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Volitional and Automatic Control of the Hand When Reaching to Grasp Objects

Zhongting Chen
East China Normal University and University of Hong Kong

Jeffrey Allen Saunders
University of Hong Kong

When picking up an object, we tend to grasp at contact points that allow a stable grip. Recent studies have demonstrated that appropriate grasp points can be selected during an ongoing movement in response to unexpected perturbations of the target object. In this study, we tested whether such online grip adjustments are automatic responses or can be controlled volitionally. Subjects performed virtual grasping movements toward target 2D shapes that sometimes changed shape or orientation during movement. Unlike in previous studies, the conditions and task requirements discouraged any online adjustments toward the perturbed shapes. In Experiment 1, target shapes were perturbed briefly (200 ms) during movement before reverting to the original shape, and subjects were instructed to ignore the transient perturbations. Despite subjects' intentions, we observed online adjustments of grip orientation that were toward the expected grip axis of the briefly presented shape. In Experiment 2, we added a stop-signal to the grasping task, with target perturbation as the stop cue. We again observed unnecessary online adjustments toward the grip axis of the perturbed shape, with similar latency. Furthermore, the grip adjustments continued after the forward motion of the hand had stopped, indicating that the automatic response to the perturbed target shape co-occurred with the volitional response to the perturbation onset. Our results provide evidence that automatic control mechanisms are used to guide the fingers to appropriate grasp points and suggest that these mechanisms are distinct from those involved with volitional control.

Public Significance Statement

Control of movement involves both volitional and automatic processes. When reaching to pick up an object, we volitionally initiate movement and can choose to grasp in different manners, but we do not consciously control details like selection of contact points and guiding the fingers to the object. This study tested whether we could exert volitional control over automatic adjustments during grasping movements. Subjects reached to "grasp" a virtual target that sometimes changed during movement. They were instructed to ignore these changes (Experiment 1) or stop their movement in response (Experiment 2). However, subjects were not able to inhibit adjustments of their hand toward the changed target, and adjustments continued even after volitional stopping had begun. Our results are consistent with neurophysiological evidence that independent brain areas are involved with volitional and automatic control of movements.

Keywords: grasping, reaching, shape processing, visuomotor, volitional control

Control of everyday actions like reaching to grasp an object is a complex process with both volitional and automatic components. When picking up an object, we generally do not think about exactly how we will grasp the object, yet we reliably select contact points that allow for a stable grip (e.g., Goodale, Meenan, Bulthoff, Nicolle, Murphy, & Racicot, 1994; Kleinholdermann, Franz, & Gegenfurtner, 2013; Lederman & Wing, 2003). The fact that stable grasping can occur without conscious attention suggests that this capability is largely because of automatic visuomotor processing. On the other hand, we are able to exert conscious control of our movements when a task requires. For example, we can choose whether to grasp an object with two fingers or enclose the object with the hand, or whether to grasp an object slowly and carefully or grasp quickly with less precision. This raises the question of how volitional and automatic processes interact.

Perturbation studies have demonstrated that online adjustments of hand movements occur spontaneously without volitional effort, or even conscious awareness. Many previous studies have observed fast corrective adjustments during movement in response to various types of perturbations, including target position (e.g.,

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Zhongting Chen, Key Laboratory of Brain Functional Genomics (STCSM & MOE), School of Psychology and Cognitive Science, East China Normal University, and Department of Psychology, University of Hong Kong; Jeffrey Allen Saunders, Department of Psychology, University of Hong Kong.

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Correspondence concerning this article should be addressed to Jeffrey Allen Saunders, Department of Psychology, University of Hong Kong, Pokfulam Road, Hong Kong, Hong Kong SAR. E-mail: jsaun@hku.hk

Bridgeman, Lewis, Heit, & Nagle, 1979; Gentilucci, Chieffi, Scarpa, & Castiello, 1992; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991a), target size (e.g., Glover, Miall, & Rushworth, 2005; Hesse & Franz, 2009; Karok & Newport, 2010; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991b; van de Kamp, Bongers, & Zaal, 2009; Zaal & Bongers, 2014), target orientation (Desmurget & Prablanc, 1997; Fan, He, & Tillery, 2006; Tunik, Frey, & Grafton, 2005; Voudouris, Smeets, & Brenner, 2013), and hand position (Saunders & Knill, 2003, 2004, 2005). Furthermore, such responses can be observed even if subjects are unaware of perturbations because of saccadic suppression (Bridgeman, Lewis, Heit, & Nagle, 1979; Pélisson, Prablanc, Goodale, & Jeannerod, 1986; Prablanc & Martin, 1992) or visual masking (Chen & Saunders, 2016; Greenwald & Knill, 2009; Greenwald, Knill, & Saunders, 2005). Thus, we clearly have online control mechanisms for guiding hand movements that do not require volition or conscious awareness.

A further question is how the online control processes revealed by these perturbation studies are affected by volition. Are these online control processes entirely automatic, or can they be influenced volitionally? Humans clearly have some capability for volitional supervision of actions. Previous studies have demonstrated that we are able to inhibit a planned action in response to a "no-go" signal (e.g., Falkenstein, Hoormann, & Hohnsbein, 1999; Falkenstein, Koshlykova, Kiroj, Hoormann, & Hohnsbein, 1995; Rubia et al., 2001), or stop an ongoing action in response to a stop-signal (e.g., Logan & Cowan, 1984; Verbruggen & Logan, 2008b), with response latencies of 100–200 ms. However, the effect of volitional intervention on online control processes is not yet known. In previous go/no-go or stop-signal studies, subjects performed tasks that required little or no continuous feedback control, such as button pressing (e.g., Logan & Cowan, 1984), arm movements without a target (Kudo & Ohtsuki, 1998; McGarry & Franks, 1997), or reaching with fixed movement direction (Brunamonti, Ferraina, & Paré, 2012; Mirabella, Pani, & Ferraina, 2008; Mirabella, Pani, Paré, & Ferraina, 2006). With these tasks, we cannot determine whether volitional inhibition of movement also prevents or interferes with the online control processes revealed by perturbation studies. The relationship between volitional actions and online control remains an open question.

Neural imaging evidence suggests that volitional control involves different mechanisms than those involved with online visuomotor control. Volitional inhibition when performing a go/no-go or stop-signal task has been found to be correlated with the activity of a fronto-basal-ganglia circuit (for review, see Verbruggen & Logan, 2008b), whereas online visuomotor control is associated with parietal lobe areas (Prabhu, Lemon, & Haggard, 2007). Given this neural dissociation, volitional and automatic control might make independent contributions to performance of a visuomotor task that has both volitional and automatic components.

Although volitional inhibition is clearly a conscious and intentional action, unconsciously processing can influence such responses. For example, many studies have found that subliminal presentation of no-go signal can delay responses to a go signal, even though the interfering signal is not consciously perceived (e.g., Chiu & Aron, 2014; van Gaal, Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008; van Gaal, Ridderinkhof, Scholte, & Lamme, 2010). Another finding is that implicit learning can facilitate volitional control: subjects are better at inhibiting their responses in a go/no-go task, and faster at stopping their actions in a stop-signal task, when specific stimulus-signal mappings are consistently repeated across training sessions (Lenartowicz, Verbruggen, Logan, & Poldrack, 2011; Verbruggen & Logan, 2008a). These findings demonstrate interactions between volitional and automatic processes.

In the present study, we test whether subjects can exert volitional control on grasp point selection during the online control phase of a reach-to-grasp movement. Grasp points for picking up an object could potentially be selected during a planning phase prior to initiating movement. To the extent that grasp point selection is preplanned, we would likely have some degree of volitional control. However, some recent studies, discussed in the next section, have demonstrated that grasp point selection can occur online during movement. Are these online adjustments because of an automatic control process, or can they be influenced volitionally? This is the main question addressed in this study.

Grasp Point Selection During Online Control

When reaching to grasp an object, information about the shape of a target object is needed to guide the hand to a successful grip. We consider the case of a two-digit precision grip, which is commonly used for manipulating small objects (Landsmeer, 1962; Napier, 1956). To make a stable grip, the contact points of the grip must satisfy some physical constraints that depend on the shape of the object (Blake & Brady, 1992; Ponce, Stam, & Faverjon, 1993; Sanz, Del Pobil, Inesta, & Recatala, 1998). Figure 1 illustrates the constraints of force closure and torque control. Studies of human grasping have found that the contact points selected for a two-finger grip effectively satisfy these constraints (Goodale, Jakobson, & Keillor, 1994; Goodale, Meenan, et al., 1994; Kleinholdermann et al., 2013; Lederman & Wing, 2003), indicating that shape information plays an important role in guiding the control of reach-to-grasp movements.

One might expect that grasp points would be selected prior to initiation of movement, but recent evidence indicates that preplanning is not necessary, and that grasp point selection can occur during online control (Ansuini, Santello, Tubaldi, Massaccesi, & Castiello, 2007; Chen & Saunders, 2015; Eloka & Franz, 2011; Voudouris, Smeets, & Brenner, 2013). These studies used a perturbation paradigm in which the orientation or shape of a target object was suddenly changed during movement on some trials, and subjects had to make online adjustments to successfully grasp the new perturbed target. The general finding from these studies is that subjects are able to smoothly adjust their grip toward appropriate grasp points for a new target, with corrective adjustments detectable after a relatively short latency (115–310 ms). Chen and Saunders (2015) included shape perturbation conditions that required online analysis of target shape to determine grasp points and found that subjects were still able to grasp at appropriate contact points, with no difference compared with unperturbed trials where the target shape was visible prior to movement.

