%. See caption of Figure 3(e-g). (a-c) Adapted from Jenmalm, P., Birznieks, I., Goodwin, A. W., and Johansson, R. S. 2003. Influences of object shape on responses in human tactile afferents under conditions characteristic for manipulation. Eur. J. Neurosci. 18, 164–176 and (d-f) from Johansson, R. S. and Birznieks, I. 2004. First spikes in ensembles of human tactile afferents code complex spatial fingertip events. Nat. Neurosci. 7, 170-177.

might all contribute information on object shape and contact forces, the SA-II population likely provides coarser information than the SA-I and especially the FA-I populations because of the lower innervation density of SA-II afferents. Because tactile afferents respond to the complex patterns of strain/stress that occur in the fingertip when objects are contacted, various contact parameters can show complex interaction effects on the afferent responses. Interactions between force

direction and object shape on the responses of SA-I, SA-II, and FA-I afferents have been demonstrated (Jenmalm, P. et al., 2003). That is, changing the direction of force generally affects an afferent's sensitivity to curvature and vice versa. Figure 4(c) illustrates such an interaction for a single SA-I afferent. How the brain deals with interactions among different parameters of fingertip stimulation in natural tasks poses important problems for future research. Presumably, many computational requirements for decoding tactile messages in manipulation tasks are satisfied by the somatosensory pathways functionally modeling the mechanics of the fingertips in the tactile sensory domain by, in effect, filtering information predictively in a manner that depends on context, task, and task phase. For example, corollary discharges associated with the execution of action plans (Sommer, M. A. and Wurtz, R. H., 2002) could, through descending corticothalamic, corticocuneate, and corticospinal projections, dynamically control the signal processing in ascending somatosensory pathways (Harris, F. et al., 1965; Adkins, R. J. et al., 1966; Ergenzinger, E. R. et al., 1998). As such, there is ample evidence that the processing of sensory stimuli is controlled by top-down influences that constantly create predictions about forthcoming sensory events (Engel, A. K. et al., 2001) including contract events (Bays, P. M. et al., 2005).

6.05.2.3 Relative Spike Timing Provides Fast Information about Mechanical Fingertip Events

Traditionally, it is posited that tactile information is coded by the firing rates of afferents. To estimate firing rates, at least two impulses in a given neuron are required and given the stochastic properties of interspike intervals, reliable rate estimation may require that neural responses be averaged over a substantial time window and over several trials. However, in manipulation, typically, the brain quickly extracts information from dynamic tactile events and expresses this information in fingertip actions faster than can be readily explained by rate codes. Recent findings indicate that the relative timing of impulses from ensembles of individual different afferents conveys information about important contact parameters faster than the fastest possible rate code and fast enough to account for the use of tactile signals in natural manipulation (Johansson, R. S. and Birznieks, I., 2004). Specifically, the sequence in which different afferents initially discharge in response to discrete fingertip events provides information about the direction of fingertip force and the shape of the contacted surface. Presumably, the order of recruitment of members of the populations of tactile afferents can code other parameters of tactile stimuli used in the control of manual actions as well.

The relative timing of the first spikes contains information about force direction and object shape because changes in either of these parameters differentially influences the first-spike latency of individual afferents rather than having systematic effects on the latencies within an afferent population (Figures 3(e) and 3(g) and 4(d) and 4(f)). For example, with a single stimulus delivered to the fingertip in a given force direction, the responsive afferents will be recruited in a particular order. With another force direction, the order will be different because some afferents are recruited earlier and others later. The efficacy of this code for conveying early information to the brain depends on the variability and noise in firstspike latencies and the speed of recruitment of afferents. The FA-I population provide correct discrimination faster than the SA-I afferents of both force direction (cf. Figure 3(f) and 3(g)) and surface curvature (cf. Figure 4(e) and 4(f)). Effective discrimination takes place after as few as some five FA-I afferents are recruited, which occur a few milliseconds after the appearance of the first impulse in the population response (Figure 3(f) and 3(e)). For the SA-Is, about twice as many (but still very few) afferents had to be recruited for reliable discrimination primarily because of a larger variability in first-spike latencies. Even under the most favorable conditions, discrimination based on firing rates (first-interspike rate) takes on average 15-20 ms longer than discrimination based on first-spike latency (cf. dashed and solid curves in Figure 3(f) and 3(g) and 4(e) and 4(f)). Populations of SA-II are much poorer in discriminating force direction or object shape based on both first-spike latencies and firing rate, in part because of the background discharge in many of these afferents. Encoding and decoding of sensory information based on the timing of neural discharges, rather than (or in addition to) their rate, has received increasing attention in the past decade and it has become clear that the timing, with precision in the order of milliseconds or even less, of individual spikes can carry far more information than average rates alone (Heil, P., 2004; VanRullen, R. et al., 2005).

