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Control strategies in object manipulation tasks

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The remarkable manipulative skill of the human hand is not the result of rapid sensorimotor processes, nor of fast or powerful effector mechanisms. Rather, the secret lies in the way manual tasks are organized and controlled by the nervous system. At the heart of this organization is prediction. Successful manipulation requires the ability both to predict the motor commands required to grasp, lift, and move objects and to predict the sensory events that arise as a consequence of these commands.

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Introduction

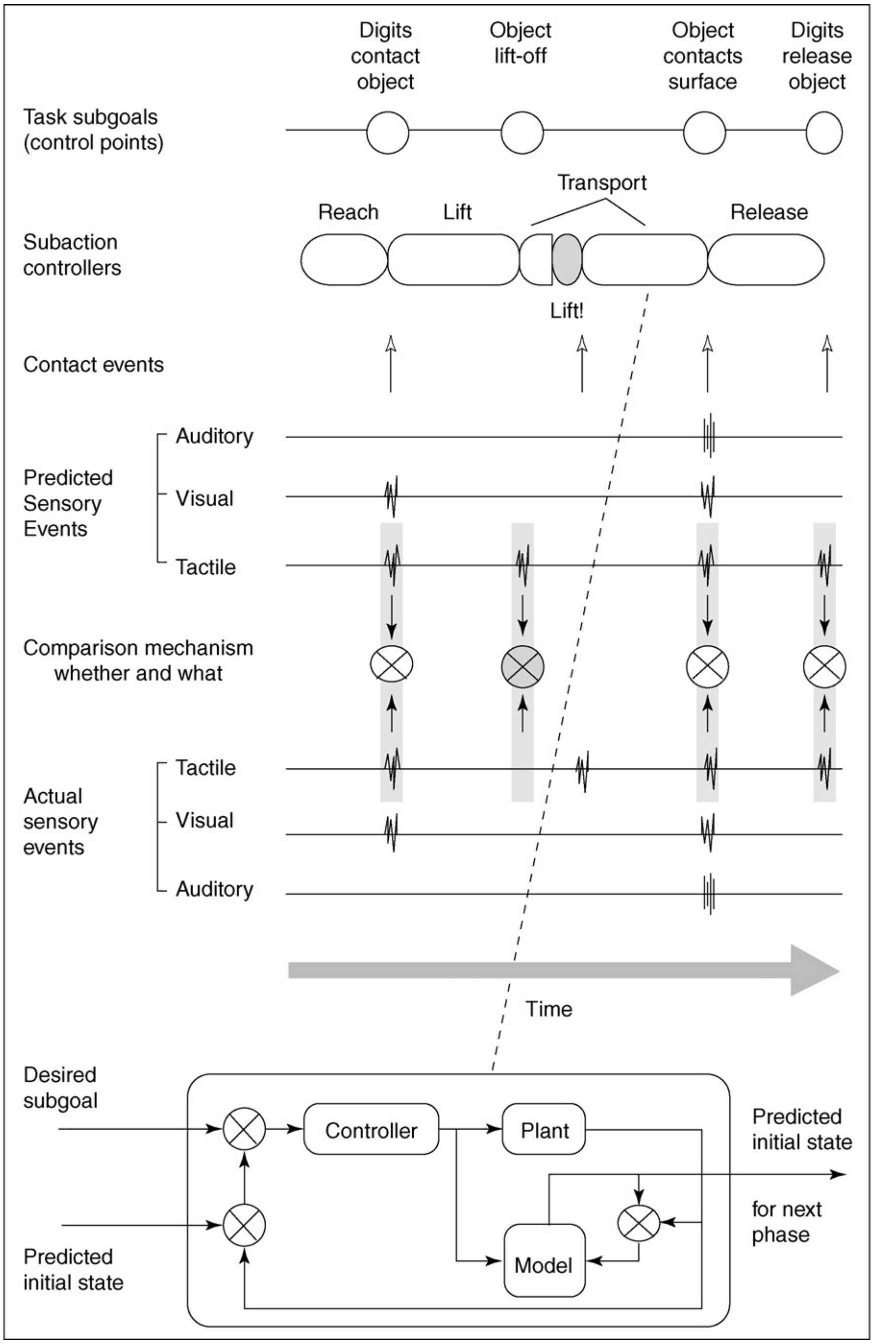
Object manipulation is a model system for the study of sensorimotor and cognitive control strategies governing skilled behavior in humans. Tasks involving object manipulation engage multiple sensorimotor systems, are explicitly concerned with mechanical interactions between the body and the objects in the environment, and involve sequentially organized action plans at various levels of complexity. Here, we review recent work on the control of hand and eye movements in object manipulation tasks. This work highlights the importance of 'contact events' in the control of manipulation tasks and the importance of predictive control mechanisms that are based on knowledge of object properties.