While the relatively fast responses suggest an automatic online control process, they do not rule out the possibility of a volitional influence. In the studies cited previously, subjects were aware that the target could be perturbed and were asked to adjust their movement in response. Results might be different if subjects were instead asked to suppress responses to perturbations, as in a stop-

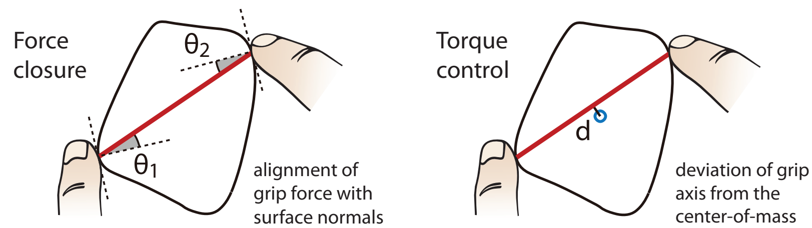

Figure 1. Two main physical constraints of grasp point selection in two-digit precision grip: force closure and torque control. Force closure requires the direction of force by the fingers (thick red line) to be close to perpendicular to the surface of the object. The angles between the force and the surface normal directions at the contact points (θ1 and θ2) provide a measure of deviation from force closure. If these angles are too large, the object may rotate or slip when force is applied. Torque control requires to minimize torque and its ideal situation is that the grip axis to pass through the object's center of mass. The distance (d) from grasp axis to the center of mass (blue circle) provides a measure of deviation from optimal torque control. If this distance is too large, then extra pressure would have to be applied to avoid rotation of the object around the grip axis. See the online article for the color version of this figure.

signal task. Note also that the smooth adjustments observed in response to target perturbations do not necessarily imply a continuous feedback control process. It is possible that perturbations prompt a discrete reprogramming of the grasping movement that is similar to the normal process of movement initiation (e.g., Gentilucci et al., 1992; Paulignan et al., 1991b), which gradually affects the movement trajectory because of momentum of the hand. Studies using a stop-signal paradigm have found that volitional responses can be initiated within 200 ms (e.g., Logan & Cowan, 1984; Mirabella et al., 2006), which is less than the response latencies observed in our previous study (Chen & Saunders, 2015). This would provide an opportunity for volitional control: Subject might be able to suppress the initiation of the secondary movement toward the new perturbed target.

In another recent study, we found that subliminal perturbations of a grasping target can produce detectable grip adjustments (Chen & Saunders, 2016), which suggests that these adjustments are because of an automatic online control process. In that study, we used backward masking to prevent subjects from perceiving brief perturbations of the orientation or size of a grasping target during movement. Despite being unaware that the target object ever changed during the grasping trials, subjects made adjustments in the orientation or size of their grip in a direction consistent with the perturbations. These results demonstrate that online adjustments to grip orientation and size can occur automatically without conscious awareness. However, it remains possible that subjects could exert volitional influence on responses to perturbations that are consciously perceived. Another limitation of Chen and Saunders (2016) is that we tested perturbations of orientation and size, but not perturbations of shape. Responses to orientation and size perturbations could potentially have been driven by rotational and radial motion signals, rather than online shape processing for grasp point selection.

Current Study

This study investigates automatic and volitional visuomotor control by combining volitional inhibition and a reaching-to-grasp task with target perturbations. As in Chen and Saunders (2015), subjects performed grasping movements toward virtual targets that were sometimes perturbed during movement. However, the instructions and task demands were different. In Experiment 1, the target shape was briefly replaced by a different shape during movement on perturbed trials, and subjects were asked to inhibit any response to these transient perturbations (Figure 2a). In Experiment 2, perturbations served as a stop signal, and subjects were asked to stop their movement and withdraw their hands immediately when a perturbation was detected (Figure 2b). In both cases, the task demands would discourage adjustments of the grip toward grasp points for the perturbed object; such responses would be either counterproductive for the task (Experiment 1) or unnecessary (Experiment 2). On the other hand, if online grasp point selection is an automatic process under limited volitional control, then these conditions might elicit the same sort of "corrective" adjustments as observed in our previous study, despite the task irrelevance of the shape perturbations.

In addition, the stop-signal task of Experiment 2 allowed us to observe the time course of volitional control of action. We measured the latency of volitional response by detecting changes in hand speed and grip aperture, which could then be compared with the latency of automatic grip adjustments to test whether these two types of responses can coexist at the same time.

Experiment 1

Method

Subjects. For Experiment 1, 12 subjects (6 men, 6 women) were recruited from the University of Hong Kong and paid for their participation. The average age of the subjects was 21.67 ($\pm$3.77 *SD*) years. All were right-handed and had normal or corrected-to-normal vision. The procedures were approved by the Human Research Ethics Committee for Non-Clinical Faculties.

We expected that 12 subjects would provide high power for detecting responses if performance was similar to the results of our previous studies. In Chen and Saunders (2016), we observed perturbation effects with Cohen's *d* in the range of 0.9–1.2, for which 8–11 subjects would provide a power of 80%. The previous study used subliminal perturbations while Experiment 1 used

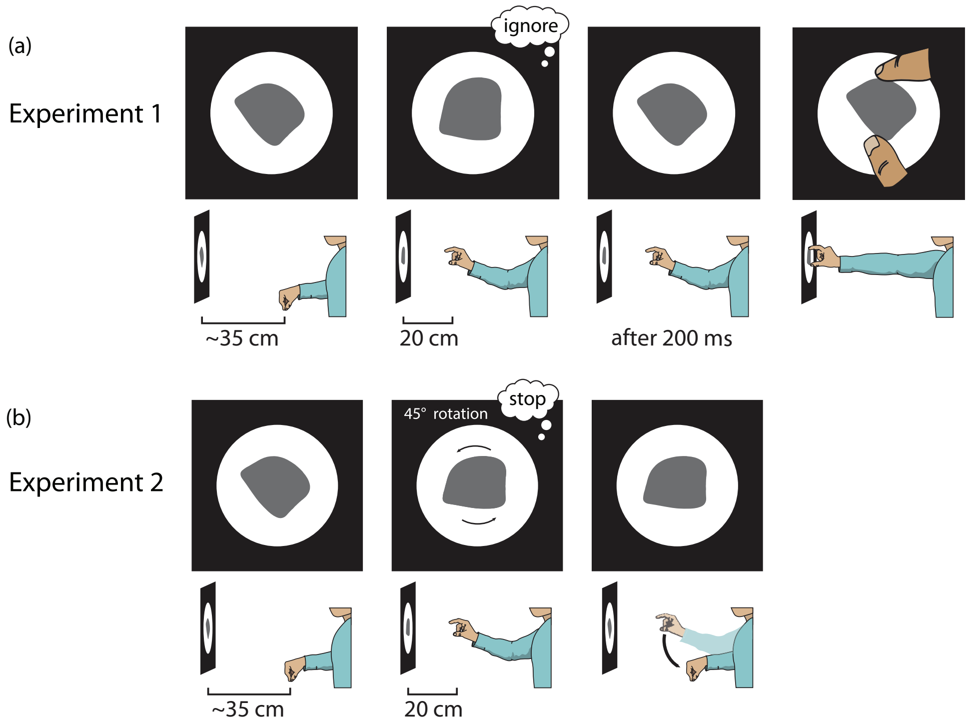

Figure 2. Illustration of the perturbed conditions and tasks in Experiments 1 and 2. Subjects performed a virtual grasping task in which they reached to touch projected shapes as they would if they were grasping a thin object. Unperturbed trials were the same for the two experiments, but the procedure and task on perturbed trials differed. (a) In Experiment 1, subjects attempted to suppress responses to brief perturbations of the target shape. On 50% of trials, the target shape was replaced by a different random shape for 200 ms during the movement. Subjects were instructed to ignore these perturbations and continue reaching toward the original target, which always reappeared after the perturbation. (b) In Experiment 2, subjects were required to stop their movement in response to perturbations. On 20% of trials, either the orientation or shape of the target was changed during movement. When this occurred, subjects were instructed to stop their hand immediately and return it to the start position. See the online article for the color version of this figure.

supraliminal perturbations, so any responses would be expected to be equal or greater than in the previous study.

Apparatus and stimulus. The targets for virtual grasping movements were computer-generated images of 2D shapes that were back-projected onto a rigid and semitransparent acrylic surface, using a BenQ 710ST DLP projector with a resolution of 1,920 × 1,080 pixels and a refresh rate of 60 Hz. Images were rendered with OpenGL using a NVIDIA Quadro FX 3700 graphics card and were antialiased with subpixel resolution. The projection surface was aligned to be perpendicular to the floor and the subject's line of sight, at a distance of 50 cm from the subject's eyes. A black board with circular aperture was placed on top of the projection surface to create a 16.8 cm diameter visible region that was centered in front of the subjects. Subjects were seated at a table and allowed free movement of their heads. The starting position for the hand was a marked location on the table, and the hand was visible throughout movements.

The 3D positions of a subject's right index finger and thumb were recorded during movements at 240 Hz using 3D Guidance trakSTAR system. Sensors were attached to back of a subject's fingernails using latex finger cots, which enclosed the tip of the finger and sensor. Because the sensors were on the back of the fingers, the distance between the sensors was slightly larger than the aperture between the fingertips. To estimate this difference, subjects performed a calibration procedure in which they touched the screen at pairs of points that were separated by 40 mm or 80 mm.

The simulated objects were random 2D shapes with smooth contours presented in gray on a black ground. Shapes were created by first generating a random polygon, which was the convex hull of 5–7 random vertices, and then applying Gaussian blur to the radial function ($\sigma = 17°$). A total of 16 unique shapes were generated in this way. Across shapes, the average radius was 2.60 cm (±.23 cm) and the average area was 21.75 (±3.87) cm^2. Each shape would appear in one of two orientations, which differed by 45°. The set of shapes was the same as used in Chen and Saunders (2015).

Procedure. The task for subjects was to reach and touch a virtual object in the way that they would if they were grasping the object. At the start of a trial, the hand was at a starting location approximately 40 cm away from the surface. Presentation of the target shape was the cue to begin movement. Subjects reached to touch the virtual object, making contact with the projection surface, and then held their hand at the end position until the stimulus disappeared. Subjects were encouraged to move at a natural speed, with no specific requirements on movement duration or speed. Our previous study using a similar method found that this instruction was sufficient to produce movements with normal transport kinematics (Chen & Saunders, 2015).