6.05.3 **Predictions and Control** Points in the Tactile Modality

6.05.3.1 Control of Reach

Most manipulation tasks require that we first reach for the object to grasp it. One goal of this reach phase is 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. Likewise, it is usually important that the fingertips contact the object at around the same time and that the fingertip force vectors sum to zero. These and other features of the contacts between the fingertips and object are robustly encoded by tactile signals. 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 (Figure 1(b) and 3). Thus, the initial contact events represent control points where predicted and actual sensory feedback related to object geometry, location, and orientation can be compared. Mismatches between predicted and actual contact responses can be used to calibrate and uphold calibration of future reach commands (Gentilucci, M. et al., 1997; Lackner, J. R. and DiZio, P. A., 2000; Rao, A. K. and Gordon, A. M., 2001; Monzée, J. et al., 2003; Säfström, D. and Edin, B. B., 2004).

6.05.3.2 Control of Grasp Stability

After contact is obtained with an object, most manipulation tasks require application of forces tangential to the contacted surfaces (load forces). For example, to lift an object with the digits at the sides, vertical load forces must be applied to overcome the weight of the object (Figure 1(a)). If we lift a bar from one end, we must also apply tangential torque to prevent it from rotating when lifted. To deal with these potentially destabilizing tangential forces, the motor system generates grip forces normal to the grasped surface that are synchronous with, and proportional to, the tangential loads applied (Figures 1(a) and 5) (Johansson, R. S. and Westling, G., 1984a; Goodwin, A. W. et al., 1998; Johansson, R. S. et al., 1999). The grip forces are strong enough to prevent the object from slipping (either linearly or rotationally), while at the same time not excessive. This coordination of grip and load force supports grasp stability in virtually all maneuvers that we perform with objects. For example, it operates at the level of individual digits when people use two or more digits of the same or both hands to lift and further manipulate objects (Edin, B. B. et al., 1992; Flanagan, J. R. et al., 1999). Likewise, grip forces predict changes in load forces on a hand-held object that occur when we jump up and down (Flanagan, J. R. and Tresilian, J. R., 1994) and in bimanual tasks where 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 (Johansson, R. S. and Westling, G., 1984a; 1988b). 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 (Flanagan, J. R. and Wing, A. M., 1997).

The control of grasp stability requires, however, that the balance between the grip and load forces be adapted to the properties of the contacted surfaces. Indeed, irrespective of surface friction and object shape, people typically use 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 5). By varying the ratio between grip force change and load force change, people parametrically adapt to different frictional conditions and use greater grip forces with more slippery surfaces (Figure 5(b)). In the same vein, they adapt the grip-to-load force ratio to the shape of the contacted surface. For example, when lifting tapered objects, a greater grip-to-load force ratio is required when the grip surfaces are tapered upward as compared to downward (Figure 5(c)). Similarly, the greater the curvature of a spherically curved grasp surface, the larger the grip force required to generate a given tangential torque (Figure 5(d)).

Tactile signals are critical for forming, updating, and upholding predictions used by action-phase controllers when adapting forces to object surface properties. Indeed, 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.* Figure 6(b) and 6(c)) (Johansson, R. S. and Westling, G., 1984a; Westling, G. and Johansson, R. S., 1984; Jenmalm, P. and Johansson, R. S., 1997; Jenmalm, P. *et al.*, 2000; Monzée, J. *et al.*, 2003; Nowak, D. A. *et al.*, 2004). Signals in ensembles of tactile afferents – primarily in FA-Is – rapidly convey information related to