Sensorimotor control points

Object manipulation tasks typically involve a series of action phases in which objects are grasped, moved, brought into contact with other objects and released. These phases are usually bound by mechanical events that are subgoals of the task. These events involve the making and breaking of contact between either the fingertips and the grasped object or the object in hand and another object or surface. Importantly, these contact events give rise to discrete and distinct sensory events, each characterized by a specific afferent neural signature. Because these sensory events provide information related to the functional goals of successive action phases, they have a crucial role in the sensory control of manipulations. In object manipulation, the brain not only forms action plans in terms of series of desired subgoals but also predicts the sensory events that signify subgoal attainment in conjunction with the generation of the motor commands. By comparing predicted sensory events with the actual sensory events, the motor system can monitor task progression and adjust subsequent motor commands if errors are detected. As discussed further below, such adjustments involve parametric adaptation of fingertip actions to the mechanical properties of objects, triggering of task-protective corrective actions, and learning of novel sensorimotor strategies. In addition, errors in performance can be used to update representations of objects in the environment (or the motor system itself), so as to improve future control and prediction [1–3].

Tactile signals, especially from contact events, are essential for skilled and dexterous manipulation [4–6,7••,8]. For example, when grasping and lifting an object, tactile afferents from different types of mechanoreceptors in the glabrous skin of the hand encode information about both the timing and the physical nature of the discrete mechanical events that occur when the digits contact the object and when the object lifts off the surface [9–11]. Signals from ensembles of tactile afferents provide information on the timing, magnitude, direction and spatial distribution of fingertip forces, the local shape of the contact site, and the friction between the skin and the object (see below). However, contact events can also give rise to distinct signals in other sensory modalities, including proprioception, vision and audition. We suggest that contact events encoded in multiple sensory modalities represent sensorimotor control points that have three crucial functions [12] (see Figure 1). First, by comparing actual and predicted sensory events in multiple sensory modalities, the sensorimotor system can simultaneously monitor multiple aspects of task performance and, if prediction errors arise, respond to the pattern of errors observed in different modalities. Second, because contact events give rise to salient sensory signals from multiple modalities that are linked in time and space, they provide an opportunity for sensorimotor integration and intermodal alignment that might facilitate learning and upholding of multimodal sensorimotor correlations that are necessary for prediction of purposeful motor commands. Third, the predicted sensory consequences of contact events can

Figure 1



Schematic illustration of the phases, separated by contact events, in a task in which an object is grasped, lifted off a surface, moved, and then replaced on the surface. The contact events shown at the top define subgoals of the task (i.e. goals of each action phase) and are signaled by distinct and discrete sensory events in one or more modalities. 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 these actual sensory events to predicted sensory events, the motor system can monitor task progression. For example, if the object is heavier than expected, the predicted tactile events associated with lift-off will not occur. As depicted in the figure, this triggers a second lift phase. (Although the figure only shows a comparison mechanism for tactile events, comparisons can be made for each task-relevant sensory event.) The predicted sensory events from each phase can be used to provide initial state estimates for the next phase. Predictive processes also operate within each phase. For example, during object transport, the motor system might use an internal model of the object in conjunction with a copy of the arm motor commands to predict the load force acting on the object, so that grip force can be suitably adjusted.

