Can Internal Models of Objects be Utilized for Different Prehension Tasks?

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INTRODUCTION

When gripping and transporting objects, we generate fingertip forces predictively, according to the physical properties of the object (Gordon et al. 1993; Jenmalm and Johansson 1997; Jenmalm et al. 2000; Johansson and Westling 1988; Salimi et al. 2003; Wing and Lederman 1998; Witney et al. 2000). Current theory holds that internal models estimate the needed motor commands and produce sensory predictions that help adapt the models (Flanagan and Wing 1997; Flanagan et al. 1993, 2003; Jordan and Rumelhart 1992; Kawato et al. 1987; Wolpert and Ghahramani 2000; Wolpert et al. 1995). In the dominant interpretation of this theory, separate forward and inverse models are thought to exist. An inverse model generates arm motor commands and copies these commands to a forward model, which generates the commands for gripping. This forward model also sends the expected sensory consequences of the load at the fingertips for comparison with the actual sensory consequences, with the resulting error used to adapt the inverse model when these sources of information do not match (Kawato and Wolpert 1998). Monzee et al. (2003) suggested that the internal models also require sensory information about grip, such as grip force or finger alignment, for efficient functioning and adaptation. However, it is unclear whether their observations of excessive grip force during digital anesthesia resulted from the lack of tactile input to internal models or the failure to detect and correct misalignment errors at the fingers which resulted in horizontal torques.

Regardless of the mechanism, the process of learning how to handle new objects is robust and efficient. Novel objects quickly become familiar, in a few to several trials, as reflected in our ability to accurately reproduce the fully adapted fingertip forces 24 h later (Gordon et al. 1993). Likewise, the grip force required to offset load forces is predicted after only a single trial, but decays over several trials when object manipulation no longer produces the expected load forces (Witney et al. 2000). However, learning the internal models for stabilizing grip and controlling arm trajectory may not proceed at the same rates. Flanagan et al. (2003) reported that grip force adapted about seven times faster than arm trajectory on novel loading of a transported object. This finding provides support to the theory of separately adapted internal models for grip and arm control, and shows that essential differences exist between the mechanisms that generate arm trajectory and those that stabilize grip.

These accurate predictions of fingertip forces require long-term memory resources for efficient prehension that, at some level, represent relevant physical properties of objects (Flanagan et al. 2001; Gordon et al. 1993). It is not clear if these memory resources can be shared across prehension tasks. In studies of arm movement, memory resources for visuomotor transformations seem to be task-specific (Tong and Flanagan 2003). In contrast, when executing reaching and drawing movements against a single rotary viscous force field, which requires a dynamic transformation, the internal model acquired during one type of movement is available for a different movement (Conditt et al. 1997).

We investigated whether learning to handle a rigid, freely moveable object in one prehension task provides an object representation that can be used to handle the same object efficiently in a new prehension task. We predict that the internal model for producing grip force can be used to scale the fingertip forces in other tasks. This is based on the assumption that grasping and lifting the same object in different ways is more akin to a dynamic transformation (Conditt et al. 1997) than to a visuomotor transformation (Tong and Flanagan 2003).
and hysteresis of the force signals were computed to be
the plates were covered with black sandpaper (320 aluminum oxide).
other, with a separation of 2.2 cm between the digit contact surfaces.
the experiments.
Subjects were assigned to one of the two groups, the self-selected
horizontal cursors on the oscilloscope screen (2.85 N/division). Sub-
provided visual feedback of the grip forces (but not lift forces).
Subjects used the thumb and index finger in a pinch grip to grasp
hands for all subjects.
cept was removed from view. All subjects performed 10 such lifts
stationery for 5 s before returning it to the table.
On Day One, subjects in the HFG were instructed to maintain their
grip force between 10 and 11.5 N (as indicated by the horizontal bars
on the oscilloscope screen) until they returned the object to the table
and were no longer applying a lift force to the object. When the
targeted grip force was met, subjects received a verbal command to
lift the object using their right (dominant) hand. This procedure
required the subject to grasp and lift the object in a way that prevented
them from matching their grip force to the physical properties of the
object and that disrupted the natural coordination of the grip and
vertical lift forces (Fig. 2). This sequence of grip, verbal command,
and lift was repeated 10 times with ~20–30 s elapsing between lifts.
Occasional rests of ≥2 min were given between lifts to prevent
muscular fatigue.
Subjects in the SSFG also lifted the novel object 10 times with their
right hand. However, they did not receive verbal instructions other
than to lift the object to a height of 5–8 cm “naturally and comfort-
ably.” The SSFG returned 4 h later with instructions to lift the same
object in the manner as described for the HFG. Although the SSFG
experienced twice as many lifting trials on the first day (20 vs. 10 lifts
for the HFG), 10 lifts is more than sufficient to learn the fingertip
forces needed to efficiently handle novel objects (Flanagan and
Beltzner 2000; Gordon et al. 1993; Johansson and Westling 1988;
Witney et al. 2000; also see RESULTS).
On Day Two, subjects returned for additional testing. We asked
them to disregard the instructions and events from the previous day
and lift the object in a natural and comfortable manner to a height
of 5–8 cm, beginning with their left (nondominant) hand. The oscillo-
scope was removed from view. All subjects performed 10 such lifts
before switching to their right hand for 10 more lifts. Then subjects
performed two trials each with their right and left hands in which they
were instructed to slowly decrease the grip force on the lifted object
until it slipped from grasp. After these “slip” trials, subjects then
performed 10 additional natural and comfortable lifts of the test object
with both their right and left hands.
Data analysis
Force and accelerometer signals were sampled at 400 samples/s
with 16-bit resolution. Grip force was calculated from the normal
force measured at the index finger and thumb (normalfingerm + nor-
malthumb). The lift force was calculated from the vertical tangential
force at both digits (tangentialfingerm + tangentialthumb). On Day Two,
slips of the test object were measured during the phase of the lift when
subjects steadily held the object 5–8 cm above the table. The slip trials
were marked by the onset of vertical acceleration along with a sharp
decrease in lift force at one digit and a simultaneous increase in lift
force at the other digit. The slip force was taken as the normal force
at the onset of acceleration for the digit with the decreased lift force.
The slip forces were measured separately at each digit across both
hands for all subjects.