Figure 5 Parametric adjustments of fingertip forces to object weight, friction between the object and skin, and shape of the contact surface. (a-c) Subject lifts an instrumented test object from a table, holds it in the air, and then replaces it, using a precision grip (cf. Figure 1). 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 corresponding data. Dashed lines indicate the minimum grip force to prevent slips; the safety margin against slips is indicated by hatching. (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. (b) The balance between grip force and load force is adjusted to deal with changes in friction. (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. (d) An already lifted object is tilted by 65° around the grip axis, which caused tangential torques at the grasp surfaces. The three superimposed curves (color coded) refer to a trial with a spherically convex grip surface (radius 5 mm; curvature 200 m⁻¹), a flat (curvature 0 m⁻¹), and a spherically concave surface (radius 20 mm; curvature 50 m⁻¹). The top traces show the grip force, the tangential torque, and the tilt angle against time. Note the effect of surface curvature on the coordination between grip force and tangential torgue, which is in the bottom graph that plots 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, b) Adapted from Johansson, R. S. and Westling, G. 1984a. Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. Exp. Brain Res. 56, 550-564; Johansson, R. S. and Westling, G. 1988a. Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. Exp. Brain Res. 71, 59-71, (c) Jenmalm. P. and Johansson, R. S. 1997. Visual and somatosensory information about object shape control manipulative finger tip forces. J. Neurosci. 17, 4486–4499. (d) Goodwin, A. W., Jenmalm, P., and Johansson, R. S. 1998. Control of grip force when tilting objects: effect of curvature of grasped surfaces and of applied tangential torque. J. Neurosci. 18, 10724–10734, respectively.

surface friction (Figure 6(d)) and shape (Figures 4 and 7(a)) when a surface is contacted. Thus, the initial contact event represents a critical control point where predicted and actual sensory feedback

related to surface properties can be compared. Mismatches between predicted and actual contact responses lead to an updating of the grip-load force coordination about 100 ms after contact. Figure 7(a) illustrates such updating when repeatedly lifting objects with tapered grasp surfaces without visual cues about object shape. The tapering was changed between trials in a pseudo-random order. In all trials, the tapering (and hence force requirements) in the previous trial determined the initial increase in grip force. This indicates that predictions based on knowledge about the status of the object obtained in previous trials specify the force coordination. After a change in tapering, the grip force output is modified about 100 ms after contact with the object and tuned for the actual object properties (Figure 7(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. Knowledge about object surface properties remains critical for controlling grip forces for grasp stability when transporting held objects and using them as tools to impose forces on other environmental objects. A coupled decrease in the load and grip forces ensuring grasp stability also applies to the unloading phase where grip and load forces decrease in parallel in order to release an object placed on a support surface (Figures 1 and 5). Sensory events, especially in ensamples of FA-I afferents, related to the breaking of contact between the digits and the surface of the object represent the sensory goal of this phase (see release responses in Figure 1(b); see also responses in FA-I afferents to the retraction phase in Figures 3 and 4).

Under favorable conditions, visual geometric cues about object shape can provide state information for predictive parameterization of fingertip forces such that the grip-to-load force coordination is adapted to the prevailing shape right from the beginning of the force application (Figure 7(b)) (Jenmalm, P. and Johansson, R. S., 1997; Jenmalm, P. *et al.*, 2000). Once the object is contacted, tactile signals also provide state information about object shape that can override visual predictions if necessary. With regard to friction between the hand and an object, it appears that vision is unhelpful for feedforward adaptation of



Figure 6 (Continued)

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Figure 6 Adjustment of grip force to frictional changes in everyday situations. (a) 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) before and after the subject's hand was washed (soap and water) and dried (towel); 48 consecutive lifts with suede as surface structure (single subject, weight constant at 400 g). (b and c) Corresponding grip force data during frictional changes between lifts caused by changing the grasped surfaces among fine-grain sandpaper, and suede and smooth rayon, during normal digital sensibility (b) and with anesthetized finger tips (c). (d) The influence of friction on force output and initial contact responses in an fast-adapting type I (FA-I) afferent. Two lifting trials are superimposed, one with the grasped surfaces being less slippery (sandpaper; black lines) and a subsequent trial with more slippery surfaces (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. (e) Digit-specific adjustments of force coordination to the frictional condition. The participant lifted a test object with low center of gravity (CG) from a support surface, and held it still in the air. The index finger contacted a more slippery surface (silk; blue curves) than that contacted by the thumb (sandpaper; black curves). The grip-to-load force ratio and corresponding slip ratios are shown for each digit; the blue and black areas indicate the safety margin to prevent slips at the index finger and at the thumb, respectively. In a previous lifting trial, both the index finger and the thumb had contacted finegrain sandpaper. An initial adjustment to the new frictional condition occurs during the load phase, ~100 ms after the object is contacted. The index finger generates less load force than the thumb, which results in a higher grip-to-load force ratio at the index finger. A slip event occurring at the index finger later in the trial triggers a secondary adjustment to the frictional condition. The slip event is evident by a rapid decrease of the load force at that digit and a concomitant increase of the load force at the thumb. Less than 100 ms later, a grip force increase raises the grip-to-load force ratio at the index finger and restores the ratio at the thumb. Nevertheless, because of the uneven load force distribution between the digits, the test object tilts a bit when aloft. The inset shows signals in single FA-I afferents reconstructed based on microneurography recordings during similar lifting trials in a study by Johansson R. S. and Westling, G. (1987). Note the influence of the surface material on the impulse rate on the initial contact responses (a), the burst response to the slip in the afferent terminating in the tip of the slipping digit (b), and the response to the increase of the load force at the opposing digit. (a) Adapted from Johansson, R. S. and Westling, G. 1984b. Influences of Cutaneous Sensory Input on the Motor Coordination During Precision Manipulation. In: Somatosensory Mechanisms (eds. C. von Euler, O. Franzen, U. Lindblom, and D. Ottoson), pp. 249–260. Macmillan Press; (b and c) from Johansson, R. S. and Westling, G. 1991. Afferent Signals During Manipulative Tasks in Man. In: Somatosensory Mechanisms (eds. O. Franzen and J. Westman), pp. 25-48. Macmillan Press; (d) from Johansson, R. S. and Westling, G. 1987. Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. Exp. Brain Res. 66, 141–154; and (e) from Edin, B. B., Westling, G., and Johansson, R. S. 1992. Independent control of fingertip forces at individual digits during precision lifting in humans. J. Physiol. 450, 547-564.

