Sensory control of object manipulation

Roland S Johansson[1] and J Randall Flanagan[2]

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

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

Correspondence should be addressed to:

Roland S Johansson

Physiology Section, IMB, University of Umeå

SE-901 87 Umeå, Sweden

Phone: +46-90-786 5490, Fax: +46-90-786 6683

e-mail: roland.s.johansson@physiol.umu.se

Keywords:

eye movements; grasp stability; grip force; human hand; manipulation; internal models; motor control; movement; sensorimotor predictions; feedforward sensory control; procedural memory; saccades; sensorimotor transformation; tactile sensibility;

Synopsis

Series of action phases characterize natural object manipulation tasks where each phase is responsible for satisfying a task subgoal. Subgoal attainment typically corresponds to distinct mechanical contact events, either involving the making or breaking of contact between the digits and an object or between a held object and another object. Subgoals are realized by the brain selecting and sequentially implementing suitable action-phase controllers that use sensory predictions and afferents signals in specific ways to tailor the motor output in anticipation of requirements imposed by objects' physical properties. This chapter discusses the use of tactile and visual sensory information in this context. It highlights the importance of sensory predictions, especially related to the discrete and distinct sensory events associated with contact events linked to subgoal completion, and considers how sensory signals influence and interact with such predictions in the control of manipulation tasks.

Sensory systems supporting object manipulation

In addition to multiple motor systems (arm, hand, posture), most natural object manipulation tasks engage multiple sensory systems. Vision provides critical information for control of task kinematics. In reaching, we use vision to locate objects in the environment and to identify contact sites for the digits that will be stable and advantageous for various actions we want to perform with the grasped object (Goodale, Meenan, Bülthoff, Nicolle, Murphy and Racicot, 1994; Santello and Soechting, 1998; Cohen and Rosenbaum, 2004; Cuijpers, Smeets and Brenner, 2004; Lukos, Ansuini and Santello, 2007). For example, when we pick up a hammer to drive in a nail, we will likely use different grasp sites than when picking it up to give it to another person. When reaching, people naturally direct their gaze to visible targets and looking at the target enables optimal use of visual feedback of hand position to guide the hand (Paillard, 1996; Land, Mennie and Rusted, 1999; Sarlegna, Blouin, Vercher, Bresciani, Bourdin and Gauthier, 2004; Saunders and Knill, 2004). In addition, proprioceptive and/or motor signals related to gaze position can be used to guide the hand; even when the hand is not visible, directing gaze to the target improves reaching accuracy (Prablanc, Pélisson and Goodale, 1986; Prablanc, Desmurget and Gréa, 2003). Once grasped, we often move the object to make or break contact with another objects or surfaces (e.g., in lift, transport and place tasks) or to contact and impose forces on other objects (e.g., when using tools such as a hammer, screwdriver or wrench). Studies of eye movements in object manipulation have shown that gaze fixations also play an important role in providing information for planning and control of motions with objects in hand (Ballard, Hayhoe, Li and Whitehead, 1992; Land et al., 1999; Johansson, Westling, Bäckström and Flanagan, 2001). In addition to providing information for motion planning, visual cues about the identity, size, and shape of an object can provide information about its mechanical properties that is useful for predicting the forces require for successful manipulation. For example, visual cues related to object weight and mass distribution can be used to predict magnitudes of required fingertip forces (Gordon, Forssberg, Johansson and Westling, 1991; Gordon, Westling, Cole and Johansson, 1993; Wing and Lederman, 1998; Salimi, Frazier, Reilmann and Gordon, 2003) and visual cues about the shape of grasp surfaces can be used to predict stable fingertip force directions (Jenmalm and Johansson, 1997; Jenmalm, Dahlstedt and Johansson, 2000).

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 provides indirect information about mechanical interactions between the hand and objects. That is, the use of vision in manipulation relies on learned associations (statistical correlations) 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. Indeed, people with impaired digital sensibility have great difficulty even with routine tasks performed under optimal 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, i.e., the palmar surfaces of the hands, the soles of the feet, and the tongue and lips. Furthermore, for the hand and the foot, the density is highest at the most distal segments. For the human hand, about 2,000 tactile afferents innervate each fingertip whereas some 10,000 afferent neurons innervate all of the remaining glabrous skin areas of the digits and the palm (Johansson and Vallbo, 1979). Four different types of tactile afferents encode complementary aspects of the deformations of the soft tissues when the hands interact with objects (Johansson and Vallbo, 1983; Vallbo and Johansson, 1984) (further details see Fig. 1B). 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 moving hand held objects (Johansson and Westling, 1987; Westling and Johansson, 1987; Macefield, Häger-Ross and Johansson, 1996). These dynamic tactile signals reliably encode various aspects of contact events around which most object manipulation tasks are organized.

Comparatively little is known about the contribution of proprioceptive and auditory signals in the control of manipulation tasks. Like vision, these modalities can only provide indirect information about mechanics. Proprioception 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 non-digital mechanoreceptive afferents (e.g., musculotendinous afferents) to fingertip events is very low in comparison to that of tactile sensors (cf. Macefield and Johansson, 1996 and Macefield et al., 1996; see also Häger-Ross and Johansson, 1996).

Contact events and action goals in manipulation tasks

Natural object manipulation tasks usually involve a series of action 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 (Fig. 1A) (Johansson and Westling, 1984). 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. That is, subgoal attainments are generally associated with distinct signals in one or more sensory modalities, each providing an afferent neural signature that encode the timing as well as the characteristics of the mechanical interaction of the corresponding contact event.

A given object manipulation task can be represented as a sensory plan wherein a sequence of sensory goals is specified in one or more sensory modalities (Flanagan, Bowman and Johansson, 2006). To achieve the sensory goals, the brain selects and executes a corresponding sequence of basic actions, or action-phase controllers (Fig. 1A). To be accurate, when possible the controllers use knowledge of object properties, combined with information about the current state of the system (including the initial configuration of the motor apparatus and objects in the environment), to predictively adapt the motor output with reference to attainment of their sensory goals. 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.

In addition to generating motor commands, implemented action-phase controllers generate predictions about the sensory consequences of the motor output, including sensory signals associated with contact events. By comparing predicted and actual sensory signals, task progression is monitored (Fig. 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. If a mismatch occurs in one or more modalities because of misleading initial state information or unpredicted external or internal events, the brain can launch corrective actions (or smart reflexes), the nature of which is specific for the sensory signals, the implemented controller, and the current state of the system and environment. If the mismatch is due to erroneous predictions about object properties, memory representations related to these properties can be updated to improve predictive control in subsequent phases of the task and in other tasks with the same object. This highly task and phase specific use of sensory information in object manipulation tasks is presumably acquired when we learn the underlying basic action-phase controllers, which occurs gradually during ontogeny until about 10 years of age (Forssberg, Eliasson, Kinoshita, Johansson and Westling, 1991; Forssberg, Kinoshita, Eliasson, Johansson, Westling and Gordon, 1992; Gordon, Forssberg, Johansson, Eliasson and Westling, 1992; Eliasson, Forssberg, Ikuta, Apel, Westling and Johansson, 1995; Forssberg, Eliasson, Kinoshita, Westling and Johansson, 1995; Paré and Dugas, 1999).

Although we have emphasized that manipulation tasks are organized as a sequence of discrete 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 state of the motor system and environment at the termination of one action phase also provide initial state information for the subsequent action-phase controller. This information allows parameterization of the next action phase in advance, which is necessary for smooth transitions between the component actions of the task. In the absence of such anticipatory control, stuttering phase transitions 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 delay, 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. In the remainder of this chapter, we will discuss experimental results from manipulation tasks that illustrate and further develop the general principles described above.