On each trial, the shape of a target either remained constant (unperturbed trials) or briefly changed during the ongoing movement (perturbed trials). Perturbations were triggered when the tip of index finger was 20 cm away from the projection surface. At this point, the target shape was replaced by a different randomly chosen shape from the set. The perturbed shape was presented for 200 ms, and then the original target shape reappeared and remained visible for the remainder of the trial. We explained to subjects that the final target shape would always be the same as the initial target shape, and asked them to try to ignore the brief perturbations and continue their planned movement.

Each subject performed 512 trials in a 1-hr session. Each combination of object shape and orientation was used as the target object on 8 unperturbed trials and 8 perturbed trials. The order of trials was fully randomized. Before the experimental trials, 12 practice trials were provided as to familiarize the subject with the task. Half of the practice trials were with perturbations and half without perturbations.

Results

Final grasp point selection and optimality. We first report analyses of the grip axes at the end of movements. The final grip axes were used to test whether subjects selected grasp points that were appropriate for the target objects, and we compared final grip axes from perturbed and unperturbed trials to test whether perturbations had effects that persisted until the end of movements. There is evidence that opposing fingers are controlled jointly during two-finger grasping (Mon-Williams & Bingham, 2011; van de Kamp & Zaal, 2007), so we analyzed the orientation and position of this axis rather than the separate positions of the fingers. Note that perturbation responses would not necessarily be revealed in final grasp points because any such responses could potentially be corrected after the original target reappeared. Nevertheless, we did observe some small differences in final grasp points consistent with involuntary responses.

Figure 3a shows examples from individual trials of a representative subject for two sample objects. As in these examples, the final grip axes tended to be similar for perturbed and unperturbed trials. To quantitatively evaluate whether final grip axes for were affected by perturbations, we performed a regression analysis using the expected grip axes for the initial/final stimuli and perturbed stimuli as predictors. We fit a linear model to the perturbed trials from each subject:

$$\alpha_{pert} = \beta_0 + \beta_1 \alpha_1 + \beta_2 \alpha_2 + \text{noise} \quad (1)$$

where α_{pert} is the angle of the final grip axis on a given perturbed trial, α_1 and α_2 are the grip axis angles that would be expected for the target stimuli and the perturbed stimuli on an individual trial, and β_1 and β_2 are regression coefficients representing the relative influence of the two stimuli. The expected grip axis angles (α_1 and α_2) for each target object were computed by averaging final grip angles from unperturbed trials, separately for each subject. For comparison, we also applied the regression analysis to data from unperturbed conditions, setting α_1 to be the expected grip axis for the presented stimulus and α_2 to be the expected grip axis for a randomly chosen alternative object. The regression results for unperturbed trials provide an indication of the range of coefficients that would be expected if the grip axes were entirely determined by a single object, given the variability across trials in the same condition.

Figure 3b shows the means of the regressed coefficients, averaged across subjects. The observed coefficients from the unperturbed trials show that the average grip axis for the presented objects was highly predictive of grip axes on individual unperturbed trials, whereas the mean coefficient for the unseen alternative objects were negligible. This observation confirms that there were systematic variations in grip axes across individual objects. For perturbed trials, the mean coefficient of initial (final) objects

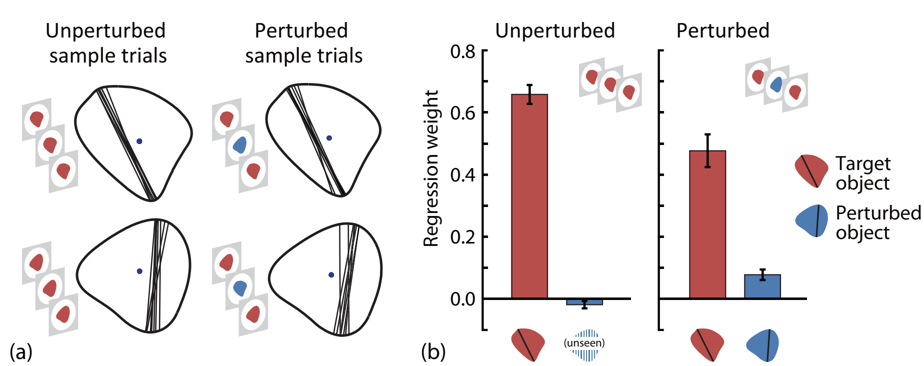

Figure 3. (a) Sample grip axes in Experiment 1 from unperturbed trials (left) and perturbed trials (right) with the same target objects, from a representative subject. (b) The fitted coefficients of the final grip axis angle as a linear function of the expected grip axis angles of the target and perturbed objects. The left set of bars shows the results of the control analysis of unperturbed trials, in which one predictor was the expected grip axis from the presented target and the other was the expected grip axis from the alternate target that was not presented but randomly selected. The right set of bars show the results from the analysis of perturbed trials, in which the predictors were the expected grip axes from target objects and perturbed objects. Error bars depict one standard error of the mean. See the online article for the color version of this figure.

was large, indicating that final grasp points on these trials were similar to those on unperturbed trials. However, there was also evidence of an influence of perturbations on final grip axes. The coefficient β_2, representing the component of final grip axes predicted by the expected grip axes of the perturbed shapes, was small but significantly larger than zero, $t(11) = 4.58$, $p < .001$, Cohen's $d = 1.32$. This shows that there remained some adjustment of the grip toward the preferred grip axes of the perturbed shapes that was not eliminated by final adjustments at the end of movement.

To test whether perturbations influenced the quality of grasp point selection, we analyzed the optimality of final grasp points with respect to the two criteria: the distance of the grip axis from the center-of-mass (COM) of the shape, and the angular deviations from force closure at the two contact points (Figure 1). These measures were computed based on the orientation and position of the grip axis in relation to the shape, as if the projected shape were a thin planar object with uniform density and opposing forces were applied along the grip axis. While there was no actual force closure for virtual grasping, and the virtual objects did not have a center of mass, a control experiment found that grip axes are selected in a similar way for virtual grasping and grasping physical objects (see the Appendix).

The mean results, averaged across subjects, are shown in Figure 4. For COM deviation, the mean distance was 3.57 mm (±.97 mm *SD*) in the unperturbed condition and 3.40 mm (±1.01 mm *SD*) in the perturbed condition, which were not significantly different, $t(11) = 2.15$, $p = .055$, Cohen's $d = .62$. These COM deviations are similar to those observed in some previous studies testing grasping of real objects (Goodale, Jakobson, et al., 1994; Lederman & Wing, 2003). For force closure, the mean angular deviation was 14.61° (±1.65° *SD*) in the unperturbed condition and 13.54° (±1.29° *SD*) in the perturbed condition. The difference in force closure was marginally significant, $t(11) = 2.28$, $p = .043$, Cohen's $d = .66$, but in the opposite direction that would be expected if the transient perturbations interfered with grasping the final target object. We suspect that this is a Type I error because our previous study using a similar method did not observe any effect or trend in this direction (Chen & Saunders, 2015), and it is not clear why perturbations would improve optimality. As an alternative, this slight improvement might be because of enhanced attention caused by the sudden change in the target.

To evaluate whether the grip axes were shape specific, we computed the force closure deviations that would be expected if the observed grip axes were paired with either the perturbed object or randomly chosen shapes, rather than the actual target shapes on each trial. The expected force closure deviation was significantly smaller for the actual shapes than either the perturbed shapes, $F(1, 11) = 61.46$, $p < .001$, partial $\eta^2 = 0.81$, or randomly paired shapes, $F(1, 11) = 86.62$, $p < .001$, partial $\eta^2 = 0.89$, indicating that grasp point selection was sensitive to the force closure constraint. These results indicate that subjects successfully adopted final grasp points that would permit a stable grip, either with or without transient perturbations.

Dynamic perturbation responses. In this section, we report an analysis of dynamics of corrective responses to perturbations. We used the same approach as for final grip axes, but applied to the grip orientations at various moments over the course of movement. The regression model was:

$$\alpha_{pert}(t) = \beta_0(t) + \beta_1(t)\,\alpha_1 + \beta_2(t)\,\alpha_2 + \text{noise} \qquad (2)$$

where $\alpha_{pert}(t)$ is the grip axis angle at a given time t, α_1 and α_2 are the grip axis angles that would be expected for the target and perturbed stimuli for each individual trial (same as before), and $\beta_1(t)$ and $\beta_2(t)$ are regression coefficients representing the relative influence of the target and the perturbed stimuli at time t. For this analysis, time was defined related to the point at which perturbations would be applied. For example, the analysis for $t = 50$ ms would use the frames that were 50 ms after the finger reached 20 cm from the target. We chose to align trials at the perturbation onset because we were primarily interested in the responses to perturbations, and this allows a measure of response latency.

One complication of this analysis is that the 3D orientation of the hand changes systematically over the course of the movement, irrespective of the final grip axis (Figure 5). To associate grip axes at different points in the movements, we computed a set of moving 2D reference frames for each subject that represents the typical range of grip orientations at various distances from the screen surface. The method was the same as used in Chen and Saunders (2015). Only unperturbed trials were used to compute reference

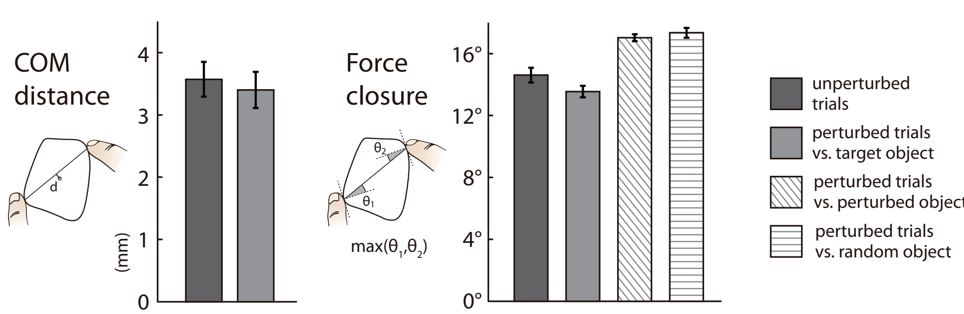

Figure 4. Optimality of final grasp points in Experiment 1. The left graph plots mean distances from the grip axis to the center of mass (torque control), and the right graph plots mean angular deviation between the grip axis and the surface normal directions at the contact points (force closure). For perturbed trials, force closure error was measured in three ways: relative to the target object (gray), relative to the perturbed object that was briefly presented (diagonal lines), and relative to a random different object that was not seen (horizontal lines). Error bars depict one standard error of the mean. See the online article for the color version of this figure.