force coordination. Presumably, this is because friction depends not only on the object surface but also on sweating rate and the greasiness and wetness of the skin (and objects) (Figure 6(a)). Thus, predictions of frictional conditions are based on the memory of recent haptic experiences with the same or similar objects. By varying the frictional condition independently at individual digits in two-digit and multidigit object lifting tasks it has been shown that the grip-toload force ratios employed at each of the digits engaged can be independently controlled (Edin, B. B. *et al.*, 1992; Burstedt, M. K. O. *et al.*, 1999). When gripping and lifting an object using a precision grip, the digit that contacts a more slippery surface can exert less vertical lifting force than the digit in contact with a less slippery surface. Unpredicted



Figure 7 Adaptation of fingertip forces to changes in object shape. Vertical load force and horizontal grip force shown as a function of time for trials (a) without and (b) with vision of the contacted surfaces from a lift series in which surface angle was unpredictably varied between lifts. 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 dashed yellow segment in the grip force curve in (a) indicates the epoch of the corrective action elicited by the new surface angle. The thin dashed red 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 about 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. (a and b) Compiled from data presented in Jenmalm, P. and Johansson, R. S. 1997. Visual and somatosensory information about object shape control manipulative finger tip forces. J. Neurosci. 17, 4486-4499.

asymmetries in the frictional conditions at the digits can influence the development of the tangential forces during the load phase some 100 ms after contact (Figure 6(e)). Likewise, the average friction of the grasped surfaces influences the rate of increase of the grip force after this point.

Occasionally, the updating of frictional and shape representations that typically occurs at initial contact is inadequate and may result in an accidental slip later in the task. When an object is held in air after being lifted, such a slip usually results in a transitory and partial unloading at one digit (the slipping digit) and this increases the loads on the other digits engaged (Figure 6(e)). Such transient redistribution of the tangential force triggers a grip force increase. The net outcome is an increased safety margin at the slipping digit for the remainder of the task but a virtually unaffected safety margin at the other digits. This updated force coordination is used as default coordination for subsequent trials with the same object, again indicating that the force coordination is controlled by memory representations related to object properties. While slips during the hold phase lead to an increase in grip force, slips during the load phase in lifting lead to a slowing down of the subsequent increase in load force at the slipping digit (Johansson, R. S. and Westling, G., 1984a; 1987). Hence, different action-phase controllers are associated with different smart reflex mechanisms that support grasp stability and help achieve the current subgoal of the task.

6.05.3.3 Control of Motion of Objects in Hand

Tactile control points can also support planning and control of transport of grasped objects. The goal of many action phases in object manipulation (including tool use) is to move a held object so as to break or form contact between it and another object. The held object transmits various features of these contact events that tactile afferents can signal. Likewise, sensory plans in manipulation tasks integrate and thus predict the occurrence and nature of such signals, which allow

for comparison of predicted and actual sensory events at the level of the appropriate action-phase controllers. This applies, for example, when we lift an object, hold it in air, and then replace it on the support surface (Figure 1). The object breaking contact with the support surface at liftoff represents the sensory goal of the load phase and constitutes a control point for the loadphase controller. Likewise, the contact event that occurs when the object lands on the support surface represents the sensory goals of the controller that replaces the object. Because of their exquisite sensitivity to mechanical transients, ensembles of FA-II afferents most quickly and reliably signal the incidence and the dynamics of both the liftoff and the landing event (Westling, G. and Johansson, R. S., 1987).