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directly furnish initial state information for subsequent phases of the manipulation tasks. This enables smooth phase transitions, in contrast to the stuttering transitions that would occur as a result of neuromuscular delays if peripheral afferent information about subgoal completions always triggered, reactively, the execution of the next phase.

Prediction and rapid updating

Because of time delays associated with receptor transduction, neural conduction, central processing and muscle activation, skilled manipulation relies on predictions about the properties of objects. People are able to use visual and (in many cases haptic) cues about object size, shape and identity to predict object weight [13–17] and mass distribution [18–22], and to estimate stable fingertip force vectors [4,5]. If initial predictions are incorrect, they can be updated over successive lifts of the object [23,24]. For example, if an object is lighter or heavier than expected, lift-off will occur either too soon or not at all at the predicted point in time. The resulting mismatch between expected sensory signals in tactile afferents and the actual sensory event triggers a learned corrective action pattern that decreases or increases fingertip forces, respectively, and leads to an updating of the representation of object weight in memory [10,13]. Thus, in this situation the sensorimotor system reacts quickly to both the presence of an unexpected sensory event and the absence of an expected sensory event. For object properties that impose constraints on the fingertip force vectors for grasp stability, such as friction [8] and the local shape of the contact surface [4,5], updating is formed on the basis of prediction errors derived from tactile signals obtained when the digits initially contact the object. When handling common inertial loads in the absence of misleading cues, updating typically takes place in a single trial. However, in the presence of misleading cues [25,26], or when manipulating objects with unusual dynamics (relating applied force to motion) [27,28], updating might require repeated lifts or movements of the object.

Although prediction underlies skilled manipulation, rapid processing of sensory events related to contact events is crucial for detecting and correcting prediction errors or for when the system is unable to predict object properties. By using microneurography (i.e. recording from human nerves using a percutaneously inserted needle) we have shown that when a digit initially contacts an object, ensembles of tactile afferents provide early information about the frictional status of the contact [10], the shape of the contact surface [29] and the direction of fingertip forces [30]. The encoding of these complex fingertip parameters is formed on the basis of signals in ensembles of afferents that reflect the patterns of stresses and strains distributed throughout the fingertip. This information begins to shape fingertip force output within about 70 ms, which is faster than can be explained by the afferents transmitting information by their firing rates, through which they are traditionally thought to convey sensory information (rate encoding). Recently, we have shown that the relative timing of first spikes in ensembles of tactile afferents (temporal codes), which are elicited in response to discrete mechanical fingertip events, encode the relevant information more rapidly than do the rate codes, and fast enough to account for the use of tactile signals in natural manipulation tasks [31]. This work has demonstrated that first, neuronal signals can be transmitted with great (millisecond) temporal precision, second, the precise timing of individual spikes carries information, and third, temporal codes are distributed and sparse.

Control of gaze in object manipulation tasks

Studies of gaze behavior in manual tasks have mainly focused on hand pointing movements that are completed the moment the target is reached [32,33]. While pointing, people direct their gaze to the target at the start of the hand movement, and gaze fixates the target until the hand arrives. The finding that fixating the target improves pointing accuracy, even when vision of the hand is blocked [34–36], suggests that gaze-related efferent and/or afferent signals participate in visual and non-visual feedback loops to ensure manual accuracy [37]. Several recent studies have examined gaze behavior in sequential object manipulation tasks [12,38–42,43•]. In these tasks, participants direct their gaze to successive contact locations as they gain salience as the task progresses over time. Gaze is directed to these locations well before the hand (or object in hand) arrives, and typically remains at the location until around the time of completion of the goal of the current manipulation phase, which is associated with a specific contact event. For example, in a task in which participants are required to pick up a bar, move the bar in hand to contact a spring-loaded target switch, and then replace the bar, gaze is successively directed to the grasp site, the target, and landing surface where the bar is replaced [12]. Gaze arrives at each location ahead of the hand (or bar in hand) but, on average, remains until the grasp is established, the target switch is released, or the bar is replaced. These results indicate that gaze fixations not only predict the spatial goals of sequential action phases but also the timing of goal attainment of each phase. Hence, the timing of contact events demarcating action phases can be predicted both in the visual and in the tactile modalities.