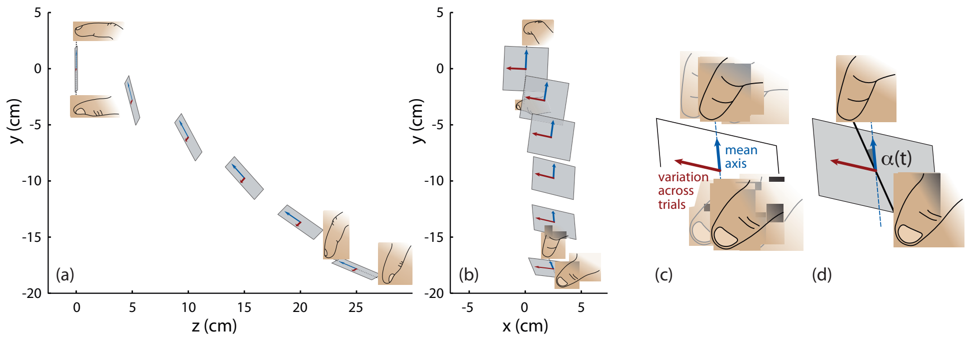

Figure 5. Example of a moving reference frame used to compare grip orientations at different points during movement, shown in a side view (a) and a front view (b). Variations in grip axis at the end of movement were in the frontoparallel plane of the target, while variations earlier in movement tended to be in a slanted plane. (c) We computed 3D reference frames at each distance using average 3D orientation of the grip axis as one basis vector (blue arrows), and the orthogonal direction that was most predictive of trial-to-trial variations as the second basis vector (dark red arrows). (d) The angle of the grip axis relative to the mean grip axis within these reference planes was used for analysis of grip dynamics. See the online article for the color version of this figure.

frames to avoid confounding with perturbation effects. Reference frames were computed for 8 nonoverlapping intervals of distance (i.e., 2–6 cm, 6–10 cm, 10–14 cm, 14–18 cm, 18–22 cm, 22–26 cm, 26–30 cm, 30–34 cm from target) and smoothly interpolated to get reference frames at each specific distance. The set of grip axes within a distance interval were represented as unit vectors on the sphere corresponding to the direction from thumb to index finger. The first basis vector was the mean 3D orientation of the grip axes at a given distance. The second basis vector was chosen to be the orthogonal direction that was most predictive of the final grip axis. To compute this, we first projected the unit vectors representing grip axes onto a plane orthogonal to the mean grip axis to remove the component in the direction of the first basis vector, resulting in a 2D representation of the residual variability. We then performed a regression analysis to find a best fitting linear mapping from this set of residual vectors onto the set of final grip angles. The gradient direction of the best-fitting map was used as the second basis vector. Trial-to-trial variations of the grip axis in this direction would be the most strongly predictive of variations in the final grip axis. The reference frame defined by these basis vectors therefore provides an optimal way to compare grip orientation at various stages during movement to the grip orientation at the end of movement.

Figure 6 plots the mean regression coefficients $\beta_1(t)$ and $\beta_2(t)$ fit to the perturbed trials using Equation (2), averaged across subjects. These functions can be interpreted as the relative influences of target object ($\beta_1(t)$) and perturbed object ($\beta_2(t)$) on the grip orientation over the course of the movement. Trials were parameterized as a function of time after perturbation so that the latency of perturbation responses could be evaluated. As can be seen in Figure 6, the average $\beta_1(t)$ was significantly above zero at the time of the perturbation onset, indicating that subjects had already started to adjust their hand movement to fit the target. If perturbations had no effect, one would expect $\beta_1(t)$ to monotonically increase until the end of movement. We instead found that $\beta_1(t)$ increased for 300 ms after the perturbation onset and then began to decrease. At the same time, the average $\beta_2(t)$ coefficient (blue dashed) started to increase from zero. The $\beta_2(t)$ coefficient represents the correlation between the orientation of the grip axis at time t and the orientation of the final grip axis expected from perturbed stimuli. Therefore, both the increase of $\beta_2(t)$ and the decrease of $\beta_1(t)$ can be interpreted evidence on that subjects were adjusting their grip axis toward the perturbed object. Later in time, one can see these trends reversing as subjects adjusted their grip back toward the target. The average $\beta_1(t)$ coefficient reached a local minimum 479 ms after the perturbation onset and then began to increase again, and the average $\beta_2(t)$ increased to its maximum 538 ms after perturbation and then started to decrease. The maximum

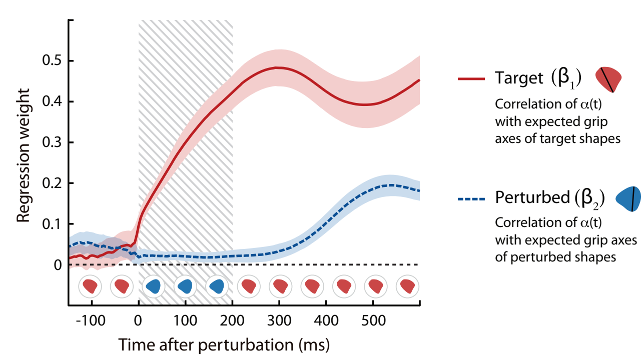

Figure 6. Effect of perturbations on grip orientation over the course of movement in Experiment 1. The graph plots the mean regression weights representing the influence of the target objects (β1, solid red) and the perturbed objects (β2, dashed blue) on the grip axis at various times after the perturbation onset trigger. Shaded regions depict ±1 standard error, and hatched region shows when perturbed objects were visible. If subjects were able to ignore perturbations and continuously guide their fingers to preferred grasp points for the target, then β1 would increase monotonically and β2 would remain close to zero. We instead observed a non-monotonic pattern. About 300 ms after the perturbation onset, β1 began to decrease while β2 began to increase from close to zero, corresponding to an adjustment away from the grip axis for the target object and toward the grip axis for the perturbed object. Later, these trends reversed and the grip was adjusted back toward the expected grip axis for the target object. See the online article for the color version of this figure.

of the average β_2(t) was substantially larger than zero, $t(11) = 7.73$, $p < .001$, Cohen's $d = 2.23$, 95% confidence interval (CI) = [.14 .25]. The observed pattern of response can be interpreted as a transient adjustment to the perturbed object followed by a correction toward the original (and final) target object.

When analyzed individually, this nonmonotonic pattern of dynamic responses was observed for all subjects except one. We computed the latency of the local maximum and minimum of β_1(t) for each individual subject that showed a nonmonotonic pattern, and found that these latencies averaged 285.2 ms and 487.5 ms, respectively, and had *SD*s of 49.7 ms and 49.3 ms. The similar mean latencies and modest variability demonstrate that the individual subjects' results showed the same patterns observed in the average coefficients.

The adjustment of the grip toward the target object on unperturbed trials began somewhat later than in our previous study using similar stimuli (Chen & Saunders, 2015). The β_1(t) weights indicating adjustment toward the target remained small until near the point where perturbations would be triggered, whereas in our previous study we observed a more graduate increase that began earlier. Subjects may have adapted to the new task by slightly delaying adjustment of their grip. However, they did not appear to be performing the task as a two-part movement, as there was no corresponding delay or discontinuity in hand transport (see Dynamics of Hand Transport and Grip Aperture).

From our analysis of grip dynamics, we can conclude that the briefly presented objects on perturbed trials had an influence on grip orientation during hand movements, despite subjects' attempt to inhibition any response. Moreover, the adjustments were toward the grasp points expected for the specific perturbed objects. The β_2 function shown in Figure 6 (blue dashed) represents the consistency between the current grip orientation and the expected final grip orientation for the perturbations objects. One can see that β_2 function temporarily increases after the perturbations, indicating that they were adjusting the grip as they would if they were reaching to grasp the perturbed object. These results demonstrate that grasp point selection can occur during online control, and suggest that this is an automatic process that resists volitional influence.

Dynamics of hand transport and grip aperture. We also analyzed the dynamics of hand transport and grip aperture to check whether perturbations had other effects on movement. There was nothing unusual about these components of movements, and there were no detectable differences across perturbed and unperturbed trials.

Figure 7a plots the mean speed of the hand as a function of time on unperturbed and perturbed trials. As in the previous analysis, trials were aligned at the moment when perturbations would be triggered. For perturbed trials, the figure plots hand speed over a time window from 250 ms before perturbation to 600 ms after perturbation. For unperturbed trials, the figure plots hand speed over the same window around the point at which a perturbation would have been triggered on perturbed trials (i.e., $t = 0$ when the hand reaches 20 cm from the target).