Predictions and control points in the tactile modality

Control points for reaches for objects

The goal of the first action phase in most manipulation tasks is to bring the hand to the object in order to grasp it, or more precisely to position the digits 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 likewise important that the fingertips contact the object at around the same time and that the fingertip force vectors sum to zero (Burstedt, Edin and Johansson, 1997; Flanagan, Burstedt and Johansson, 1999; Reilmann, Gordon and Henningsen, 2001). This is particularly important when initially contacting a light object that might otherwise be displaced or rotated. Signals in ensembles of tactile afferents robustly and rapidly encode these and other features of the contacts between digits and objects (Johansson and Westling, 1987; Westling and Johansson, 1987; Macefield et al., 1996; Birznieks, Jenmalm, Goodwin and Johansson, 2001; Jenmalm, Birznieks, Goodwin and Johansson, 2003; Johansson and Birznieks, 2004). Thus, the contact events between the digits and objects provide control points for reach phases where tactile signals can be compared with predicted tactile input concerning contact timing, geometry, and forces, and errors can be assessed regarding the outcome of the executed action phase-controller. Not surprisingly, weak single pulse transcranial magnetic brain stimulation (TMS) delivered to the hand area of the contralateral primary sensorimotor cortex just before the instance of contact can interfere with this process (Lemon, Johansson and Westling, 1995). That is, it causes a disruption of the transition from the reach phase to the subsequent load phase and results in a significant and variable delay of the onset of the load phase. This effect might result from the TMS influencing the motor output causing a mismatch between the actual and predicted spatio-temporal pattern of afferent information related to contact, disruption of the sensory prediction and/or disturbed processing of tactile afferent information. Various lines of evidence indicate that tactile contact information is important both for calibration and upholding of accuracy of reach commands (Gordon and Soechting, 1995; Gentilucci, Toni, Daprati and Gangitano, 1997; Lackner and DiZio, 2000; Rao and Gordon, 2001; Rabin and Gordon, 2004; Säfström and Edin, 2004).

Tactile contact responses. 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, Jenmalm, Goodwin and Johansson, 2001; Jenmalm, Birznieks, Goodwin and Johansson, 2003). The non-linear deformation properties of the fingertip, with stiffness increasing with the contact force (Westling and Johansson, 1987; Pawluk and Howe, 1999), implies that it deforms quite briskly when an object is initially contacted. This deformation causes clear contact responses in SA-I and often in FA-II afferents, but most distinctly in FA-I afferents (Westling and Johansson, 1987). The spatial centroid of the afferent population response has been proposed to represent the primary contact site on the finger (Wheat, Goodwin and Browning, 1995), while the recruitment of afferents and their firing rates reflect force intensity (magnitude and rate) (Knibestöl, 1973, 1975; Johansson and Vallbo, 1976; Macefield et al., 1996; Goodwin and Wheat, 2004). For force direction, firing rates of individual tactile afferents distributed over the entire 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 (Fig. 2A–C) (Birznieks, Jenmalm, Goodwin and Johansson, 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, Schwartz and Kettner, 1986).

Control points supporting grasp stability

Practically all manipulation tasks require application of forces tangential to the contacted surfaces (load forces). For example, to lift an object with the digits contacting the sides, vertical load forces must be applied to overcome the weight of the object (Fig. 1A). 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) application of forces normal to the surface (grip forces) is required to create stabilizing frictional forces. To that end, action-phase controllers used in manipulation support grasp stability by automatically generating grip forces normal to the grasped surface that are synchronous with, and proportional to, the applied tangential loads (Fig. 1A; see also Fig. 3) (Johansson and Westling, 1984; Westling and Johansson, 1984). This grip-load force coordination supports grasp stability in virtually all maneuvers that we naturally perform with objects in unimanual (Flanagan and Tresilian, 1994; Flanagan and Wing, 1995; Goodwin, Jenmalm and Johansson, 1998; Wing and Lederman, 1998; Johansson, Backlin and Burstedt, 1999; Flanagan, Burstedt and Johansson, 1999; Santello and Soechting, 2000; LaMotte, 2000) and bimanual tasks (Johansson and Westling, 1988b; Flanagan and Tresilian, 1994; Burstedt, Edin and Johansson, 1997; Flanagan, Burstedt and Johansson, 1999; Witney, Goodbody and Wolpert, 1999; Bracewell, Wing, Soper and Clark, 2003; Gysin, Kaminski and Gordon, 2003; Witney and Wolpert, 2007). Thus the implemented action-phase controllers predicts continuously the consequences of arm and hand motor commands regarding tangential loads acting on the object so that grip force can be suitably adjusted.

Control of grasp stability requires, however, that the balance between the grip and load forces be adapted to the properties of contacted surfaces. The friction between digits and object surfaces determines the minimum ratio between grip and load forces required to prevent slip. Accordingly, people parametrically adapt grip-to-load force ratios for different frictional conditions, using greater ratios with more slippery surfaces (Johansson and Westling, 1984; Westling and Johansson, 1984; Flanagan and Wing, 1995; Cadoret and Smith, 1996). In fact, the local frictional condition can tailor the grip-to-load force ratios employed at individual digits within limits imposed by the overall force requirements for maintaining object equilibrium (Edin, Westling and Johansson, 1992; Birznieks, Burstedt, Edin and Johansson, 1998; Burstedt, Flanagan and Johansson, 1999; Quaney and Cole, 2004; Niu, Latash and Zatsiorsky, 2007). 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 (Fig. 2D) (Goodwin et al., 1998; Jenmalm, Dahlstedt and Johansson, 2000). Similarly, when lifting tapered objects, a greater grip-to-load force ratio is required when the grip surfaces are tapered upwards as compared to downwards (see Fig. 3A) (Jenmalm and Johansson, 1997). 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.

Tactile contact responses. Tactile sensibility is critical for adaptation of grip-to-load force ratios to object surface properties (Johansson and Westling, 1984; Westling and

Johansson, 1984; Jenmalm and Johansson, 1997; Jenmalm, Dahlstedt and Johansson, 2000; Monzée, Lamarre and Smith, 2003; Nowak and Hermsdörfer, 2003; Cole, Steyers and Graybill, 2003; Nowak, Glasauer and Hermsdorfer, 2004; Schenker, Burstedt, Wiberg and Johansson, 2006). In addition to forces and contact sites on the digits, the contact responses in ensembles of tactile afferents – primarily in FA-Is – rapidly convey information related to object surface properties, including friction (Johansson and Westling, 1987) and local shape (Fig. 1 and 2E–F) (Jenmalm, Birznieks, Goodwin and Johansson, 2003; Johansson and Birznieks, 2004). For example, changes in the curvature of contacted surfaces, which markedly influence the grip forces in tasks involving tangential torque loads (Fig. 2D) (Goodwin et al., 1998; Jenmalm, Dahlstedt and Johansson, 2000), robustly influence firing rates in the majority of responsive tactile afferents. Roughly, one half of the afferents for which response intensity correlates with curvature show a positive correlation and half a negative correlation (Fig. 2E – F); responsive afferents terminating at the sides and end of the fingertip tend to show negative correlations. Consequently, there is a curvature contrast signal within the population of tactile afferents.