Because gaze is aligned in both time and space with the contact events marking task subgoals [12], visual events related to contact are registered in central vision. These events can include vision of contact between two objects or the hand and an object, or motion of a contacted object. According to our control point hypothesis, these visual events can be compared to predicted visual events and

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aligned with tactile, sensory and auditory events that might arise from the same mechanical contact events. Thus, in sequential manipulation tasks, we argue that in addition to improving the accuracy of hand movement towards target objects, gaze plays a complementary role in the monitoring of task progression and the upholding of sensorimotor correlations important for prediction (see also [40]).

Sensorimotor control points in action observation

An important hypothesis in psychology and neuroscience is that understanding others' actions results from a mechanism that maps observed action onto sensorimotor representations of that same action in the observer's brain. Numerous neurophysiological and imaging studies have shown that neural systems that are engaged when performing actions are also active during action observation (see [44–46] for reviews). These findings have given rise to the direct matching hypothesis that posits that when people observe action, they implement covert action plans that, in real time, match the action plans executed by the actor [44,47]. We have investigated this issue by measuring gaze behavior in observers while they watch an actor perform visually guided object manipulation tasks [42]. Because the pattern of eye movement in object manipulation is driven by sensorimotor representations of the task [12,40,48], the matching hypothesis predicts that observers' eye movements should mirror those of the actor, even though observers' manual actions might be suppressed or inhibited. We confirmed this prediction by showing that when people observe a familiar block-stacking task, the coordination between their gaze and the actor's hand is very similar to the gaze–hand coordination adopted when they perform the task themselves [42]. Both actors and observers direct their gaze to forthcoming contact sites (where blocks are grasped and replaced) and maintain their gaze at each site until the goal is completed. This predictive gaze behavior, recently shown to emerge between 6 and 12 months of age [49•], appears to require vision of the actor's hand. When the hand cannot be seen, gaze tends to track the moving blocks and is reactive rather than proactive and action-like [42,49•].

In a follow-up study, we have shown that even when observers do not know in advance which of two possible blocks the actor will grasp, they still shift their gaze, proactively, to the target block well before the hand arrives [50•]. These proactive eye movements are elicited after a short period of vision of the actor's unfolding hand movement and as soon as the observer is certain about which block the actor will pick up. Although the timing of these eye movements does not directly match that of the actor, they nevertheless reveal that the observer proactively directs gaze to sites at which contact events occur and fixates the site until the subgoal is completed. We have suggested that by directing gaze to predicted contact events, observers — like actors — can monitor task progression. That is, contact events can function as sensorimotor control points in both actors and observers. Of course, the observer does not obtain tactile and proprioceptive signals related to contact. However, visual and — if the action takes place within earshot — auditory events can be registered and compared with predictions of these events. By predicting and monitoring these contact events, observers (again like actors) can also gain information about the properties of objects in the environment. For example, if an observer watches an actor pick up an object that is heavier than the observer expects (on the basis of visual cues), and assumes that the actor has similar expectations about weight as they do, the observer might be able to discern that the object is heavier than expected on the basis of the actions of the actor [51]. Taken together, these results suggest that, in manipulation tasks, contact events have a key role in linking the actor and observer. In both actors and observers, eye movements are driven by sensory predictions and the matching between actor and observer is achieved through common sensory predictions and monitoring. We believe that recording gaze during action observation has great research potential. This novel paradigm has already been used effectively to study the development of action understanding [49•] but can also be used to examine control mechanisms and levels of understanding during learning, potential impairments in action understanding in, for example, individuals with autism or attention deficit and hyperactivity disorder, and to test whether deficits in action production, that are associated with stroke and other impairments, are linked with deficits in action perception.