FIG. 1. Test object. Subjects grasped the object at the black, sandpaper-
covered vertical surfaces with a pinch grip of the thumb and index finger. Force
transducers embedded in the object measured horizontal grip force (GF) and
vertical lift force (LF) at each surface. Total mass of the test object was 230 g.
An accelerometer attached to the object measured vertical acceleration and
lift-off from the support surface.
For each trial we determined the grip and lift forces at lift-off of the object from the table, the peak grip and lift forces, and the grip force once the object stopped moving in the vertical direction. ANOVA was used to assess the effects of group on these dependent variables. Statistical comparisons between the first and last lifts in a series were made using matched-pair t-test. Data in the text and figures refer to group means and SE.

RESULTS

We hypothesized that the internal model that generates grip force commands for one prehension task can be exploited for other prehension tasks with the same object. If true, the HFG should show grip forces at the start of Day Two scaled for the object mass. Accordingly, the HFG grip forces on Day Two would be similar in magnitude to those used by the SSFG at end of the first session on Day One.

Grip force and memory

DAY 1. Subjects who used self-selected forces (SSFG) to lift the test object on Day One used grip forces at the time the object lifted-off from the table (lift-off) that averaged 5.8 ± 0.46 N on the first lift (Figs. 2B and 4). They rapidly decreased their grip forces across the next four lifts and then more slowly across the last five lifts. By the 10th lift of this session, the grip force at lift-off averaged 2.6 ± 0.21 N, which is consistent with previous studies of healthy young adults when lifting this same object (Cole and Rotella 2002).

The peak lift force was similar between groups on Day One across all testing sessions (t(1,18) = 1.32; P = 0.28). For the HFG, the peak lift force on Day One averaged 3.1 ± 0.18 N. The average peak lift force for the SSFG on Day One was 2.9 ± 0.10 N when lifting the object with self-selected grip forces and 3.0 ± 0.14 N for the lifts using 10-N grip force.

DAY 2. During this session, both groups lifted the object naturally and comfortably with the opposite hand (left hand) from the previous day. Subjects in both groups used low peak lift forces that remained stable across all lifts of the object (3.2 vs. 2.8 N for HFG and SSFG, respectively; t(1,18) = 4.33; P = 0.07) and were no different from the peak lift forces of Day One. The mean peak acceleration of the object was also equivalent between the HFG and SSFG across lifts (0.75 and 0.91 m/s², respectively; t(1,18) = 1.04; P = 0.31). These observations suggest that a long-term memory of the load was consolidated and that an internal model of the arm and object was accurately adapted for controlling lift force.