Traditionally, it is posited that afferents information is coded by firing rates. However, in manipulation, typically, the brain quickly extracts information from discrete tactile events and expresses this information in fingertip actions faster than can be readily explained by rate codes. That is, based on the delays in sensorimotor control loops (see above) and the firing rates of tactile afferents in manipulation tasks, it can be deduced that tactile events typically influence fingertip actions when most afferents recruited have had time to fire only one impulse (Johansson and Birznieks, 2004). Recent findings in humans indicate that the relative timing of impulses from ensembles of individual 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 tasks (Johansson and Birznieks, 2004). Specifically, the sequence in which different afferents initially discharge in response to discrete fingertip events provides information about the shape of the contacted surface and the direction of fingertip force. The relative timing of the first spikes contains information about object shape and force direction because changes in either of these parameters differentially influenced the first-spike latency of individual afferents rather than having systematic effects on the latencies within an afferent population. For example, when the fingertip contacts a surface with a given curvature, the responsive afferents will be recruited in a particular order. With another curvature, the order will be different because some afferents are recruited earlier, and others later. Presumably, the order of recruitment of members of the populations of tactile afferents can code other contact parameters used in the control of manual actions as well, such as the friction between fingertips and contacted surfaces.

A mismatch between predicted and actual contact responses triggers a corrective action commencing ~100 ms after contact that is accompanied with an updating of the representation of the object used to control forces in future interactions with the object. Figure 3A illustrates this process when repeatedly lifting objects with tapered grasp surfaces where the tapering was changed between trials in an unpredictable order. First, for all trials the tapering (and hence force requirements) in the previous trial determines the initial increase in grip force, indicating that predictions based on knowledge obtained in previous trials specify the grip-load force coordination. After an unpredicted change in tapering, the grip force output is modified about 100 ms after contact with the object and tuned for the actual object properties (Fig. 3A). By the second trial after the change, the force coordination is appropriately adapted right from the onset of force application. 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.

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 (Jenmalm and Johansson, 1997; Jenmalm, Dahlstedt and Johansson, 2000)**.** However, 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 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). Thus, predictions of frictional conditions are based on memory of recent haptic experiences with the same or similar objects.

Accidental slips. Occasionally, the updating of frictional and shape representations that occurs at initial contact is inadequate and may result in an accidental slip later in the task. 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. Such transient shifts in tangential forces, reliably signaled by FA-I afferents (Johansson and Westling, 1987; Macefield et al., 1996), trigger a corrective action (onset latency 70 – 90 ms) that results in an updating of grip–to–load force ratios and an increase in the safety margin primarily at the slipping digit (Edin et al., 1992; Burstedt, Edin and Johansson, 1997). This updated force coordination is maintained in subsequent phases of the same trial and in subsequent trials with the same object. While an increase in grip force accounts for the adjustment of the grip–to–load force ratio triggered by slip events during the hold phase in lifting trials, during the load phase it is implemented by a slowing down of the subsequent increase in load force (Johansson and Westling, 1984). Hence, different action phase controllers are associated with different smart corrective reflex mechanisms that support grasp stability and enable the task to progress.

Control points for object motion

The goal of many action phases in object manipulation (including tool use) is to move a held object to form or break contact with another object. The held object transmits various features of these contact events to the hand that tactile afferents can signal, including mechanical transients. For example, when we lift an object from a support surface, ensembles of FA-II afferents terminating throughout the hand and wrist signal the incidence and dynamic aspects of the lift-off event (Fig. 1B) (Westling and Johansson, 1987). Because no sensory information is available about object weight until lift-off, a smooth and critically damped lifting motion requires that the load (lift) force drive at lift-off, which accelerates the object, be scaled predictively to object weight. People regularly form such predictions based on sensorimotor memory of the object derived from previous lifts (Johansson and Westling, 1988a). Familiar objects can be identified visually (or by haptic exploration) for retrieval of weight related predictions, and size-weight associations can be used to predict the weights of categories of familiar objects where the items can vary in size (e.g., cups, books, loafs of bread) (Gordon, Forssberg, Johansson and Westling, 1991; Gordon, Westling, Cole and Johansson, 1993). In a similar vein, visual cues about object geometry can be used for anticipatory tuning of fingertip forces to the mass distribution of the object (Wing and Lederman, 1998; Salimi, Frazier, Reilmann and Gordon, 2003).

However, if such predictions are erroneous, compensatory control processes programmed to correct for performance errors and reduce future errors are automatically elicited (Johansson and Westling, 1988a). For example, when a lifted object is lighter than predicted, the lift movement becomes faster and higher than intended (Fig. 3B, T2). As a result, a mismatch is registered at the control point for the load phase controller because sensory events related to lift-off occur before the predicted time. This error automatically triggers a compensatory process that involves abortion of the implemented action phase controller and execution of a corrective action program that generates motor commands that bring the object back to the intended position. However, because of delays in the sensorimotor control loops (~100 ms), the corrective action kicks in too late to avoid an overshoot in the lifting movement (see position signal in Fig. 3B, T2). Conversely, if the object is heavier than expected, the increase in load force generated by the load phase controller finishes without giving rise to sensory events signaling lift-off (Fig. 3C, T2). This absence of predicted sensory events triggers a corrective action program that generates slow, probing increases in fingertip forces until terminated reactively by sensory events signaling lift-off. Thus, the sensorimotor system reacts to both the presence of an unexpected sensory event and the absence of an expected sensory event and various corrective action programs can be associated with a given controller and executed depending on the characteristics of the sensory mismatch. Importantly, in addition to triggering corrective action programs, these sensory mismatches update weight related memory for anticipatory parametric control of subsequent action phases and tasks that engage the same object (see T3 in Fig. 3B and C). With natural objects, usually a single lift efficiently brings about such updating (Johansson and Westling, 1988a; Gordon, Westling, Cole and Johansson, 1993)while in the presence of misleading cues or unfamiliar objects, repeated interactions with the object are usually required for establishing adequate internal representations of objects' mass and mass distributions (Gordon, Forssberg, Johansson and Westling, 1991; Gordon, Westling, Cole and Johansson, 1993; Flanagan and Beltzner, 2000; Salimi, Hollender, Frazier and Gordon, 2000; Salimi, Frazier, Reilmann and Gordon, 2003).

When transporting and holding an object, knowledge about object weight, mass distribution and surface properties remains critical for controlling action and maintaining grasp stability. When replacing 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 FA-II afferents that encode the timing and nature of the event (Fig. 1B). The contact event is followed by an unloading phase where grip and load forces decreases in parallel, maintaining a grip-to-load force ratio providing grasp stability. 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 the unload phase (see "release responses" in Fig. 1B; see also responses in FA-I afferents to the retraction phase in Fig. 2B and E).

Predictions and control points in the visual modality

Studies of eye movements in object manipulation indicate that contact events that demarcate action phases also can be predicted in the visual modality. People use saccadic eye movements to direct their gaze to successive contact locations as they gain salience during task progression (Biguer, Jeannerod and Prablanc, 1982; Ballard et al., 1992; Land et al., 1999; Johansson, Westling, Bäckström and Flanagan, 2001). For example, when people pick up a bar, move the bar 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 (Fig. 4A – B) (Johansson, Westling, Bäckström and Flanagan, 2001). Furthermore, people may direct fixations to points where contact must be avoided, including obstacles that must be circumnavigated with the hand or by an object moved by the hand (Fig. 4A – B). Notably, people almost never fixate their hand or objects being moved by the hand. Thus, when people direct actions towards visible objects, the implemented action-phase controllers appear to provide instructions for task- and phase-specific eye movements so as to acquire visual information optimized for guidance of the hand (Land and Furneaux, 1997; Flanagan and Johansson, 2003).