Gaze behavior in visuomotor learning

The acquisition of most motor skills requires learning novel transformations relating actions to their sensory consequences [3,52]. Studies of motor learning in manual tasks have focused on how hand movements are adapted to altered visual feedback (e.g. [53–58]) or to forces applied to the hand or arm as a whole (see [59••] for a review). Recently, we investigated gaze behavior during learning of a novel visually guided manual task [60••]. Land and McLeod [61] reported differences in gaze behavior across skill levels in cricket batsman; however, previous studies have not examined gaze during the course of skill acquisition. In our task, participants were required to move a cursor to successive targets presented on a screen by applying forces and torques to a rigid tool held between the two hands. Implementation of different complex mappings between hand actions (twisting torques and lateral forces) and cursor motion typically resulted in three distinct stages of learning: an initial exploratory stage, in which participants were unable to control the cursor effectively; a skill acquisition stage, during which control began to develop and performance improved rapidly; and a skill refinement stage, during which performance improved more slowly. During the exploratory stage, participants attempt to discover the basic mapping rules relating motor and sensory signals that can then be implemented to improve performance [62,63]. Like a child learning to ride a bike, the basic coordination needed for stability needs to be discovered before the task can even be performed. Note that most previous studies that have examined adaptation of reaching movements to novel loads or visuomotor perturbations (see above) do not require an exploratory stage. In these tasks, performance improves from the first trial onwards, suggesting that learning involves adaptation of previously acquired basic sensorimotor mapping rules rather than the discovery of novel rules.

During the exploration stage, gaze tended to 'chase' the cursor, reactively, through saccades directed to successive cursor locations. As participants started to gain control over the cursor during the skill acquisition stage, proactive gaze behavior gradually emerged with gaze leading the cursor to the vicinity of the target or to locations en route to the target. As learning progressed, fewer reactive saccades were observed and, eventually, gaze was directed almost exclusively to the target, similar to the situation in reaching and pointing movements under normal sensorimotor conditions [32,33]. The reactive or 'chasing' gaze behavior observed during early learning enables the spatial and temporal alignment of the cursor and gaze, and the locations at which this alignment occurs might function as sensorimotor control points, in much the same way that targets do once the skill is acquired. That is, by directing saccades to successive cursor positions, the consequences of hand actions can be monitored in foveal vision. Moreover, this gaze strategy (whereby cursor and saccadic eye movements are launched from the same locations, albeit at different times) might help to establish a mapping between hand actions and eye movements in gaze-centered coordinates [33,64,65]. Once established, this map could be inverted such that spatially congruent hand and eye movements — based on peripheral vision of target locations — can be programmed concurrently [36].

Sensory cancellation and contact events

As discussed above, the control of object manipulation depends on sensorimotor mechanisms that exploit predicted and actual contact events. One can ask whether contact events are also important in shaping conscious perceptions related to the consequences of our actions. It has been proposed that sensations caused by our own actions are attenuated to increase the salience of sensations with an external cause [66]. Such perceptual attenuation of our own actions could explain why we cannot tickle ourselves [67], and why externally imposed constant forces applied to the fingertip are perceived as more intense than the same forces applied by ourselves [68]. In a recent study, we examined perceptual attenuation in a tapping task, and asked whether attenuation is linked to self motion or to predicted contact events [69]. Participants used their right index finger to tap a force sensor mounted above their left index finger (Figure 2a). A motor generated a tap on the left finger either at the same time as the right finger tap or before or after the right finger tap. When taps on the left and right fingers were synchronous, simulating a self-generated mechanical event, the perception of force on the left finger was attenuated compared with that of similar taps on the left finger experienced during rest (i.e. without right finger tapping). The attenuation gradually reduced when the left tap was either delayed or time advanced relative to the active right tap (Figure 2b). However, taps on the left finger triggered by movements of the right finger that stopped above or passed wide of the sensor did not result in attenuation. These results indicate that perceptual attenuation occurs over a broadly tuned window of time that is centered on the self-generated and predictable contact event. In addition, the results demonstrate that perceptual attenuation is linked to specific contact events arising from movement rather than the movement itself [69].