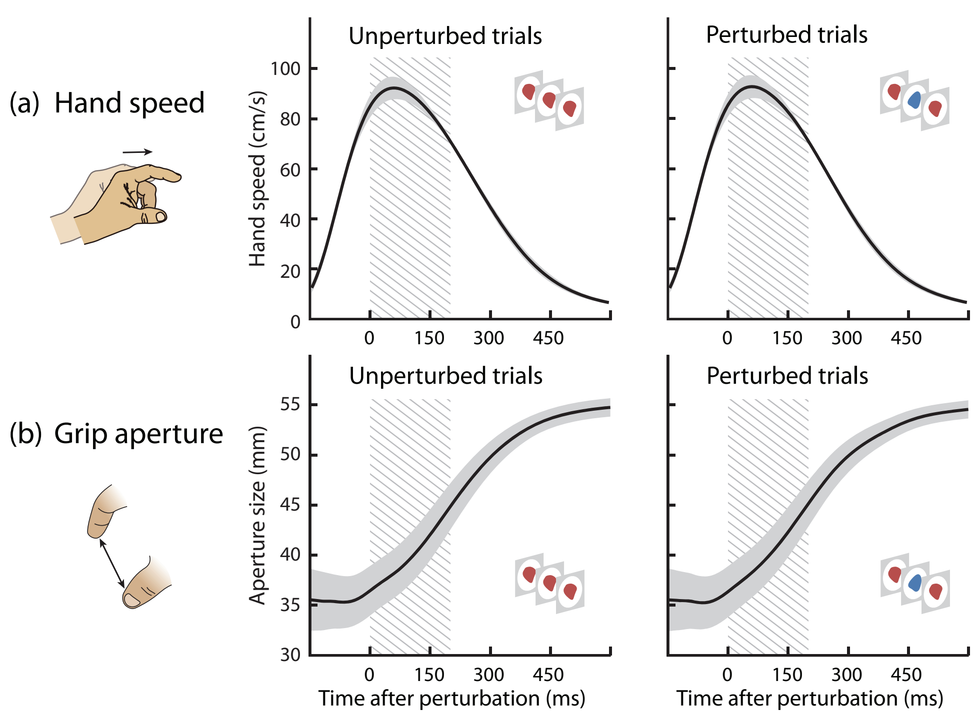

Figure 7. Hand speed (a) and grip aperture size (b) as a function of time after the perturbation onset trigger (20 cm away) for unperturbed trials (left) and perturbed trials (right) in Experiment 1. The curves show mean speed and grip aperture functions averaged across subjects, with gray regions showing ±1 standard error. Hatched regions show the time range when perturbations would be presented. See the online article for the color version of this figure.

The speed profiles were almost identical in the unperturbed and perturbed conditions, showing a typical pattern of smooth acceleration and deceleration. To test whether the presentation of perturbation delayed the hand movement, we also compared overall movement durations. Overall movement duration was measured from the onset of the initial target to when subjects touch the screen surface. The mean movement duration, averaged across subjects, was 1157 ms (±201 ms *SD*) for unperturbed trials and 1181 ms (±213 ms *SD*) for perturbed trials, which were not significantly different, $t(11) = 1.93$, $p = .079$, Cohen's $d = .56$. Our previous study using similar methods found a small but significant delay in the perturbed conditions relative to unperturbed conditions, which would be consistent with the marginal trend observed in the present data. A small delay, if it occurred, could be attributed to some slight hesitation in response to the sudden change in target. Our results suggest that any such delay was small (2.7%). Overall, the observed speed profiles and movement duration indicate that the brief perturbations of the grasping targets caused little or no delay of the ongoing hand movements.

The maximum speed of the hand over the course of movement, averaged across trials and subjects, was 98.18 cm/s (±15.50 cm/s *SD*). This is comparable to the speeds observed in previous studies (e.g., Fan et al., 2006; Gentilucci et al., 1992; Paulignan et al., 1991a, 1991b), suggesting that subjects did not intentionally delay their hand movement despite that we did not encourage them to make the movement fast. No significant difference was found in the maximum speed profile between unperturbed and perturbed trials, $t(11) = 1.20$, $p = .256$, Cohen's $d = .025$.

Figure 7b plots the mean size of the grip aperture as a function of time after perturbation in unperturbed and perturbed conditions. Online adjustments of the grip aperture in response to the size of the perturbed target would not be expected to cause any systematic difference between the average grip aperture on unperturbed and perturbed trials because the perturbed targets were selected randomly from the same set. However, if perturbations caused movement to be reinitialized, this could cause the grip aperture dynamics to change (e.g., Bock & Jungling, 1999; Castiello, Bennett, & Paulignan, 1992; Paulignan et al., 1991b). Like the speed profiles, the dynamics of grip aperture appeared almost the same in two perturbation conditions. We compared the maximum grip apertures (MGA) and times to reach MGA in unperturbed and perturbed conditions and found no significant difference, MGA: $t(11) = 1.08$, $p = .30$, Cohen's $d = .31$; time to reach MGA: $t(11) = .44$, $p = .67$, Cohen's $d = .13$. The shape perturbations did not appear to have any effect on control of grip aperture.

Summary. In Experiment 1, we found that subjects made corrective grip adjustments automatically in response to the brief perturbations despite being asked to inhibit such responses. Around 300 ms after perturbation onset, we detected adjustments of the grip orientation toward the preferred grip axis of the perturbed object, which began to reverse around 300 ms after the target object reappeared (Figure 6). These unnecessary adjustments were mostly corrected by the end of movement, but there was still a detectable influence of the perturbed object on the final grip axes (Figure 3b).

Experiment 2

Method

Subjects. Eighteen right-handed subjects (9 men, 9 woman) with normal or corrected-to-normal vision were recruited from the University of Hong Kong and paid for their participation. None had participated in Experiment 1 or our previous grasping experiments. Data from one subject was excluded from the analysis because she used a conscious strategy of slowing her initial movement to facilitate stopping her hand, contrary to instructions. The remaining subjects had an average age of 25.50 (±6.92 *SD*) years. The procedures were approved by the Human Research Ethics Committee for Non-Clinical Faculties.

Based on the results of our previous study that used a similar method (Chen & Saunders, 2016), we expected that 12 subjects would be sufficient to detect perturbation responses with a power ≥80%. We used a slightly larger sample size of 18 subjects because this was the first experiment conducted for this study (Experiment 1 was sequentially later).

Apparatus and stimulus. The apparatus for presenting stimuli and recording hand movements was the same as in Experiment 1. The rendering and calibration procedure were also identical. Experiment 2 used a subset of the shape set from Experiment 1. Twelve individual object shapes were used, with an average radius of 2.36 cm (±.21 cm) and an average area of 17.82 cm^2 (±3.21) cm^2), and each shape was presented at two different orientations that differed by 45°, as before.

Procedure. Subjects performed virtual grasping movements like in Experiment 1 but with different instructions for perturbed trials. When a perturbation of the target was detected, subjects were to immediately stop their grasping movement and move their hand back to the starting position. On unperturbed trials, task was the same as before.

Two types of perturbations were tested: shape perturbations where the target was replaced by a different random shape, and orientation perturbations where the target was rotated by ±45°. Perturbations were triggered when the tip of the index finger was 20 cm away from the projection surface, as in Experiment 1, but the perturbed targets remained visible rather than reverting to the original targets.

The need to stop the hand on some trials could potentially encourage subjects to make unnaturally slow movements. To prevent this, we added a requirement that the initial movement from 30 cm to 20 cm away from the target was completed within 250 ms. This criterion was chosen based on performance in our previous experiments. During practice trials, subjects received a warning when the initial movement duration was too long. This training was effective: Initial movement duration was in a normal range for all experimental trials from all subjects.

To further encourage natural grasping movements, we limited the proportion of trials with perturbations to be 20% of the total trials. Subjects performed 480 trials in a 1-hr session with breaks, which included 384 unperturbed trials, 48 orientation perturbation trials and 48 shape perturbations trials. Each shape and orientation was presented as a final target on 16 unperturbed trials, 2 orientation perturbation trials, and 2 shape perturbation trials. On shape perturbation trials, the initial object was randomly chosen from other shapes. Before the experimental session, subjects performed

12 practice trials to familiarize themselves with the task, which included 2 trials with perturbations.

On a small number of trials (77 trials, 4.72%), subjects did not successfully respond to the stop signal. In some cases, they did not withdraw their hand (36 trials, 2.2%), or they took over 1000 ms (after perturbation) to begin withdrawing their hand (41 trials, 2.5%). These trials were excluded from analysis.

Results and Discussion

Optimality of grasp point selection. We analyzed the optimality of final grasp points on unperturbed trials and found that grasp points were well adapted to the target shapes, consistent with the results of Experiment 1 and Chen and Saunders (2015). The mean deviation of the grip axis from the COM was 2.10 mm (±.50 mm *SD*), and the mean angular deviation from force closure was 14.11° (±3.17°). The angular deviations were significantly smaller than if a random object was paired with the grip for each trial, $t(16) = 5.51$, $p < .001$, Cohen's $d = 1.34$, confirming that the grasp points were dependent on the specific shapes of the targets. Final grasp points could not be analyzed for perturbed trials because subjects were able to successfully stop their movement before making contact with the surface on most trials (97.8%). The optimality of grasp points on unperturbed trials suggests that the additional stop-signal task did not substantially interfere with performing the basic grasping task.

Dynamics of hand movement: intentionally stopping movement. We analyzed the speed of the hand over time to detect the intentional response to the perturbations, which were the signal to stop movements. Figure 8a plots the mean hand speed as a function of time for the unperturbed trials (red line) and perturbed trials (blue dashed). For this analysis, time was encoded relative to the moment when a perturbation would be triggered (20 cm from the target). There was no indication that subjects slowed their movement or hesitated when performing the reaching movement, and the maximum hand speed was not significantly different from the previous experiment, $t(27) = 1.12$, $p = .274$, Cohen's $d = .421$. On unperturbed trials, hand speed smoothly decreases to zero at the end of the trials, as is typical of grasping movements. On perturbed trials, hand speed is initially similar but becomes negative as subjects stop their movement and begin to withdraw their hand.