The spatiotemporal coordination of gaze and hand movements emphasizes the segmentation of manipulation tasks into distinct action phases (Fig. 4C). At the start of most action phases, congruent hand and eye movements are launched concurrently to the contact location representing the goal of the current phase. 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), which enables optimal use of vision for guiding the hand (Paillard, 1996; Land et al., 1999; Prablanc, Desmurget and Gréa, 2003; Saunders and Knill, 2004). 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 passed closest to the obstacle in the target contact task) (Fig. 4). Thus, the gaze shift to the contact location associated with the next action phase occurs around 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, smooth transition between successive phases of the manipulation task would not be possible because of the substantial time-delays in sensorimotor control loops. Hence, contact events that demarcate action phases can be predicted in both the tactile modality and the visual modality.

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 at the surface. Here, sensory feedback related to contact is only available through vision and/or audition. Thus, the visual, auditory, and tactile systems can play complementary roles in predicting contact events. Prediction of contact events in the visual modality without the tactile modality engaged is evident from studies of eye movements in people who observe an actor performing familiar manipulation tasks (Flanagan and Johansson, 2003). 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). By comparing actual and predicted visual feedback related to contact events, 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, Fogassi and Gallese, 2001; Flanagan and Johansson, 2003; Rotman, Troje, Johansson and Flanagan, 2006).

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, auditory, and proprioceptive mechanisms in planning and control of object-oriented manual actions depends on learned associations between visual, auditory, and proprioceptive cues and their mechanical meaning primarily 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 contact events that represent the outcomes of motor commands to the hand. Furthermore, populations of tactile afferents encode information related to surface properties of contacted objects such as the shape and texture of contacted surfaces and the frictional conditions between these surfaces and the skin.

Manipulatory tasks involve a sensory plan that specifies the sequence of task subgoals in terms of specific afferent neural signatures in the tactile and other modalities. This plan provides a scaffold for the selection and shaping of the action-phase controllers implemented for achieving the sensory subgoals, which generally corresponds to distinct contact events. When a given contact event give rise to afferent signals that are adequately predicted by the implemented controllers, the task runs in a pre-defined way based on knowledge of object properties derived from internal representations gained in previous interactions with objects (and representations related to the current state of the sensorimotor system). Invalid internal representations result in mismatches between predicted and actual signals that trigger learned corrective actions – the nature of which depends on the task and its action phase and the characteristics of the error – along with updating of representations of object properties. Prediction of the terminal sensorimotor state of an active action-phase controller can also be used as a prediction of the initial state by the controller responsible for the next action phase. If the brain regularly relied on peripheral afferent information to obtain this state information, stuttering phase transitions would occur because of sensorimotor delays.

We suggest that the brain encodes, in multiple sensory modalities, planned contact events that represent sensorimotor control points where predicted and actual sensory signals can be compared. Multimodal encoding of sensorimotor control points likely allows the sensorimotor system to simultaneously monitor multiple aspects of task performance and, if prediction errors are detected, respond to the pattern of errors observed in different modalities. Furthermore, 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.

Acknowledgments

The Swedish Research Council (project 08667), the sixth Framework Program of the EU (project IST-001917, IST-028056), and the Canadian Institutes of Health Research supported this work.

References

Ballard, D.H., Hayhoe, M.M., Li, F. and Whitehead, S.D. (1992). Hand-eye coordination during sequential tasks. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **337**, no. 1281, 331-8.

Biguer, B., Jeannerod, M. and Prablanc, C. (1982). The coordination of eye, head, and arm movements during reaching at a single visual target. *Experimental Brain Research*, **46**, no. 2, 301-4.

Birznieks, I., Burstedt, M.K.O., Edin, B.B. and Johansson, R.S. (1998). Mechanisms for force adjustments to unpredictable frictional changes at individual digits during two-fingered manipulation. *Journal of Neurophysiology*, **80**, 1989-2002.

Birznieks, I., Jenmalm, P., Goodwin, A. and Johansson, R. (2001). Encoding of direction of fingertip forces by human tactile afferents. *Journal of Neuroscience*, **21**, no. 20, 8222-37.

Bracewell, R.M., Wing, A.M., Soper, H.M. and Clark, K.G. (2003). Predictive and reactive co-ordination of grip and load forces in bimanual lifting in man. *European Journal of Neuroscience*, **18**, no. 8, 2396-402.

Burstedt, M.K.O., Edin, B.B. and Johansson, R.S. (1997). Coordination of fingertip forces during human manipulation can emerge from independent neural networks controlling each engaged digit. *Experimental Brain Research*, **117**, 67-79.

Burstedt, M.K.O., Flanagan, R. and Johansson, R.S. (1999). Control of grasp stability in humans under different frictional conditions during multi-digit manipulation. *Journal of Neurophysiology*, **82**, 2393–2405.

Cadoret, G. and Smith, A.M. (1996). Friction, not texture, dictates grip forces used during object manipulation. *Journal of Neurophysiology*, **75**, 1963-9.

Cohen, R.G. and Rosenbaum, D.A. (2004). Where grasps are made reveals how grasps are planned: generation and recall of motor plans. *Experimental Brain Research*, **157**, no. 4, 486-95.

Cole, K.J., Steyers, C.M. and Graybill, E.K. (2003). The effects of graded compression of the median nerve in the carpal canal on grip force. *Experimental Brain Research*, **148**, no. 2, 150-7.

Cuijpers, R.H., Smeets, J.B. and Brenner, E. (2004). On the relation between object shape and grasping kinematics. *Journal of Neurophysiology*, **91**, no. 6, 2598-606.

Edin, B.B., Westling, G. and Johansson, R.S. (1992). Independent control of fingertip forces at individual digits during precision lifting in humans. *Journal of Physiology*, **450**, 547-64.

Eliasson, A.C., Forssberg, H., Ikuta, K., Apel, I., Westling, G. and Johansson, R. (1995). Development of human precision grip V. Anticipatory and triggered grip actions during sudden loading. *Experimental Brain Research*, **106**, 425-33.

Flanagan, J.R. and Beltzner, M.A. (2000). Independence of perceptual and sensorimotor predictions in the size–weight illusion. *Nature Neuroscience*, **3**, no. 7, 737-41.

Flanagan, J.R., Bowman, M.C. and Johansson, R.S. (2006). Control strategies in object manipulation tasks. *Current Opinion in Neurobiology*, **16**, no. 6, 650-9.

Flanagan, J.R., Burstedt, M.K.O. and Johansson, R.S. (1999). Control of fingertip forces in multi-digit manipulation. *Journal of Neurophysiology*, **81**, 1706-17.

Flanagan, J.R. and Johansson, R.S. (2003). Action plans used in action observation. *Nature*, **424**, 769-71.

Flanagan, J.R. and Tresilian, J.R. (1994). Grip load force coupling: A general control strategy for transporting objects. *Journal of Experimental Psychology Human Perception and Performance*, **20**, 944-57.

Flanagan, J.R. and Wing, A.M. (1995). The stability of precision grip forces during cyclic arm movements with a hand-held load. *Experimental Brain Research*, **105**, 455-64.

Forssberg, H., Eliasson, A.C., Kinoshita, H., Johansson, R.S. and Westling, G. (1991). Development of human precision grip. I: Basic coordination of force. *Experimental Brain Research*, **85**, 451-7.

Forssberg, H., Eliasson, A.C., Kinoshita, H., Westling, G. and Johansson, R.S. (1995). Development of human precision grip IV. Tactile adaptation of isometric finger forces to the frictional condition. *Experimental Brain Research*, **104**, 323-30.

Forssberg, H., Kinoshita, H., Eliasson, A.C., Johansson, R.S., Westling, G. and Gordon, A.M. (1992). Development of human precision grip. 2. Anticipatory control of isometric forces targeted for objects weight. *Experimental Brain Research*, **90**, 393-8.

Gentilucci, M., Toni, I., Daprati, E. and Gangitano, M. (1997). Tactile input of the hand and the control of reaching to grasp movements. *Experimental Brain Research*, **114**, 130-7.