It is not known whether the neural mechanisms that account for the attenuation of percepts caused by prediction of contact events are related to those accounting for predictions of contact events in the sensorimotor control of action. This question is touched on in Figure 2d, which shows grip and (vertical) load forces recorded during a task in which participants dropped a ball into a cup that was suspended from a handle held with a precision grip [23] (Figure 2c). The solid gray trace is from catch trials in which the ball was caught by the experimenter, and reveals the purely predictive grip force response that prevents the handle from slipping at impact. This trace has been superimposed on Figure 2b after inversion and scaling in height but not time. The time course of grip force modulation in anticipation of ball contact is strikingly similar to the time course of perceptual attenuation observed in the tapping experiment.

Representing object dynamics in manipulation

When lifting an object with a precision grip, with the digits on either side, people scale their grip and tangential load (or lift) forces to the expected weight of the object, which is predicted on the basis of visual and haptic cues and sensorimotor memory from previous lifts [13–15,17,18]. Similarly, when translating and rotating familiar hand-held objects, grip force is precisely modulated in parallel with changes in movement-dependent forces and torques tangential to the grasped surfaces [18,20,21,70–73]. Importantly, the close coupling between grip force and load force has been demonstrated for objects with different complex dynamics (elastic, viscous and inertial

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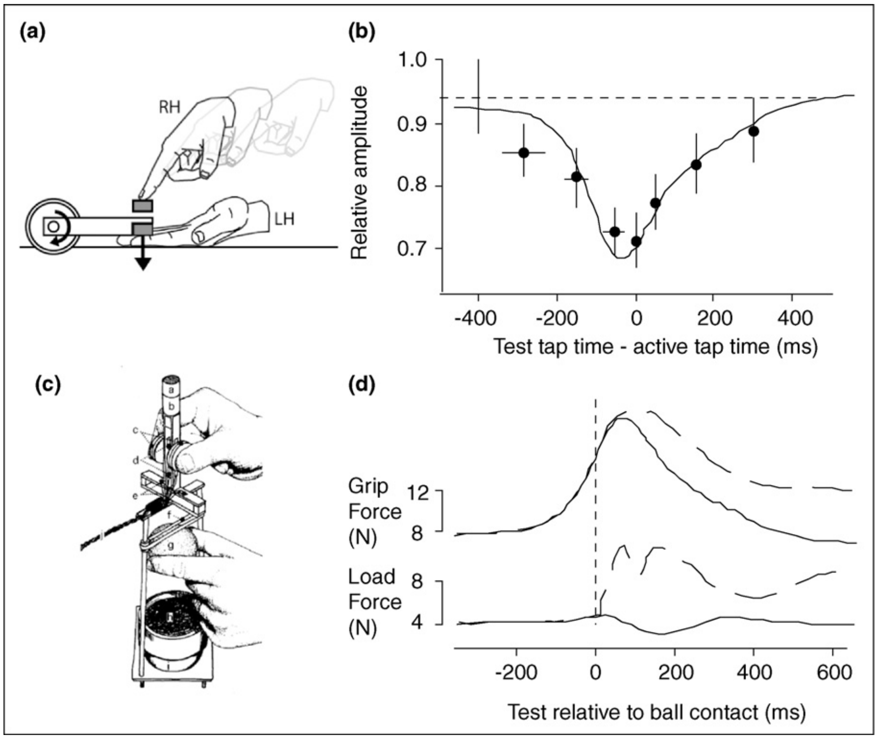
Figure 2