In contrast, the two groups used substantially different grip force for the first lift of the object on Day Two, even though both groups ended Day One handling the object by applying a 10-N grip force prior to applying the lift force (Figs. 3 and 4). Only the HFG on Day Two seemed to be affected by the high grip force task from the previous day. On the first lift of Day Two, the grip force at lift-off was 6.9 ± 0.72 N for the HFG versus 2.5 ± 0.13 N for the SSFG (t(1,18) = 20.46, P < 0.0002). No subject in the SSFG began Day Two using a grip force >2.9 N, whereas no subject in the HFG began Day Two with a force <4.8 N. Grip force for the SSFG on the first lift of Day Two did not differ from the grip force used on their last lift of the self-selected grip force session on Day One (2.5 ± 0.13 vs. 2.6 ± 0.21 N; t(1,9) = 0.35; P = 0.73). Moreover, the SSFG subjects did not decrease their grip force across the remaining nine lifts on Day Two (t(1,9) = 0.43; P = 0.67).

Subjects in the HFG rapidly adapted their grip forces on Day Two. After their first lift, subjects in the HFG substantially decreased their grip force across the remaining nine lifts (Fig. 4). The grip force at lift-off for the first lift of Day Two (6.9 ± 0.72 N) significantly differed from the average of lifts 9 and 10 (2.8 ± 0.21 N) of this day (t(1,9) = 6.16; P < 0.0002). Their grip force levels on lifts 9 and 10 were comparable with those of the SSFG’s lifts on Day Two (F(1,18) = 0.38; P = 0.55).

Differences in grip force between groups on Day Two cannot be attributed to differences in hand slipperiness. The
grip force at which the object would slip from subject's grasp (slip force) in each group was similar (HFG = 1.1 ± 0.07 N; SSFG = 1.1 ± 0.08 N). Likewise, differences between days cannot be attributed to differences in slipperiness between the right hand (Day One) and the left hand (Day Two). The difference in slip force between hands never exceeded 0.2 N.

On considering reasons for the large unexpected differences in grip force between the two groups on the second day of testing, we became concerned that, at the start of Day Two, subjects in the HFG merely persisted with the instructions of the previous day. We compared the grip force across trials when each group was first asked to lift the test object naturally and comfortably (Day One for the SSFG; Day Two for the HFG). Both the SSFG and HFG applied about 6–7 N of grip force for the first lift and rapidly decreased the applied grip force across subsequent lifts (Fig. 4). The group × trial interaction was not significant ($F_{9,180} = 0.42; P = 0.93$), indicating both groups used a similar pattern of grip force across the 10 lifts in this comparison. The 3- to 4-N decrease in grip force between the end of Day One and the start of Day Two indicates that most subjects in the HFG were not merely beginning Day Two by performing the task learned on Day One. Taken at face value, the HFG seemed to start Day Two by treating the object as the SSFG had at the start of Day One, when the object was unfamiliar or novel.

Inspection of the data from individual subjects further reveals that the ability of the HFG to adapt their grip force on Day Two was not compromised by the instructions they received on Day One, with the possible exception of two subjects. All but two subjects in the SSFG used a grip force of 6–8 N for the first lift and steadily decreased the grip force across the remaining trials (Fig. 5). One subject in the HFG (Fig. 5, inset, S1) used nearly twice the force of all other HFG subjects during the first few lifts. The other subject, (Fig. 5, inset, S2) used unusually high grip force over trials five through seven. The behavior of only these two subjects is consistent with the interpretation that subjects in the HFG began Day Two by repeating the task they learned on Day One, at least with regard to grip force level. The remaining subjects used forces across the first 10 lifts that were remarkably similar to the SSFG on Day One (Fig. 5, cf. △ and ■; $F_{1,180} = 0.94; P = 0.34$). It also seems unlikely from these data that the SSFG’s performance on Day Two reflected the opportunity to lift the object 20 times on Day One (10 lifts under each condition) compared with 10 lifts (high force condition) for the HFG. That is, the HFG began the process of rapidly adapting their grip force on the first lift of Day Two (lift 11 overall), which matched the behavior of the SSFG on their first lift overall.