Because no sensory information is available about weight until liftoff in object lifting, a natural, smooth, and critically damped lifting motion requires that the load force drive at liftoff, which accelerates the object, be scaled predictively to object weight. People form such predictions based on sensorimotor memory of the object derived from previous interactions with the object (Johansson, R. S. and Westling, G., 1988a). Familiar objects can be identified visually (or by haptic exploration) for retrieval of weight estimates (Gordon, A. M. et al., 1991), and size-weight associations can be used to predict the weights of familiar objects that are organized into families of objects where the items can vary in size (e.g., cups, books, loafs of bread) (Gordon, A. M. et al., 1993). Erroneous weight predictions often result in pronounced performance errors. For example, when we lift an object that is lighter than predicted and the load phase is programmed for a heavier weight, we typically make jerky movements and lift the object higher than intended (Figure 8(a), T2). The sensory events elicited by the liftoff occur before the predicted events that are part of the sensory plan (cf. predicted and actual neural events in Figure 8(a)). This mismatch automatically triggers a learned corrective action (smart reflex) 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 the substantial 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 8(b)). When lifting an object that is heavier than expected, the load phase becomes slow and hesitant because the force drive is targeted for a lighter weight and additional increases in force are required to bring the object aloft (Figure 8(b), T2). In

this case, the predicted sensory event related to liftoff does not occur at the predicted time (cf. predicted and actual neural events in Figure 8(b)). Hence, again there is a mismatch between actual and predicted sensory events. The corrective action triggered by the mismatch now involves slow, probing increases in fingertip forces until terminated reactively by sensory events signaling liftoff. Thus, the sensorimotor system reacts to both the presence of an unpredicted event and the absence of a predicted sensory event. Importantly, 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 Figure 8) while with objects with unusual dynamics (relating applied force to motion) (Flanagan, J. R. and Wing, A. M., 1997; Flanagan, J. R. et al., 2003) or in the presence of misleading cues (Gordon, A. M. et al., 1991; Flanagan, J. R. and Beltzner, M. A., 2000), updating may require repeated lifts or movements of the object.

6.05.4 Predictions and Control Points in Other Modalities

Studies of eye movements in object manipulation indicate that contact events that demarcate action phases can also be predicted and monitored in the visual modality (Land, M. et al., 1999; Johansson, R. S. et al., 2001; Land, M. F., 2006). Accordingly, people use saccades to direct their gaze to successive contact locations as they gain salience in the evolving manipulation task. 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 (Johansson, R. S. et al., 2001). Both hand and eye movements are specified based on peripheral vision about the contact location (or on memorized landmark locations), but gaze reaches the contact location well before the hand (or object in hand) because the saccadic eye movements are quick. 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). This indicates that the visual system, like the tactile system, can monitor control points linked to the completion of task subgoals.



Figure 8 Adaptation of motor output to object weight. Single-unit tactile afferent responses and adjustments in force to unexpected changes in object weight. Data from single lift trials aligned on initial touch (vertical line). Gray circles and vertical lines indicate the moment of liftoff for each trial and the arrowheads point at the actual sensory events generated by the liftoff in a fast-adapting type II (FA-II) afferent. The circles behind the nerve traces indicate the corresponding predicted sensory events. (a) Three successive trials (T1–T3) in which the subject lifted an 800 g object (blue curves), a 200 g object (solid red curves), and then the 200 g object again (dashed red curves). The forces exerted in the first lift are adequately programmed - they had previously lifted the 800 g object. The forces are erroneously programmed in the first 200 g lift (T2), i.e., 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 (cf. actual and predicted sensory events), which initiates a corrective action (yellow-dashed red curves). The strong force drive of the ongoing load phase is terminated but still results in overshoots in position due to the reflex delay and a corrective motor command is launched that brings the object back to the intended position. (b) The participant performed an adequately programmed lift with a 400 g weight (T1, green curves), followed by a lift with 800 g, erroneously programmed for the lighter 400 g weight lifted in the previous trial (T2, solid blue curves), and then a lift with the 800 g object again (T3, dashed blue curves). The absence of burst responses in fast-adapting type II (FA-II) afferents at the predicted point for the erroneously programmed 800 g trial (cf. actual and predicted sensory event) 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 liftoff. The top diagram in (a) and (b) represents the status of the sequentially implemented action-phase controllers. In T1 they are parameterized for the 800 g (b) and 400 g (b) weight throughout. In T2, a corrective action (Corr) is triggered about 100 ms after the occurrence of the mismatch between predicted and actual sensory information related to object liftoff. This action involves abortion of the operation of the current action-phase controller and the implementation of corrective 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. (a-b) Developed from Johansson, R. S. and Cole, K. J. 1992. Sensory-motor coordination during grasping and manipulative actions. Curr. Opin. Neurobiol. 2, 815-823.