Perceptual attenuation in a tapping task. **(a)** Apparatus and task. While resting their left index finger beneath a force sensor fixed to the lever of a torque motor, participants produced a brief force pulse with their right index finger on a second force sensor fixed above their left index finger (active tap). The motor delivered a similar force pulse (test tap) to the left index finger with a variable lead or lag. Participants compared the magnitude of the test tap to that of a comparison tap delivered to the left index finger a short amount of time later. **(b)** Relative amplitude of the comparison tap to the test tap at the point of perceptual equality, as a function of time difference between the test tap and the active tap. Filled circles and vertical bars represent the mean and ±1 S.E. of 12 participants, and the dashed line shows the mean relative amplitude in a control condition in which no active tap was produced. The horizontal error bars represent ±1 S.D. **(c)** Apparatus used in the ball drop experiment. Participants used their left hand to drop a ball into a cup suspended by a handle instrumented with force sensors that measured grip and load forces applied by the right hand. **(d)** Dashed curves show average grip and load forces as a function of time with 0 representing the time of impact. The solid traces show mean grip and load forces in catch trials during which impact did not occur. The grip force profile from these catch trials is also shown in (b) but has been inverted and scaled in height. Modified from [69] and [23].

loads) [27,28]. Because the mapping between arm motor commands and load force is determined by object dynamics, these findings show that arm motor commands and grip motor commands are independently controlled. This conclusion is supported by recent studies in which the loads acting at the hand and on the arm have been dissociated. Danion and colleagues [74,75•] examined grip forces when holding or moving objects with an additional inertial or spring load attached to either the object or the arm. Grip force was clearly modulated for additional loads applied to the object but not for equivalent loads applied to the arm.

Taken together, these results indicate that the motor system makes use of internal models of object dynamics to predict the load forces that will arise when acting on objects (Figure 1). By combining knowledge about object dynamics with knowledge of the intended arm motor commands (i.e. efference copy), the system can predict load force and adjust grip force accordingly [3,23,28,52].

The ease with which people seamlessly and skillfully handle objects in natural manipulation tasks suggests that they can recruit and de-recruit internal models of object dynamics when grasping and releasing objects that are distinct from internal models used to control limb dynamics alone. Direct support for this idea comes from recent studies of adaptation to hand-held loads in reaching, which demonstrate that the after-effects of adaptation are not observed if the object in hand is released [59••,76].

As noted above, when the weight of an object that has been lifted repeatedly is unexpectedly changed, grip and load forces are typically updated within a single lift. The standard interpretation of this adaptation is that the internal model of the object, incorporating information about its weight or inertia, is updated. However, Quaney *et al.* [77] have shown that the grip force used to lift an object can also be influenced by previous fingertip actions that do not involve lifting the object. For example, if a

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participant strongly pinches an object and then lifts a test object, the grip force used during lifting will be substantially increased compared with that used when the test object is lifted without prior pinching. Similarly, if a participant is explicitly asked to use excessive grip forces for several lifts, they will employ an elevated grip force when lifting the object a day later, even when told to use a normal grip force [78]. However, the load forces used when lifting are not affected by these interventions. On the basis of these results, these authors suggested that separate internal representation of object properties could be used to predict grip and load forces when lifting [78]. It is important to remember that whereas the load force required for lifting depends solely on object weight (i.e. dynamics), grip force also depends on the friction between the fingertips and the object, in addition to the grip force safety margin used to guard against slip, and that can vary idiosyncratically. Thus, instructing participants to use particular grip force behaviors could influence implicit memory mechanisms that are related to scaling of grip force to load force, independently of the internal model of the dynamics of the object.

Although it is clear that people store and recall information about object dynamics, relatively little is known about how this information is represented or encoded. Several studies have examined how we represent loads applied to the hand by robotic manipulanda during reaching movements; these studies concluded that these loads are represented in arm-centered coordinates as opposed to Cartesian coordinates (e.g. [79,80]). Mah and Mussa-Ivaldi [81] examined how object dynamics are represented using a task in which participants learned to balance a virtual inverted pendulum by applying isometric forces that moved the base of the pendulum on a computer screen according to a simulated equation of motion. They found that learning did not transfer across different arm configurations, which suggests that participants did not learn the dynamics of the object (i.e. the mapping between applied force and object motion), but instead learned a mapping between observed object motion and motor commands to the arm and hand muscles [81]. Thus, these results are consistent with the idea that novel dynamics are encoded (at least initially) in intrinsic coordinates.