Georgopoulos, A.P., Schwartz, A.B. and Kettner, R.E. (1986). Neuronal population coding of movement direction. *Science*, **233**, 1416-9.

Goodale, M.A., Meenan, J.P., Bülthoff, H.H., Nicolle, D.A., Murphy, K.J. and Racicot, C.I. (1994). Separate neural pathways for the visual analysis of object shape in perception and prehension. *Current Biology*, **4**, no. 7, 604-10.

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. *Journal of Neuroscience*, **18**, no. 24, 10724-34.

Goodwin, A.W. and Wheat, H.E. (2004). Sensory signals in neural populations underlying tactile perception and manipulation. *Annual Review of Neuroscience*, **27**, 53-77.

Gordon, A.M., Forssberg, H., Johansson, R.S., Eliasson, A.C. and Westling, G. (1992). Development of human precision grip. 3. Integration of visual size cues during the programming of isometric forces. *Experimental Brain Research*, **90**, 399-403.

Gordon, A.M., Forssberg, H., Johansson, R.S. and Westling, G. (1991). Integration of sensory information during the programming of precision grip: comments on the contributions of size cues. *Experimental Brain Research*, **85**, 226-9.

Gordon, A.M. and Soechting, J.F. (1995). Use of Tactile Afferent Information in Sequential Finger Movements. *Experimental Brain Research*, **107**, 281-92.

Gordon, A.M., Westling, G., Cole, K.J. and Johansson, R.S. (1993). Memory representations underlying motor commands used during manipulation of common and novel objects. *Journal of Neurophysiology*, **69**, 1789-96.

Gysin, P., Kaminski, T.R. and Gordon, A.M. (2003). Coordination of fingertip forces in object transport during locomotion. *Experimental Brain Research*, **149**, no. 3, 371-9.

Häger-Ross, C. and Johansson, R.S. (1996). Non-digital afferent input in reactive control of fingertip forces during precision grip. *Experimental Brain Research*, **110**, 131-41.

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. *European Journal of Neuroscience*, **18**, no. 1, 164-76.

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

Jenmalm, P. and Johansson, R.S. (1997). Visual and somatosensory information about object shape control manipulative finger tip forces. *Journal of Neuroscience*, **17**, 4486-99.

Johansson, R.S., Backlin, J.L. and Burstedt, M.K.O. (1999). Control of grasp stability during pronation and supination movements. *Experimental Brain Research*, **128**, 20-30.

Johansson, R.S. and Birznieks, I. (2004). First spikes in ensembles of human tactile afferents code complex spatial fingertip events. *Nature Neuroscience*, **7**, no. 2, 170-1177.

Johansson, R.S. and Cole, K.J. (1992). Sensory-motor coordination during grasping and manipulative actions. *Current Opinion in Neurobiology*, **2**, 815-23.

Johansson, R.S. and Vallbo, Å.B. (1976). Skin mechanoreceptors in the human hand: An inference of some population properties. in: Zotterman, Y. (ed) *Sensory Functions of* *the skin in Primates, with special reference to Man*, pp 171-84.Pergamon Press Ltd., Oxford

Johansson, R.S. and Vallbo, A.B. (1979). Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptive units in glabrous skin. *Journal of Physiology*, **286**, 283-300.

Johansson, R.S. and Vallbo, Å.B. (1983). Tactile sensory coding in the glabrous skin of the human hand. *Trends in Neurosciences*, **6**, 27-31.

Johansson, R.S. 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**, 550-64.

Johansson, R.S. and Westling, G. (1987). Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. *Experimental Brain Research*, **66**, 141-54.

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

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

Johansson, R.S., Westling, G., Bäckström, A. and Flanagan, J.R. (2001). Eye-hand coordination in object manipulation. *Journal of Neuroscience*, **21**, no. 17, 6917-32.

Knibestöl, M. (1973). Stimulus-response functions of rapidly adapting mechanoreceptors in human glabrous skin area. *Journal of Physiology*, **232**, no. 3, 427-52.

Knibestöl, M. (1975). Stimulus-response functions of slowly adapting mechanoreceptors in the human glabrous skin area. *Journal of Physiology*, **245**, no. 1, 63-80.

Lackner, J.R. and DiZio, P.A. (2000). Aspects of body self-calibration. *Trends in Cognitive Sciences*, **4**, 279-88.

LaMotte, R.H. (2000). Softness discrimination with a tool. *Journal of Neurophysiology*, **83**, no. 4, 1777-86.

Land, M., Mennie, N. and Rusted, J. (1999). The roles of vision and eye movements in the control of activities of daily living. *Perception*, **28**, no. 11, 1311-28.

Land, M.F. and Furneaux, S. (1997). The knowledge base of the oculomotor system. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **352**, no. 1358, 1231-9.

Lemon, R.N., Johansson, R.S. and Westling, G. (1995). Corticospinal control during reach, grasp and precision lift in man. *Journal of Neuroscience*, **15**, 6145-56.

Lukos, J., Ansuini, C. and Santello, M. (2007). Choice of contact points during multidigit grasping: effect of predictability of object center of mass location. *Journal of Neuroscience*, **27**, no. 14, 3894-903.

Macefield, V.G., Häger-Ross, C. and Johansson, R.S. (1996). Control of grip force during restraint of an object held between finger and thumb: responses of cutaneous afferents from the digits. *Experimental Brain Research*, **108**, 155-71.

Macefield, V.G. and Johansson, R.S. (1996). Control of grip force during restraint of an object held between finger and thumb: responses of muscle and joint afferents from the digits. *Experimental Brain Research*, **108**, 172-84.

Monzée, J., Lamarre, Y. and Smith, A.M. (2003). The effects of digital anesthesia on force control using a precision grip. *Journal of Neurophysiology*, **89**, no. 2, 672-83.

Niu, X., Latash, M.L. and Zatsiorsky, V.M. (2007). Prehension synergies in the grasps with complex friction patterns: local versus synergic effects and the template control. *Journal of Neurophysiology*, **98**, no. 1, 16-28.

Nowak, D.A., Glasauer, S. and Hermsdorfer, J. (2004). How predictive is grip force control in the complete absence of somatosensory feedback? *Brain*, **127**, no. PT 1, 182-92.

Nowak, D.A. and Hermsdörfer, J. (2003). Digit cooling influences grasp efficiency during manipulative tasks. *European Journal of Applied Physiology*, **89**, no. 2, 127-33.

Paillard, J. (1996). Fast and slow feedback loops for the visual correction of spatial errors in a pointing task: a reappraisal. *Canadian Journal of Physiology and Pharmacology*, **74**, no. 4, 401-17.

Paré, M. and Dugas, C. (1999). Developmental changes in prehension during childhood. *Experimental Brain Research*, **125**, no. 3, 239-47.

Pawluk, D.T. and Howe, R.D. (1999). Dynamic lumped element response of the human fingerpad. *Journal of Biomechanical Engineering*, **121**, 178-83.

Prablanc, C., Desmurget, M. and Gréa, H. (2003). Neural control of on-line guidance of hand reaching movements. *Progress in Brain Research*, **142**, 155-70.

Prablanc, C., Pélisson, D. and Goodale, M.A. (1986). Visual control of reaching movements without vision of the limb. I. Role of retinal feedback of target position in guiding the hand. *Experimental Brain Research*, **62**, no. 2, 293-302.

Quaney, B.M. and Cole, K.J. (2004). Distributing vertical forces between the digits during gripping and lifting: the effects of rotating the hand versus rotating the object. *Experimental Brain Research*, **155**, no. 2, 145-55.