Furthermore, the gaze behavior indicates that goal completion can be predicted in sensorimotor systems. That is, the time of gaze shift to the contact location associated with the next action phase occurs around the time of goal completion and is not delayed until sensory feedback verifying goal completion triggers the gaze shift. The latter strategy would lead to substantial lags in gaze behavior because of the time delays in sensorimotor control loops. That both gaze and hand movement commands are initiated in anticipation of goal completion reinforces the idea that sensory predictions about the terminal state of each action phase provide initial state information for the controller responsible for executing the subsequent action phase.

Although there is no question that contact points predicted and monitored in the tactile modality are essential for skilled object manipulation, there are contact events 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 only available through vision (and possibly audition). Thus, vision and the tactile system can play complementary roles in predicting and monitoring contact events. Prediction of contact events in the visual modality without the tactile modality being engaged is evident from studies of eye movements when people observe an actor performing familiar manipulation tasks. In this situation, the gaze of both the actor and observer predicts forthcoming contact sites (e.g., where blocks are grasped and replaced in a predictable block stacking task) and gaze is maintained at each contact site until around the time of goal completion (grasp contact and block landing) (Flanagan, J. R. and Johansson, R. S., 2003). By comparing actual and predicted visual feedback related to contact events, both observers and actors may be able to obtain valuable information about outcomes of actions that can be exploited by the sensorimotor system when learning, planning, and controlling future actions. These findings also support the notion that understanding of observed actions performed by others involves a mechanism that maps observed actions onto sensorimotor representations in the observers' brain implemented in real time (Rizzolatti, G. et al., 2001; Flanagan, J. R. and Johansson, R. S., 2003; Rotman, G. et al., 2006).

6.05.5 Conclusions

Dexterity in object manipulation tasks depends on anticipatory control policies that rely on knowledge about movement-effect relationships when interacting with environmental objects. The tactile modality plays a pivotal role in gaining such knowledge because signals from tactile afferents provide direct information about mechanical interactions between the body and objects in the environment. The usefulness of visual and proprioceptive mechanisms in guiding the hands in object manipulation depends on learned associations between visual and proprioceptive cues and their mechanical meaning derived from tactile mechanisms. Signals in ensembles of tactile afferents of different types convey complementary information related to both the timing and the physical nature of the various kinds of contact events that represent the outcomes of motor commands to the hand. Populations of tactile afferents encode time courses, magnitudes, directions, and spatial distributions of contact forces relative to the hand. They likewise encode information related to surface properties of contacted objects such as shape and texture of contacted surfaces and frictional conditions between these surfaces and the skin. In addition to critically supporting the control of fingertip actions in manipulation, the brain uses tactile afferent information for establishing sensorimotor correlations that underlie haptic object identification as well as representations of object affordances used in planning of object manipulation activities.

Such action plans are composed of sequences of action phases implemented to attain task subgoals specified (and verified) in terms of sensory signals. Thus, manipulatory tasks involve a sensory plan that specifies the sequence of task subgoals and provides a scaffold for the selection and shaping of the actionphase controllers implemented for achieving sensory subgoals. Distinct contact events signaled in the tactile modality generally represent subgoals, but these subgoals can also be represented in the visual and auditory modalities. 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 feedforward fashion based on predictions derived from internal representations of object properties gained in previous interactions with objects. 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. Prediction of the terminal sensorimotor state of each action phase prevents stuttering phase transitions that would result if the brain relied on peripheral afferent information to confirm subgoal completion and update state information before launching the next action phase. The fact that contact events give rise to distinct sensory signals in multiple modalities permits the sensorimotor system to simultaneously monitor multiple aspects of task performance and, if prediction errors arise, respond to the pattern of errors observed in different modalities. Finally, contact events often give rise to multimodal sensory events that are linked in time

and space and this provides an opportunity for intermodal alignment helpful for learning and upholding multimodal sensorimotor correlations necessary for prediction of purposeful motor commands.

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