It is an open question as to whether, with sufficient practice manipulating objects with novel dynamics using different arm configurations, people are able to form a single object-centered representation of dynamics or retain multiple arm-centered representations. Salimi *et al.* [24] examined fingertip forces employed when lifting a box with an asymmetric weight distribution that could not be discerned from visual cues. On the first lift, the box tilted but, after one or two lifts, participants adapted by generating unequal load forces at the two digits. However, participants were unable to transfer this learning when the object was rotated (or they rotated the object themselves), requiring a switch in the digit load forces to avoid tilt (see also [19]). This result suggests that participants stored the specific digit forces (or motor commands) required to lift the object rather than the dynamics of the object itself. However, it is also possible that the dynamics (i.e. the weight distribution) were encoded but that participants failed to apply this knowledge appropriately when the object was rotated. A similar failure to account for object rotation has previously been described when lifting objects with different frictional conditions at the opposing grasp surfaces [82]. When lifting under these conditions, people learn, within a single lift, to apply less vertical lifting force with the digit contacting the more slippery surface. (This predictive strategy tilts the object and reduces the tangential load at the more slippery surface.) When the object is rotated 180°, the predictive scaling of vertical forces is lost. Recently, Quaney and Cole [83] replicated this finding but also found that after 180° hand rotation, participants correctly anticipated the new digit–friction relationships. Thus, internally driven motor plans can access the relevant memories for predictively partitioning the vertical tangential forces according to the frictional demands with changes in hand orientation relative to the object, but not when the orientation of the object is changed relative to the hand.

We have shown, within the context of the size–weight illusion, that the brain maintains independent representations of object weight for sensorimotor control and perception [26]. The size–weight illusion refers to the fact that people judge the smaller of two equally weighted (and otherwise similar) objects to be heavier when lifted. We asked participants to repeatedly and alternately lift a large cube and an equally weighted small cube and measured their fingertip forces in each lift. As expected, participants initially scaled fingertip forces to object size such that they generated larger forces when lifting the large cube. However, they quickly adapted their force output to the true object weights and exhibited accurate sensorimotor predictions about weight (see also [84]). Nevertheless, the size–weight illusion persisted and was unaffected by lifting each object 20 times. This result indicates that the sensorimotor and perceptual systems use separate and independent representations of object weight and also demonstrates that the illusion does not result from errors in sensorimotor prediction. Instead, we have suggested that the illusion stems from errors in perceptual prediction. That is, participants judge the small cube to be heavier because it is heavier than expected at the perceptual level. Note that the size–weight illusion cannot be explained on the basis of Bayesian integration. Assuming that sensory information about object weight is uncertain, Bayesian integration predicts that participants should rely, at least to some extent, on prior expectations about object weight based

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on object size. In other words, in the face of sensory uncertainty, they should judge the small object to be lighter than the equally weighted large object.

Conclusions

The work reviewed here highlights the important role of contact events in object manipulation tasks. These events give rise to discrete and distinct sensory events in multiple sensory modalities and are sensorimotor control points at which predicted and actual sensory events can be compared and aligned. In visually guided object manipulation tasks, gaze is directed to contact points enabling visual contact events to be captured in central vision. During action observation, gaze is also directed to contact points, and we propose that observers predict and monitor sensory events in the same way that actors do. We also emphasized, in this review, the key role of predictive control in object manipulation. There is now ample evidence that people make use of internal models of object dynamics in skilled tasks, and recent studies have started to examine how this information is represented.

The notion of sensorimotor control point still requires a great deal of elaboration and we expect that future empirical and modeling studies will investigate the contributions of different sensory events, registered by different modalities, to the learning and control of object manipulations tasks. In addition, we anticipate that future studies will uncover how different physical properties of objects are represented by the motor system.

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