Rabin, E. and Gordon, A.M. (2004). Tactile feedback contributes to consistency of finger movements during typing. *Experimental Brain Research*, **155**, no. 3, 362-9.

Rao, A.K. and Gordon, A.M. (2001). Contribution of tactile information to accuracy in pointing movements. *Experimental Brain Research*, **138**, no. 4, 438-45.

Reilmann, R., Gordon, A.M. and Henningsen, H. (2001). Initiation and development of fingertip forces during whole-hand grasping. *Experimental Brain Research*, **140**, no. 4, 443-52.

Rizzolatti, G., Fogassi, L. and Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, **2**, no. 9, 661-70.

Rotman, G., Troje, N.F., Johansson, R.S. and Flanagan, J.R. (2006). Eye movements when observing predictable and unpredictable actions. *Journal of Neurophysiology*, **96**, no. 3, 1358-69.

Säfström, D. and Edin, B.B. (2004). Task requirements influence sensory integration during grasping in humans. *Learning & Memory*, **11**, no. 3, 356-63.

Salimi, I., Frazier, W., Reilmann, R. and Gordon, A.M. (2003). Selective use of visual information signaling objects' center of mass for anticipatory control of manipulative fingertip forces. *Experimental Brain Research*, **150**, no. 1, 9-18.

Salimi, I., Hollender, I., Frazier, W. and Gordon, A.M. (2000). Specificity of internal representations underlying grasping. *Journal of Neurophysiology*, **84**, no. 5, 2390-7.

Santello, M. and Soechting, J.F. (1998). Gradual molding of the hand to object contours. *Journal of Neurophysiology*, **79**, no. 3, 1307-20.

Santello, M. and Soechting, J.F. (2000). Force synergies for multifingered grasping. *Experimental Brain Research*, **133**, no. 4, 457-67.

Saunders, J.A. and Knill, D.C. (2004). Visual feedback control of hand movements. *Journal of Neuroscience*, **24**, no. 13, 3223-34.

Schenker, M., Burstedt, M.K., Wiberg, M. and Johansson, R.S. (2006). Precision grip function after hand replantation and digital nerve injury. *J Plast Reconstr Aesthet Surg*, **59**, no. 7, 706-16.

Vallbo, Å.B. and Hagbarth, K.-E. (1968). Activity from skin mechanoreceptors recorded percutaneously in awake human subjects. *Experimental Neurology*, **21**, 270-89.

Vallbo, A.B. and Johansson, R.S. (1984). Properties of cutaneous mechanoreceptors in the human hand related to touch sensation. *Human Neurobiology*, **3**, 3-14.

Westling, G. and Johansson, R.S. (1984). Factors influencing the force control during precision grip. *Experimental Brain Research*, **53**, 277-84.

Westling, G. and Johansson, R.S. (1987). Responses in glabrous skin mechanoreceptors during precision grip in humans. *Experimental Brain Research*, **66**, 128-40.

Wheat, H.E., Goodwin, A.W. and Browning, A.S. (1995). Tactile resolution: peripheral neural mechanisms underlying the human capacity to determine positions of objects contacting the fingerpad. *Journal of Neuroscience*, **15**, no. 8, 5582-95.

Wing, A.M. and Lederman, S.J. (1998). Anticipating load torques produced by voluntary movements. *Journal of Experimental Psychology Human Perception and Performance*, **24**, 1571-81.

Witney, A.G., Goodbody, S.J. and Wolpert, D.M. (1999). Predictive motor learning of temporal delays. *Journal of Neurophysiology*, **82**, 2039–2048.

Witney, A.G. and Wolpert, D.M. (2007). The effect of externally generated loading on predictive grip force modulation. *Neuroscience Letters*, **414**, no. 1, 10-5.

Figure legends

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 the digits contact the object, the grip force increases in parallel with the tangential load force applied under isometric conditions. 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 addition to issuing motor commands, the action-phase controllers predict their sensory consequences in one or more modalities (predicted sensory subgoal events). For example, when the object is replaced on the surface, the contact between the object and the surface gives rise to both predicted and actual 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. **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 (Vallbo and Hagbarth, 1968). 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; Meissner) and slowly adapting type I (SA-I; Merkel) afferents when the object is first contacted, (2) responses in the fast-adapting type II (FA-II; Pacinian) afferents related to the mechanical transients at lift-off, 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; Ruffini) 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. (Compiled from data presented in Westling and Johansson, 1987).

Figure 2

Encoding of fingertip force direction and contact surface shape by human tactile afferents under conditions representative for object manipulation tasks. **A.** Superimposed on a 0.2 N normal force (F_n), force was applied to the fingertip in the normal direction only (N), and 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 either a flat or a spherically curved 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.** Impulse ensembles exemplifying responses in single highly responsive FA-I, SA-I and SA-II afferents to repeated force stimuli (n = 5) applied in each force direction (P, U, D, R and N) with the flat contact surface. The top trace in each set shows the instantaneous discharge frequency averaged over five trials (bottom 5 traces). 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 crosses indicate the primary site of stimulation. **C.** Distributions of preferred directions 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. Preferred directions were estimated by vector summation of the mean firing rates during the force protraction phase (grey zone in B) obtained with different directions of the tangential force component. **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) in each of the right hand panels illustrate trials with two curved surfaces (5 and 10 mm radius) and a flat surface (curvature: 200, 100 and 0 m^{-1}, respectively). Curves show the grip force, tangential torque and tilt angle against time. Note the effect of surface curvature on the coordination between grip force and tangential torque. **E.** Impulse ensembles show responses to repeated stimuli (n = *5*) of two single FA-I and SA-I afferents with forces applied in the normal direction with each of the three surface curvatures used in D. Traces as in B. 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. **F.** 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 (grey zone in E) with each curvature. Circles on the fingertip as in B. (A – C adapted from Birznieks, Jenmalm, Goodwin and Johansson, 2001, D from Goodwin et al., 1998 and E – F from Jenmalm, Birznieks, Goodwin and Johansson, 2003).

Figure 3

Adaptation of fingertip forces to changes in object shape and weight. **A**. Vertical load force and horizontal grip force in trials from a lift series in which the angle of the grasped surfaces was unpredictably varied between lifts without useful visual cues. Blue curves refer to a trial with 30° upward tapered grasp surfaces (T1) preceded by a trial with 30° upward taper. The solid red curves show the next trial (T2) performed with 30° downward tapered grasp surfaces and thus illustrate adjustments to a change in shape. The force output was initially tailored for the object shape in the previous lift before a corrective action was elicited (yellow-dashed segment in the grip force curve) that adjusted the balance between grip and load forces to better suit the 30° downward tapered surfaces. The thin red dashed curves show the following trial (T3) performed without a change in surface taper. The top diagram represents the status of the sequentially implemented action-phase controllers. Throughout T1 and in the beginning of T2 they are parameterized for the 30° upward tape. In T2 a corrective action ("Corr") is triggered about 100 ms after contact based on a detected mismatch between predicted and actual tactile information obtained at contact. This corrective action, inserted during the load phase, updates the controllers to the 30° downward taper for the remainder of the trial. In T3, the controllers remain updated to the new shape. **B – C**. Single unit tactile afferent responses and adjustments in force to unexpected changes in object weight based on data from single lifts. Gray circles and vertical lines indicate the instance of lift-off for each trial and the arrowheads point at the signals generated by the lift-off in a FA-II (Pacinian) afferent. The circles behind the nerve traces indicate the corresponding predicted sensory events. **B**. Three successive trials (T1 – T3) 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 were adequately programmed because the participant had previously lifted the 800 g object. The forces were erroneously programmed in the first 200 g lift (T2), i.e., they were tailored for the heavier 800 g object lifted in the previous trial. The sensory information about the start of movement occurs earlier than expected which initiates a corrective action (yellow-dashed red curves) that terminates the strong force drive and brings the object back to the intended position after the marked overshoot in the vertical position. **C**. An adequately-programmed lift with a 400 g weight (T1, green curves) was followed by a lift with 800 g (T2, blue solid curves) that was erroneously programmed for the lighter 400 g weight lifted in the previous trial. The absence of lift-off responses in FA-II afferents at the predicted point for the erroneously programmed 800 g trial elicited a corrective action (yellow-dashed blue curves) that involved abortion of the lift-phase command followed by triggering of a second load phase command that slowly and discontinuously increased grip and load forces until terminated by sensory input signaling lift-off. In the subsequent trial (T3, blue dashed curves), the participant again lifted the 800 g object. The top diagrams in B and C represent the status of the sequentially implemented action-phase controllers. In T1 they were parameterized for the 800 g (B) and 400 g (C) weight throughout. In T2, a corrective action ("Corr") was triggered about 100 ms after the occurrence of the mismatch between predicted and actual sensory information related to object lift-off. This action involved 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 was linked to an updating of the subsequently implemented controllers for the new weight. In T3, the controllers remain updated to this weight. (A. Compiled from data presented in Jenmalm and Johansson, 1997; B – C. Developed from Johansson and Cole, 1992).