To estimate the latency of the intentional response, we first temporally de-correlated the data series using an autoregressive model (see Saunders & Knill, 2003). When subjects smoothly continue their movements, as expected on unperturbed trials, the state of the hand at a given moment would be highly predictable from the hand state at preceding moments. We modeled the temporal correlation on unperturbed trials as a linear function:

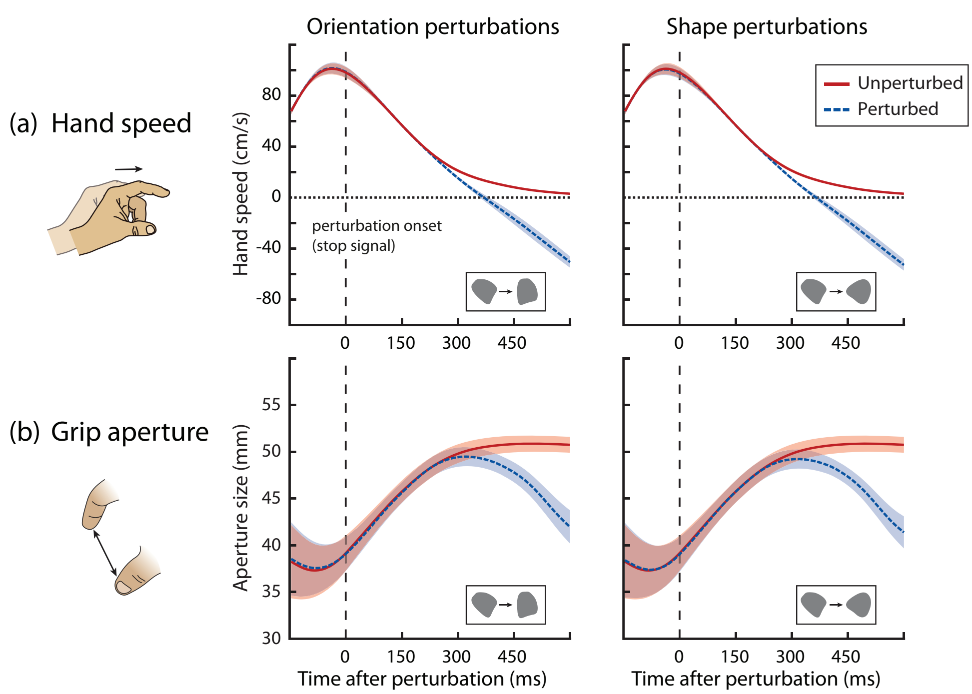

Figure 8. Mean head speed (a) and grip aperture (b) as a function of time after the perturbation onset trigger in Experiment 2. The graphs plot results from unperturbed trials (red line) and perturbed trials (dashed blue) with either orientation perturbations (left) or shape perturbations (right). Shaded regions depict ±1 std. error. Vertical dashed lines show the perturbation onset time, which was the stop signal on perturbed trials. The speed profiles diverge as subjects respond to the stop signal and withdraw their hand rather than continuing to the target. There is also a reduction in grip aperture as subjects withdraw their hand. See the online article for the color version of this figure.

$$S(t) = w_1(t) \cdot S(t-1) + w_2(t) \cdot S(t-2) + \ldots + W_n(t) \cdot S(t-n), \quad (3)$$

where $S(t)$ is the hand state at given time t after perturbation, 00 $S(t-1)$, $S(t-2)$ . . . $S(t-n)$ are the states on the preceding n moments in time, and $w_1(t)$, $w_2(t)$ . . . $w_n(t)$ are weights computed from a linear regression fit across the set of unperturbed trials. The weights were allowed to vary as a function of time, and were fit separately for each individual subject. We found that $n = 12$ was sufficient to account for most of the variability across unperturbed trials, and adding more preceding frames produced little improvement in fitting.

Online adjustments in response to perturbations would introduce changes that cannot be predicted from preceding states using the autoregressive model derived from unperturbed trials. Systematic deviations would provide evidence for a perturbation response. After fitting the autoregressive model to unperturbed trials for each subject and time, we applied the model to perturbed trials and computed the residual errors. For all subjects, residual errors were initially near zero and later became negative as they began to withdraw their hand, as expected. We derived thresholds for statistical significance ($p < .05$) for each subject and time by resampling unperturbed trials. A bootstrapping procedure was used to find the 95% CI for residuals at each time frame for unperturbed trials, using 10,000 unperturbed trials sampled with replacement. We then detected the earliest moment when the observed residual error started to be below the lower edge of the 95% CI for 12 successive time frames (50 ms). We found that the mean latency across subjects was 170.8 ms ($\pm$13.0 ms *SD*). This implies that subjects began to inhibit their hand movement within about 170 ms of the perturbation onset.

While hand speed is a direct measure of subjects' intentional response to the stop signal, we also observed an effect on grip aperture. As seen in Figure 8b, deceleration of the hand on perturbed trials was accompanied by a decrease in the mean grip aperture. On unperturbed trials, in contrast, grip aperture remained scaled for the target object until the end of movement. All subjects showed the pattern of reduced grip aperture as the hand was decelerated in response to perturbations, with the exception of one subject who increased rather than decreased grip aperture. This is likely a relaxation of the grip toward a default or preparatory state when subjects were no longer reaching toward a target. We estimated the latency of perturbation effects on grip aperture with the same method used to analyze hand speed, and found that changes in grip aperture emerged within an average of 270.6 ms ($\pm$54.8 ms *SD*) after the perturbation onset. The effect on grip aperture appeared to occur later than the effect on hand movement speed. This is not surprising given that deceleration of the hand was directly related required for the task, while reduction in grip aperture was likely an indirect consequence of stopping the movement. Even in normal grasping these components are not tightly coupled, and in this situation there is less need for grip aperture and transport to be coordinated. The apparent difference in latencies of the detected responses could also be because of lower signal-to-noise ratio for the grip aperture response. The task did not require changes in grip in response to the perturbation, so changes might be smaller and more gradual than the task-relevant deceleration of the hand. The grip aperture dynamics on perturbed trials indicates that the volitional deceleration of the hand was accompanied by a relaxation of grip size, with a latency that was either longer or overestimated by our methods.

Taken together, the perturbation effects on hand movement speed and aperture size clearly indicate that subjects were able to initiate the required intentional response with a reasonable latency after the onset of the stop signal.

Dynamics of hand movement: Automatic grip adjustments. The task in Experiment 2 did not require any adjustments of the grip toward the perturbed objects, but perturbations might nevertheless cause automatic online adjustments, as observed in Experiment 1. We measured the influence of target object and perturbed object on grip orientation over the course of movement using the same method as before (Equation 2). Because there were fewer perturbed trials in Experiment 2, we combined trials with orientation perturbations and shape perturbations to increase statistical power.

Figure 9 shows the mean regression coefficients for target and perturbed object as a function of time after perturbation. For perturbed conditions, the mean coefficient $\beta_1(t)$ representing the influence of the target object reached a peak at 312.5 ms after onset of the perturbation, and then began to reduce. This would be expected from either volitional or automatic online control; neither would predict a lasting influence of an object that was no longer either task-relevant or visible. However, we also found that the coefficient $\beta_2(t)$, which represents the influence of the perturbed object, began to increase around the same time that $\beta_1(t)$ began to decrease. The maximum of the average $\beta_2(t)$ occurred at 488 ms after perturbation. At this time, $\beta_2(t)$ was significantly larger than zero, $t(16) = 3.65$, $p = .002$, Cohen's $d = .89$, 95% CI = [.06 .23]. This clearly shows that subjects made online grip adjustments that were toward their preferred grip axis for the perturbed object. The influence of the perturbed object appears to increase around the same time when $\beta_1(t)$ began to decrease, but was not statistically detectable until 400 ms after perturbation, $t(16) = 2.14$, $p = .048$, Cohen's $d = .52$. Even at the earliest apparent influence, the latency of the grip adjustment is larger than the latency of hand deceleration in response to perturbations ($\sim$170 ms), indicating that grip adjustments occurred after subjects had already begun to stop their movements. Even while subjects were intentionally stopping their hand movement, they continued to adjust their grip toward the new potential grasping target, which was no longer relevant to the task. This strongly suggests that grip adjustments are because of automatic visuomotor control processes.

Compared with Experiment 1, grip adjustments toward the target object ($\beta_1(t)$) on unperturbed trials appeared to begin earlier in the course of movement, similar to performance in our previous study (Chen & Saunders, 2015). This suggests that the speed requirement and smaller number of perturbed trials in Experiment 2 successfully discouraged subjects from delaying grip adjustments in an unnatural manner.

Summary. In this experiment, both volitional and stimulus-driven adjustments to hand movements were observed over the course of a perturbed trial. Subjects responded to the stop signals as instructed, and were able to initiate backward movements of their hand within 170 ms of the perturbation onset. In addition to this volitional response, subjects also made online adjustments of the grip axis to fit the perturbed shape, which were unnecessary for the task. The co-occurrence of volitional and automatic responses observed here suggests that separate neural mechanisms

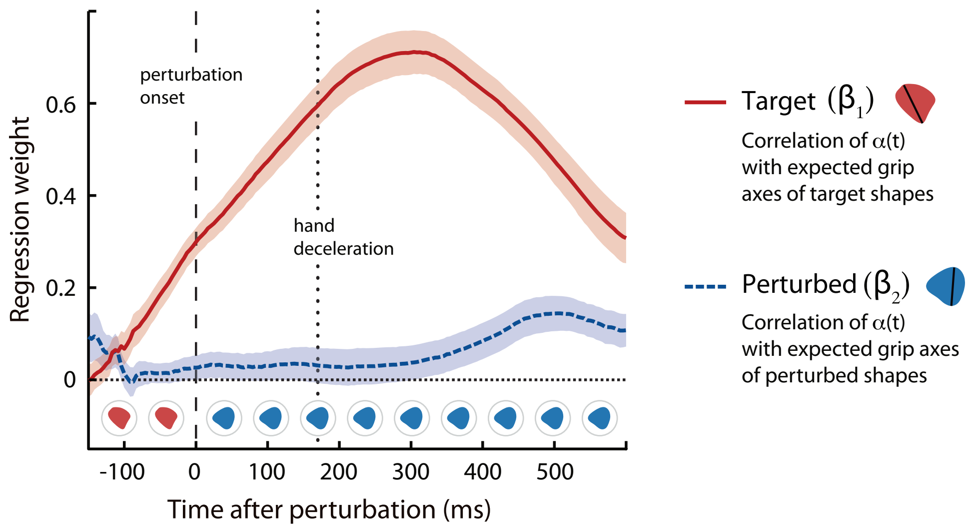

Figure 9. Effect of perturbations on grip orientation over the course of movement in Experiment 2. The graph plots the influence of the target objects (β1, solid red) and the perturbed objects (β2, dashed blue) as a function of time after the perturbation onset trigger. Shaded regions around the lines depict ±1 standard error. The vertical dashed line indicates the time of perturbation onset, and the vertical dotted line indicates the average time that subjects began to decelerate their hand in response to the stop signal. See the online article for the color version of this figure.

are involved with these two components of visuomotor control, as discussed in a later section.