Both groups applied low grip forces during Day Two on resuming lifting with their right hand (3.3 ± 1.43 and 3.1 ± 0.72 N for the HFG and SSFG, respectively; $F_{1,18} = 0.06; P = 0.81$). This indicates that the adaptation in grip force exhibited by the HFG over the previous 10 trials with the left hand also was expressed in the grip force at the right hand. Nor did subjects alter their grip forces based on the slip trials, when the minimum grip force needed to maintain a stable grip was experienced. On Day Two, the grip force applied by each hand before and after the slip trials did not change ($F_{1,18} = 2.81; P = 0.60$). Thus when first lifting the object without artificially imposed grip forces, the HFG used a similar efficient process

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**Fig. 4.** Lifts of the object for the HFG (△, left-handed lifts) on Day Two and SSFG (Day One: ■, right-handed lifts; Day Two: ○, left-handed lifts) during their sessions using self-selected grip force. Both groups began by initially lifting the object with greater grip force than needed. With each subsequent lift, they decreased their grip forces until reaching a stable level across trials 9–10. On Day Two, the SSFG (○) used grip forces similar to those they used during the last lifts (trials 8–10) on Day One (■).

**Fig. 5.** Average grip force used by the HFG on Day Two (∆) after removing 2 subjects (S1 and S2) who may have persevered with the instructions from the previous day to use a high grip force (see inset). The remaining 8 subjects in the HFG developed their grip forces across the 10 trials in a similar manner to subjects in the SSFG.
as the SSFG to quickly reach their preferred minimum grip force.

**Availability of sensory signals while gripping at 10 N**

We were also concerned that the 10-N grip force may have impaired the ability to encode, detect, or respond to cutaneous information about the physical properties of the object. Although this seems unlikely (see DISCUSSION), we examined this issue in a single subject (42-yr-old female; right hand dominant) who did not participate in the main experiment. The subject held a test object using 10 N of grip force while the experimenter randomly pulled vertically on a cord suspended from the object. The cord and experimenter were shrouded from the subject’s view. The pulls on the object produced slow load perturbations at a peak rate of $25.80 \pm 5.93$ N/s, similar to the object lifts (Fig. 6). Grip force increased reliably on each pull at a latency of $\sim 100$ ms, consistent with previous studies when random load perturbations were applied to grasped objects (Cole and Abbs 1988; Cole and Johansson 1993; Johansson et al. 1992a,b; Macefield and Johansson 1996).

**DISCUSSION**

Our observations challenge the concept of a general purpose object representation for prehension or the robustness of such a resource. Both groups obtained an accurate object representation during Day One, because peak lift forces at the start of Day Two were scaled to object weight. Contrary to our predictions, subjects who only handled the novel object using a moderately high grip force failed to apply grip force efficiently the next day when these restrictions were removed. Conversely, no subject who handled the object in a natural manner on Day One used high grip forces the next day, despite ending Day One with instructions to handle the object with a high grip force. Taken together, these observations support a theory of separate, independently adapted internal models for producing grip and lift commands (Flanagan et al. 1996, 2003; Salimi et al. 2000, 2003). Furthermore, our results are consistent with the conclusion of Tong and Flanagan (2003) that memory resources are task-specific, in contrast to the report of Conditt et al. (1997) that different arm movement tasks performed under a single, novel force field shared the same internal model.

**High force task versus natural grasping**

High force task on Day One was unusual in its combination of a moderately high grip force and a strictly enforced sequential application of grip and lift force (Johansson and Westling 1984). These complex grasping and lifting requirements that were enforced for the high force task on Day One may have interfered in various ways with the ability of a grip controller to access putative general memory resources about the object on Day Two. This interpretation would not support our conclusion that internal models are task-specific. We entertain such speculation, but in doing so note that one conclusion remains secure; the object was represented in the nervous system by Day Two, and this resource was not used to scale grip force.

Cognitive strategies can intrude in otherwise automatic motor tasks, as was showed when comparing perceptually intrusive limb loads versus less-intrusive loads (Malfait and Ostry 2004). The high force task most likely demanded considerable attention by the HFG, raising the possibility that their behavior was dominated by unusual cognitive strategies on Day Two. First, we dismiss the possibility that subjects in the HFG used the memory of a faulty weight perception on Day Two. Grasping an object with a high grip force causes us to perceive the object as lighter than when grasped with a lower grip force (McCloskey et al. 1974). Therefore if subjects in the HFG had...
used a cognitively driven strategy guided by perceptually established memories of object weight, we would expect smaller grip forces on the second day compared with the control group. Similarly, it is implausible that all subjects in the HFG failed to understand the implied instruction to lift the object using a lower grip force on Day Two, whereas no one in the SSFG persevered with the final instructions of the previous day. Thus merely instructing subjects to lift with a high grip force does not induce a similar behavior the following day.

Along similar lines, the added attentional demands of the conditioning task may have produced the equivalent of a noisy learning environment, impairing the acquisition of an object representation or adaptation of an internal model. If so, one should observe better performance on Day Two if the HFG is allowed to lift the object more often during the conditioning task on Day One. Conversely, the control group should perform worse, thus generating higher grip forces on Day Two, if required to lift the object many times using a high grip force on Day One. This interpretation remains a possibility.