Figure 4

Predictions and control points in the visual modality.

A – B. Gaze and hand movements for a single trial of a target contact task where the participant reached for and grasped a bar, moved it to press a target-switch (A) and moved it away from the target-switch and replaced it on the support surface (B). A triangular obstacle was located between the bar and target. Dashed black lines 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), the protruding part of the obstacle (orange), target (blue) and the support surface (pink). 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 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 correspondingly numbered circle 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. (Adapted from Johansson, Westling, Bäckström and Flanagan, 2001.)

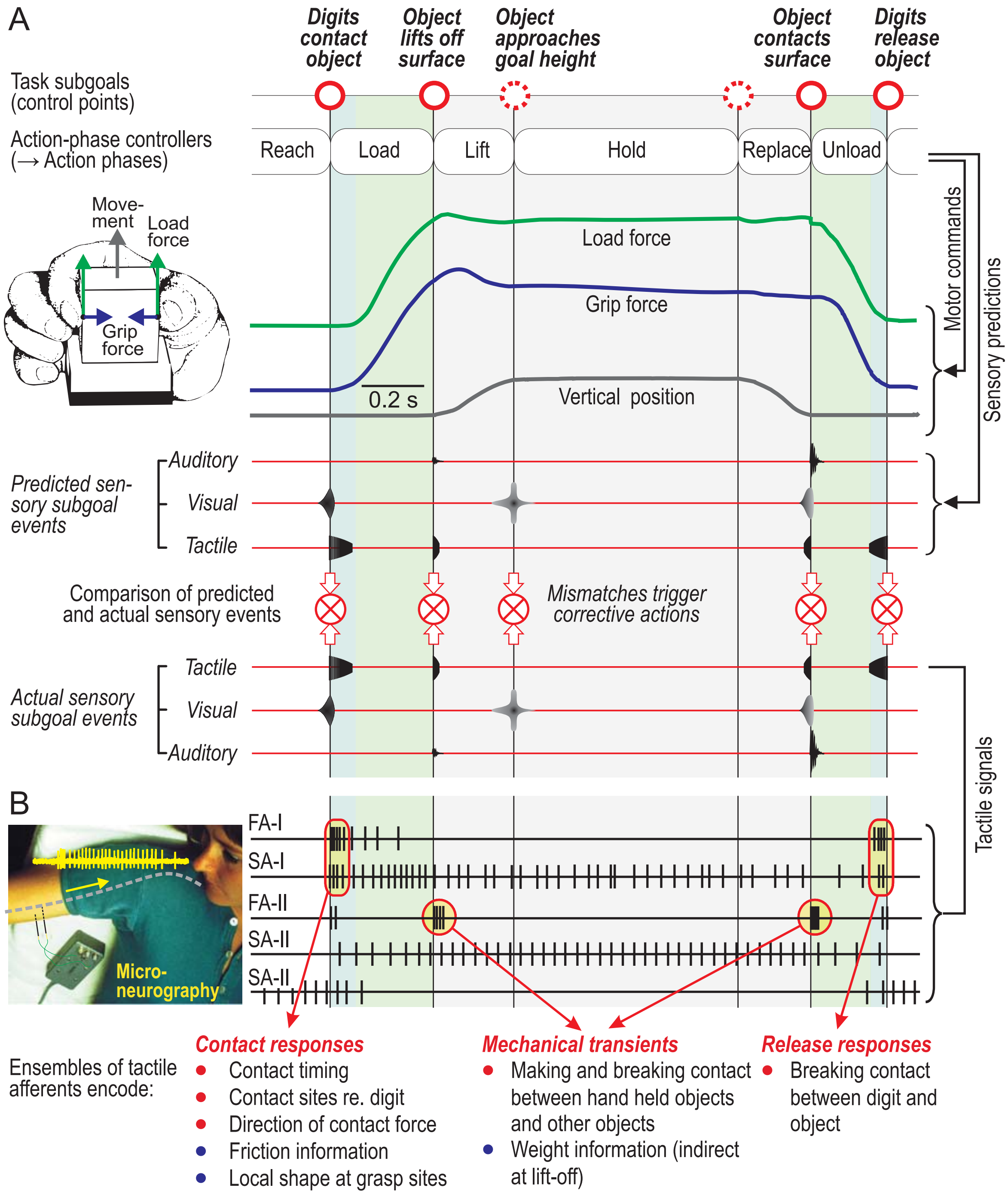

Figure 1
Johansson and Flanagan

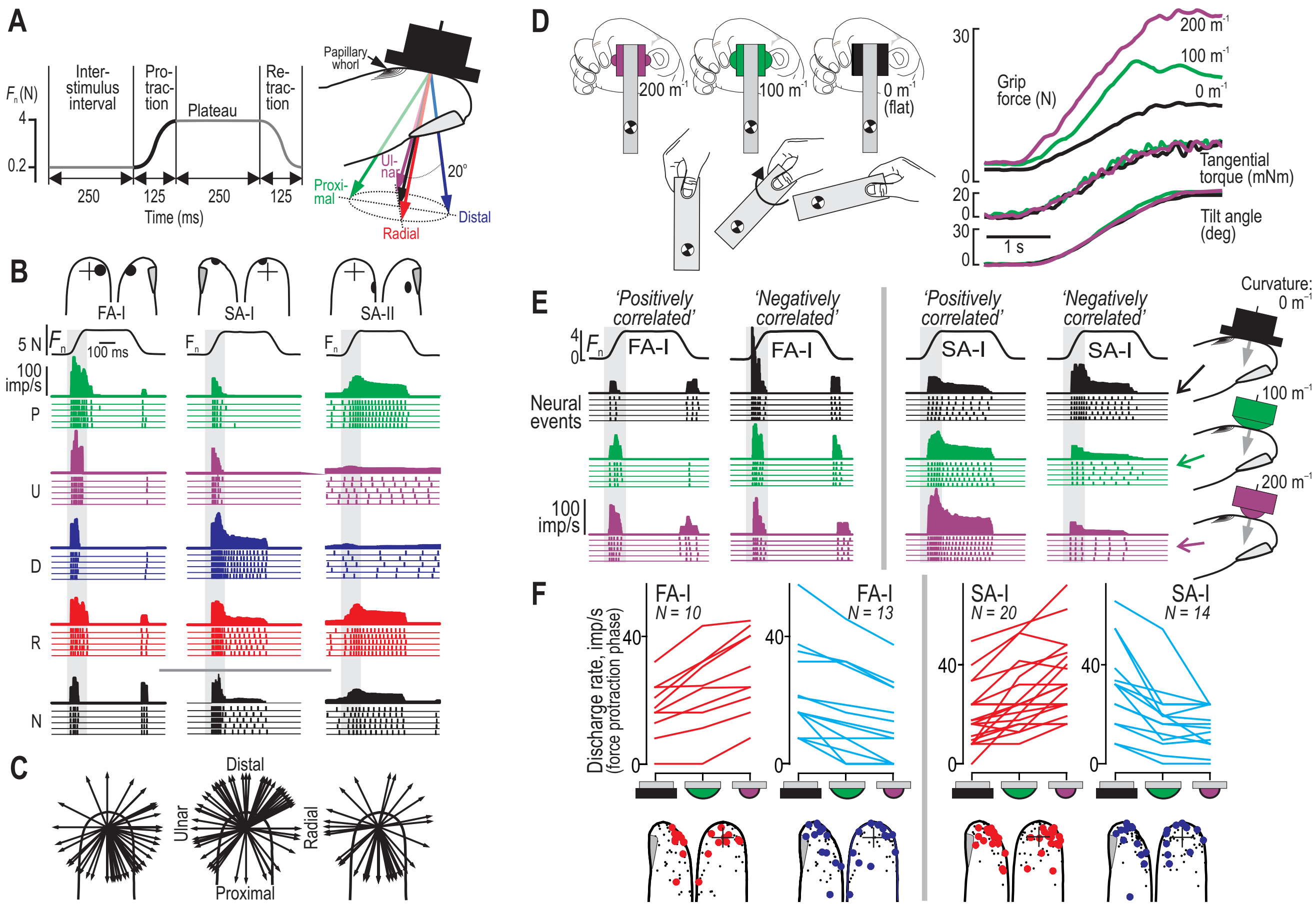

Figure 2
Johansson and Flanagan

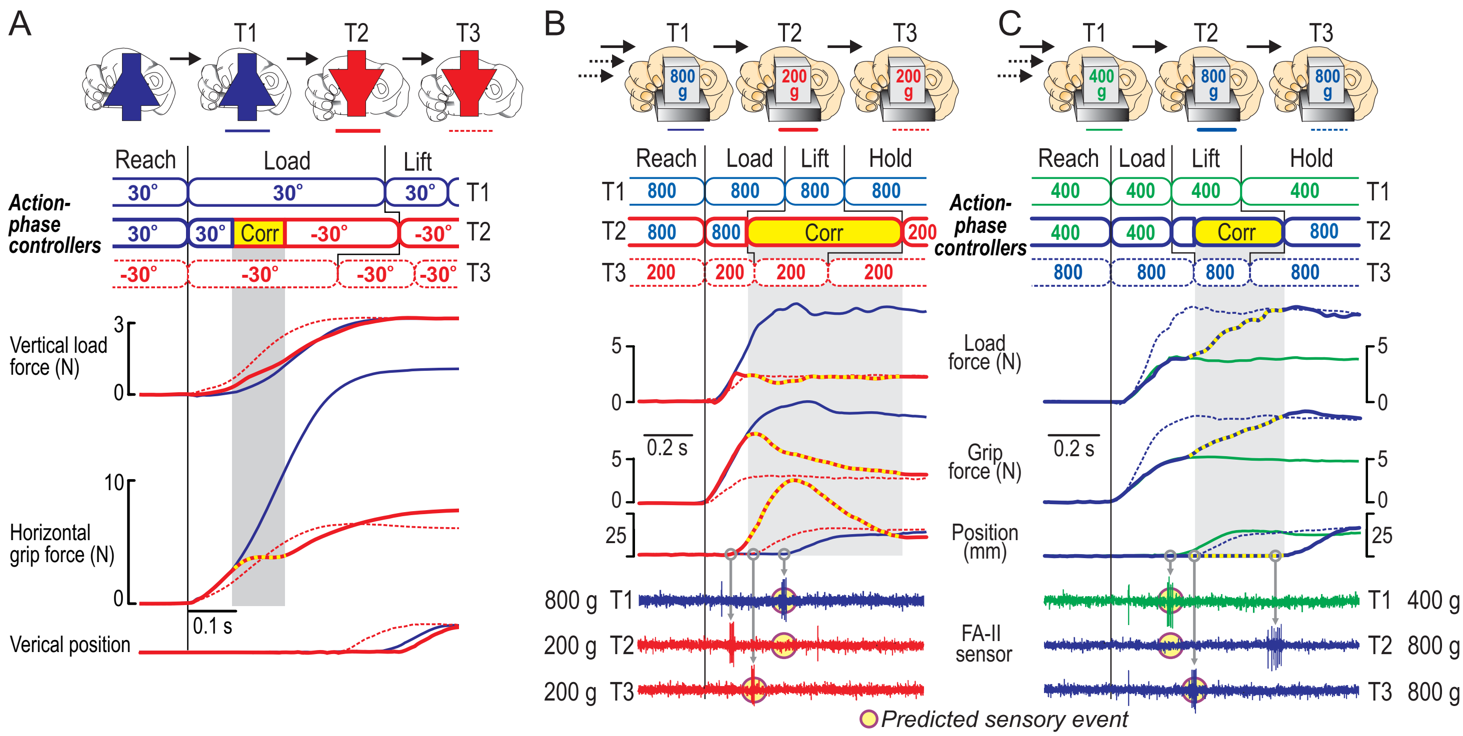

Figure 3
Johansson and Flanagan

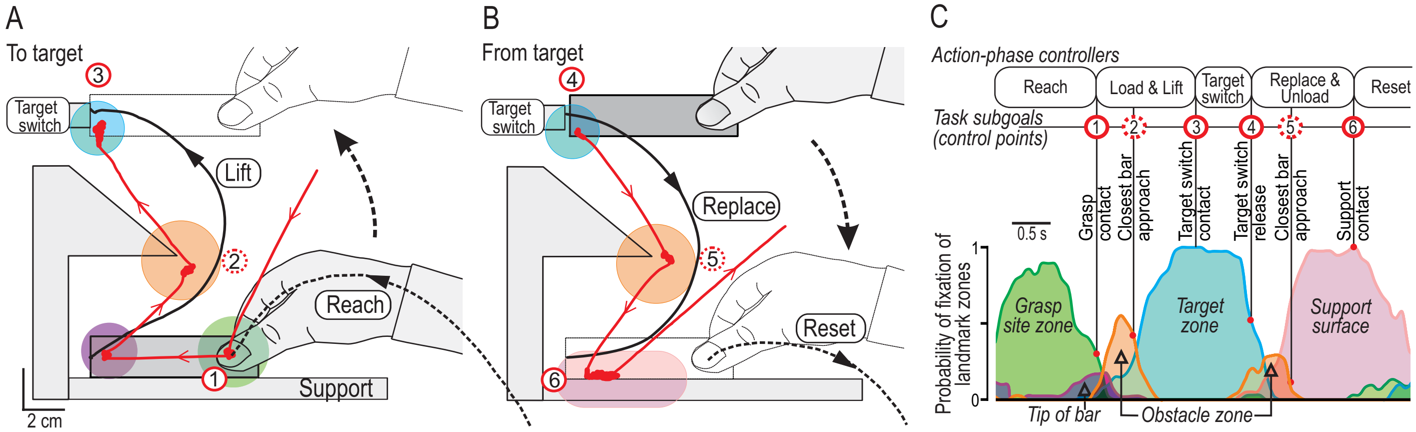

Figure 4
Johansson and Flanagan