General Discussion

Automatic Online Visuomotor Control

The two experiments investigated whether the process of guiding the hand to shape-dependent grasp points is automatic or can controlled by volition. The role of volition was tested using two task variations: subjects were instructed to inhibit any response to shape perturbation (Experiment 1) or stop their hand movement as soon as noticing the perturbation (Experiment 2), so any "corrective" adjustments in response to the perturbed shape was unnecessary. Despite these task demands, perturbation responses were clearly observed in both experiments, indicating automatic online control of the hand.

Previous studies have shown that online visuomotor corrections can occur when people are unaware of the perturbations that elicited the corrections (Bridgeman, Lewis, Heit, & Nagle, 1979; Pélisson et al., 1986; Prablanc & Martin, 1992), and can be driven by subliminal stimuli that are not consciously perceived (Chen & Saunders, 2016; Cressman, Franks, Enns, & Chua 2007; Cressman, Lam, Franks, Enns, & Chua, 2013). These findings suggest a substantial degree of independence between online control and conscious awareness.

The findings in the current study further show that automatic online corrections are resistant to volitional suppression. Responses to subliminal stimuli observed in previous studies demonstrate that visuomotor corrections can occur automatically without conscious awareness. However, these results do not rule out the possibility that the automatic responses could be intentionally modulated if subjects were aware of the changes. In our experiments, subjects were explicitly required to inhibit responses or stop movement in response to perturbations, yet they still made corrective adjustments of the grip toward appropriate contact points for the perturbed stimuli. In the case of Experiment 1, the automatic grip adjustments were potentially counterproductive for the task, and required online adjustments back toward the target object. Subjects appear unable to suppress grip adjustments in response to changes in the grasping target. This was not simply because of slow initiation of intentional control. In Experiment 2, subjects were able to stop their ongoing movement in response to perturbations, but grip adjustments continued after subjects had begun their volitional response. The results from the two experiments suggest that guiding the fingers to appropriate grasp points during reaching is an automatic process that is beyond volitional control.

Are these automatic adjustments because of a continuous control process or a discrete reprogramming of the movement? In some previous studies, kinematic changes accompanying perturbation responses have been interpreted as evidence for a reprogramming process. Paulignan et al. (1991b) and Castiello et al. (1992) found that perturbations of target size increased movement duration, and Bock and Jüngling (1999) found that the size perturbations increased peak velocity as well as movement duration. We observed no such effects. The only difference in transport may have been a slight increase in movement duration (24 ms). Otherwise, the kinematics of transport and grip aperture were almost identical in perturbed and unperturbed trials. It is possible that kinematic differences would have emerged if our perturbations had required larger changes in grip, as was observed in Paulignan et al. (1991b). However, our results provide no evidence that the responses were because of a reprogramming process rather than continuous control. Either could potentially account for the automatic adjustments observed here.

The current results extend our previous finding of online shape processing for grasp point selection. Chen and Saunders (2015) tested perturbations of the target shape during reaching, similar to the shape perturbations tested here, and found that subjects adjusted their grip toward grasp points that were appropriate for the perturbed shape. Such adjustments necessarily required online processing of the new target shape. However, the task in our previous study was to grasp the perturbed objects, so we could not draw conclusions about whether the responses were automatic or required volition. The results reported here demonstrate that shape-specific grip adjustments occur even when subjects are trying to suppress responses, and the responses had similar latency as the intentional responses in our previous study. These results strongly suggest that shape processing for grasp point selection occurs automatically during online control of grasping, and that grasp point selection does not necessarily require volitional planning.

Independent Components of Visuomotor Control

Experiment 2 used a stop-signal paradigm, which has been used in other studies of volitional control. Previous studies have found that normal people are able to selectively inhibit actions or stop actions within 100–200 ms after the onset of stop signal (Falkenstein et al., 1995, 1999; Rubia et al., 2001). Consistent with these previous results, we detected effects of volitional stopping with a comparable latency (170 ms).

Our experiment tested whether the volitional inhibition would also prevent online adjustments of the grip after the inhibition has been initialized. We found that grip adjustments in response to perturbations were not fully suppressed. During the time that subjects were volitionally stopping their hand movements, they simultaneously made automatic grip adjustments toward the expected grasp axis for the perturbed shape. This finding suggests that two independent control processes may coexist: automatic online control processes for guiding the hand during movement, and a more general volitional control process that can allow initialization or inhibition of overall movements.

This interpretation in terms of separate automatic and volitional control processes would be consistent with existing neurophysiological evidence. Studies of neuroanatomy have identified at least two neural circuits that contribute to visuomotor control. One frontal-basal-ganglia circuit is generally thought to be involved with volitional control (Brass & Haggard, 2007; Jahanshahi et al., 1995; Jenkins, Brooks, Nixon, Frackowiak, & Passingham, 1994; Lang et al., 1991; Soon, Brass, Heinze, & Haynes, 2008; Yazawa et al., 2000). Another separate circuit is through parietal areas, and evidence suggests that this circuit is more involved with fast stimulus-driven adjustments (Prabhu, Lemon, & Haggard, 2007). For example, if parietal areas in this circuit are lesions, people are no longer able to make fast online adjustments, and instead relay on slower cognitive strategies (Rossetti et al., 2005).

Some neurophysiological studies have found evidence for independent mechanisms for volitional and automatic control. Many studies have observed that volitional inhibition of visuomotor control is strongly correlated with activity of the right inferior frontal gyrus (rIFG) in go/no-go and stop-signal tasks (e.g., Aron & Poldrack, 2006; Garavan, Ross, & Stein, 1999; Konishi, Nakajima, Uchida, Kikyo, Kameyama, & Miyashita, 1999; Menon, Adleman, White, Glover, & Reiss, 2001; Rubia, Smith, Brammer, & Taylor, 2003). In addition, inhibitory responses can be impaired by either TMS applied to rIFG (Chambers et al., 2006) or lesions of rIFG (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Hodgson et al., 2007). While volitional inhibition is associated with rIFG, automatic inhibition has been found to be correlated with activity in parietal areas by the cases of optic ataxic patients (e.g., Gréa et al., 2002; Pisella et al., 2000) and neuroimaging studies (Manuel, Bernasconi, Murray, & Spierer, 2012; Manuel, Bernasconi, & Spierer, 2013). Optic ataxic patients, who generally suffer from lesions of parietal areas but have intact rIFG, remain capable of volitional action control but have problems in online control. Manuel et al. argue that the connectivity from parietal areas to basal ganglia is because of an automatic visuomotor control whereas the connectivity between rIFG and basal ganglia is because of detection and volitional correction of visuomotor errors. Thus, various lines of evidence suggest that there are multiple independent mechanisms for automatic and volitional control, which could potentially explain our finding of overlapping volitional and automatic responses.

Automatic and volitional components would not be expected to be entirely independent, and there is also evidence for interactions between volitional and automatic control. For example, performance in go/no-go and stop-signal tasks can be facilitated through repeated stimulus presentation and automatic associate learning (Chiu & Aron, 2014; Verbruggen & Logan, 2008a). This kind of automatic associative learning has been found to be correlated with activity in the rIFG (Lenartowicz et al., 2011), which is also involved with volitional control. These findings suggest a more complicated relationship between the mechanisms of volitional and automatic control, which is worth further study.

Grasping a Virtual Target

One limitation of our method was that subjects were asked to reach to touch a virtual object at grasp points rather than pick up a physical object. One important difference is that virtual grasping does not provide haptic feedback about the grasp points relative to the target shape. When grasping real objects, suboptimal contact points for the particular shape could produce an unstable grip. This potential feedback is absent in our virtual grasping task. Another difference is that real grasping requires the grip to contract at the end of movement, while in our task subjects could simply move until they made contact with the flat projection surface. Thus, it is reasonable to expect some differences in performance of real and virtual grasping. In the current study, we found a relatively small ratio between maximum grip aperture (MGA) and final grip aperture (FGA) of 1.1–1.2, compared with the MGA/FGA ratio of 1.4–1.7 in real grasping tasks (e.g., Eloka & Franz, 2011; Voudouris et al., 2013; Westwood, Danckert, Servos, & Goodale, 2002). Previous studies have also reported smaller MGA/FGA ratios for virtual grasping tasks (Chen & Saunders, 2015, 2016; Westwood et al., 2002), and this finding can be explained by an affordance model (Bingham, Snapp-Childs, Fath, Pan, & Coats, 2014; Mon-Williams, Bingham, 2011), which argues that MGA is an implication of “a safety margin for collision avoidance” and would decrease without the risk of collision.

However, such differences do not necessarily imply that people are less sensitive to shape information or less careful in grasp point selection when performing a virtual grasping task. The optimality of grasp points observed for virtual grasping in the present study and Chen and Saunders (2015) is similar to the optimality observed in studies of real grasping (Goodale, Meenan, et al., 1994; Lederman & Wing, 2003). In a control experiment, reported in the online Appendix, we compared virtual grasping and real grasping of physical objects with the same 2D shapes. While there were some differences in performance, the grasp points for virtual and real grasping were correlated and showed similar optimality. This consistency suggests that similar mechanisms are used for grasp point selection for both tasks. While our virtual grasping task may be a limited approximation of real grasping in some ways, there is reason to think that our findings from virtual grasping would generalize to control of grip axis in more natural conditions.