The high force task also was unusual because a grip force target was externally set. With the predetermined 10-N grip force and visual guidance, there was no need for a forward model of arm and object to set grip force or to scale the grip force according to inertial loads predicted from efference copy of arm commands. This possibility must be allowed, but it remains consistent with the interpretation that separate models exist for scaling grip and lift forces. That is, some memory of the object was accessed to provide for accurately scaled lift forces on Day Two, and this memory apparently was not sufficient to stimulate a process for scaling grip force.

Availability of load information

The strength of our conclusions relies on the availability and fidelity of sensory information about object properties in the face of a moderately high grip force (10 N). There are several logical and empirical reasons to believe that accurate information about load forces was available, apart from the evidence that lift forces were well-scaled on Day Two. Sensory information about load seems to be encoded in central commands used as efference copy (McCloskey 1981) and in muscular receptors (McCloskey et al. 1974). Muscles generating torque at the elbow, which are minimally affected by grip force, may provide an important source of load information in the present task. Cutaneous information about lateral forces at the grasping digits also remains available, via slowly adapting (SA I) mechanoreceptive afferents located in the skin adjacent to the contact patch and in the sides and ends of the finger (Bisley et al. 2000). Likewise, the large receptive fields and sensitivity to lateral strain allow SA II afferents to encode vertical load despite high compressive forces in the skin patch directly at grip contact (Johansson and Vallbo 1983; Macefield et al. 1996). As the skin stiffens under compressive load, we presume that lateral strain is realized at skin regions more distant from the grip contact patch. Finally, there is direct evidence that grip forces remain sensitively graded to small changes in load even when grip force is 10 N or greater (Cole and Johansson 1993). Cole and Johansson (1993) showed graded responses of grip force when a ramp load applied to an object slowed to a constant load, even though the grip force was >10 N. Similarly, Johansson et al. (1992b) showed that the grip force rate fell shortly after the onset of a ramp decrease in load when grip force was ~10 N. This latter finding is consistent with a threshold value of 0.21 N change in load and a minimum response latency of 150 ms (Johansson et al. 1992a). Finally, Johansson and Westling (1984) showed that grip force smoothly scales with load force even with an initial grip force of 10 N when subjects pulled on an object tethered by a spring.

Sensory information for fingertip forces

It is possible that memory resources were shared across prehension tasks, but the forward model for grip control was not adapted/updated in the face of the high grip force. When handling objects under tactile anesthesia, coordination is retained between the grip and load forces, but high grip forces are observed despite prior knowledge about object properties (Johansson and Westling 1984; Monzee et al. 2003; Nowak and Hermsdorfer 2003; Nowak et al. 2003). One interpretation is that the internal model for grip commands requires either continuous or intermittent cutaneous sensory information about grip (Monzee et al. 2003; Nowak and Hermsdorfer 2003) and this sensory information must match the model prediction (Blakemore et al. 1998).

A separate issue of sensory information transfer arises from the fact that the lifting task on the second day began with the left (nondominant) hand. Handling a novel object with the right hand imparts accurate scaling for load on a following lift with the left hand (see RESULTS; also Gordon et al. 1993; Johansson and Westling 1984). However, it is not known if load information obtained during the high force task similarly transfers. This question is relevant because some force fields or visuomotor adaptations fail to transfer across limbs (Shadmehr and Mussa-Ivaldi 1994). Thus it remains possible that transfer might have occurred from the conditioning task to the normal task if the same limb had been used between days.

The stark differences in performance between the two groups in their grip forces, along with similar lift forces, provides evidence that the internal models for grip and lift forces can be independently adapted. The inability of one group to scale grip force appropriately on the second day, despite evidence that an accurate representation of object weight was acquired, is consistent with a task-specific internal model for grip force commands. The data are inconsistent with interpretations based on faulty perceptions of object load or cognitive strategies driven by the unusual conditioning task. Future studies that address motor learning when handling objects are warranted. For example, requiring multiple groups of subjects to repeatedly lift a novel object at different magnitudes of grip force could resolve several issues. If the specific grip force levels used by each group transfers to object lifts on a following day, subjects learned the forces required for the task rather than the object properties. And, as previously suggested, requiring additional lifting trials could control for potential effects of the noisy environment produced by the incompatibility of the somatosensory and visual systems to produce force.

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References