Conclusion

In the current study, we investigated automatic and volitional components of visuomotor control and their potential interactions during grasping. Specifically, we tested whether stimulus-driven online grip adjustments can be volitionally suppressed. In both experiments, we observed unintentional grip adjustments during movements in response to task-irrelevant perturbations, with similar latency as in previously tested conditions where grip adjustments were required for the task (Chen & Saunders, 2015). The online adjustments depended on the particular shape of the perturbed stimulus, implicating automatic shape processing during online control. For our stop-signal task, we found that volitional and automatic adjustments overlapped in time. This suggests that these responses may be because of independent control mechanisms, which would be consistent with some recent neural evidence. Guiding the hand to appropriate grasp points appears to be an automatic online control process with limited volitional supervision.

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Appendix

Real Versus Virtual Grasping

This experiment compared grasping real objects and virtual grasping of projected objects to investigate whether contact points were selected in the same manner. For real grasping, the choice of contact points would determine the stability of the grip, and haptic feedback is available. For virtual grasping, there are no physical constraints on contact points, and no haptic feedback about whether contact points are optimal for the target shape. These differences could potentially affect selection of contact points for grasping.

Method

Subjects

Eight right-handed subjects (6 female and 2 male) with normal or corrected-to-normal vision were recruited from the University of Hong Kong for each experiment and were paid for their participation. Their average age was 22.63 years (±4.47 *SD*). The procedures were approved by and conform to the standards of the Human Research Ethics Committee for Non-Clinical Faculties.

Stimulus and Apparatus

In this experiment, a subset of irregular shapes was selected from those used in Experiments 1 and 2. For the real grasping task, physical objects were constructed by laser-cutting plexiglass. A LEGO piece was glued to the back of each object and used to attach the objects to a background acrylic surface (Figure A1). For the virtual grasping task, the stimuli were images of 2D shapes back-projected on the same acrylic surface, using a BenQ 710ST DLP projector with a resolution of 1,920 [times] 1,080 pixels and a refresh rate of 60 Hz as in Experiments 1 and 2. Each object was presented with the same orientation and size in the two tasks. The real objects had an average weight of 7.90 g (±1.20 *SD*). The average radius of the objects was 2.63 (±.21) cm, and the average area was 22.30 cm2 (±3.30 *SD*). In both tasks, the objects were gray on a dark background.

The movement of the index finger and thumb of a subject's right hand was recorded at a rate of 240 Hz with 3D Guidance trakSTAR system. A sensor was attached to the back of the fingernails using latex finger cots, which wrapped over the tip of the finger.

Procedure

Each subject performed two tasks in separate blocks: grasping real objects and virtual grasping with the same set of target shapes. The real grasping task was performed before virtual grasping for all subjects. Each unique target object was repeated 10 times in each block, yielding 100 trials for each task. Practice trials were

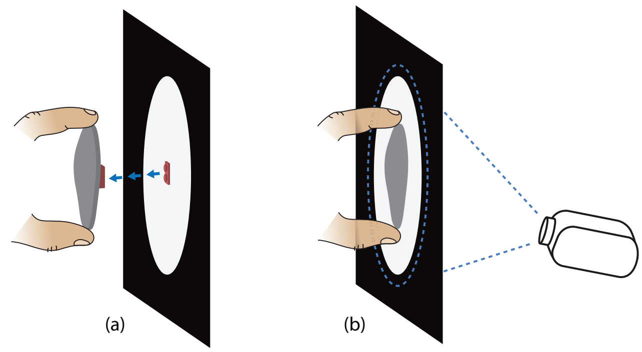

Figure A1. Illustration of real and virtual grasping tasks used in the supplementary control experiment. (a) For real grasping, thin planar objects with smooth random shapes were attached to a plastic background with LEGO pieces. Subjects reached to grasp the object and lift it off the background. (b) For virtual grasping, 2D shapes were back-projected onto a plastic screen and subjects touched the screen at the locations where they would grasp the object. See the online article for the color version of this figure.

performed before each block to familiarize the subjects with the tasks.

On a real grasping trial, a subject first placed their index finger at a starting position, closed their eyes, and waited while the experimenter positioned the target object on the background surface. An auditory signal cued the subject to open their eyes and reach to grasp the object. Subjects were instructed to grasp the object on its edge with their index finger and thumb (precision grip), and then lift the object off the background surface. No instructions about contact points were given, and subjects were encouraged to grasp the objects in a natural manner. Subjects were asked to initiate movement immediately after the auditory cue, but there was no speed requirement. They were encouraged to make their movements at a natural speed. After lifting the object, the subject moved it to an end location and then returned their hand to the starting location, which initialized the next trial.

The procedure of virtual grasping task was similar. The target objects were projected images with the same shapes and orientations as objects in real grasping trials. Subjects were instructed to reach and touch a virtual object in the way that they would if he or she were grasping the object. Trials began with a subject's index finger at a starting location, and the appearance of the virtual target cued the start of movement. The starting position was the same as for real grasping trials, and the projection surface was at the same depth as the real objects. Subject reached to touch the virtual object, making contact with the projection surface, and then held

(*Appendix continues*)

the hand at the end position until the stimulus disappeared. As in the real grasping trials, there was no speed requirement, but subjects were asked to begin their movement immediately on seeing the stimuli and move at a natural speed.

For the real grasping task, there were a few occasions where the subject dropped the target object when lifting it off the background surface (seven trials from four subjects). These trials were excluded from analysis.

Results and Discussion

Grip Axes

Figure A2 shows the relationship between the average angle of the final grip axis in the real and virtual grasping conditions. The colors and shapes indicate results from different subjects, and points with the same color and shape correspond to the different objects. Overall, there was a strong correlation between the mean grip angles in two tasks, $r(78) = .742$, $p < .001$, indicating that subjects used similar contact points used for real and virtual grasping. However, this correlation is partially because of individual differences in subjects' preferred grip angle rather than the shape of objects. When we subtracted the average grip angle from each subject, the correlation was reduced but still significant, $r(78) = .223$, $p = .046$. This demonstrates that real and virtual grasping had correlated variations in grip angle across objects, though not necessarily for all subjects. Considered individually, some subjects showed a clear relation between mean grip angles in the two tasks, whereas others did not.

One issue with using mean grip angles for analysis is that subjects often showed bimodal responses, with multiple separate clusters of grip axes for a given object. To further investigate the relationship between grip angles in real and virtual grasping, we computed the joint likelihood distributions for each individual subject, shown in Figure A3. The likelihood functions $p(\alpha_{virt}, \alpha_{real})$ correspond with the relative frequency of observing grip angles of α_{virt} and α_{real} and on a randomly selected pair of virtual and real grasping trials with the same object shape, estimated by sampling from an individual subject's data. Density near the diagonal would indicate that a subject tended to use the same grip angles on virtual and real grasping trials. For some subjects, the density was concentrated on the diagonals. These were the subjects that showed a correlation between mean grip angles. In other cases, subjects showed a wider range of grip angles for real grasping than virtual grasping, and density was distributed away from the diagonals. However, one can still see some relation between the grip angles in these cases. The joint distributions have discrete clusters rather than being randomly spread, with some clusters near the diagonal. The off-diagonal clusters could be because of bimodal responses for specific objects.

We used the normalized mutual information of these joint distributions to test whether responses across trials with the same object were independent for the two tasks. Mutual information provides a measure of how a joint distribution differs from the product of marginalized distributions, and would be zero if two variables vary independently. Unlike correlation, this could detect similarities in multimodal distributions. We computed the normalized mutual information from distributions shown in Figure A3 and compared with the expected results under a null hypothesis that the effect of object shape on grip angles was independent for real and virtual grasping. The null distribution was estimated using a resampling procedure. Real and virtual grasping trials were randomly paired without regard to the object shape, and the mutual information from these samples was computed in the same way as the analysis of the actual pairings. This was repeated 10,000 times to determine a 99.9% threshold under the null hypothesis. For all subjects, the mutual information of the actual joint likelihood distributions was much higher than this threshold, indicating the grip angles from real and virtual grasping were related in a way that depended on object shapes. Even for subjects that showed different distributions of grip angles for the two tasks, there remained a detectable relationship between real and virtual grasping toward the same target shape.

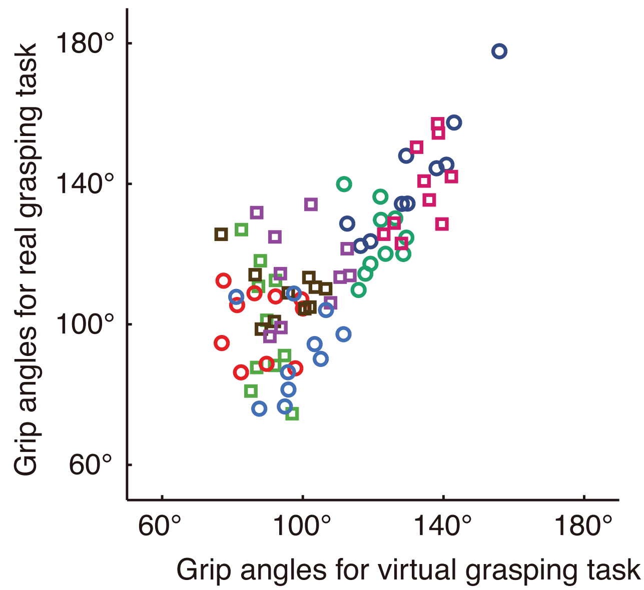

Figure A2. Relation between the final grip angles of real and virtual grasping tasks. Each point plots the mean grip angle for one object and one individual subject in two grasping tasks. Points with the same color and shape are data from the same individual subject but different objects. See the online article for the color version of this figure.

Optimality

We also compared optimality of grip axes from real and virtual grasping. As a measure of the optimality of torque control, we used the deviation from the grip axis to the center of mass (COM) of an object. As a measure of the optimality of force closure, we computed the angular deviation between grip axis and the normal

(*Appendix continues*)

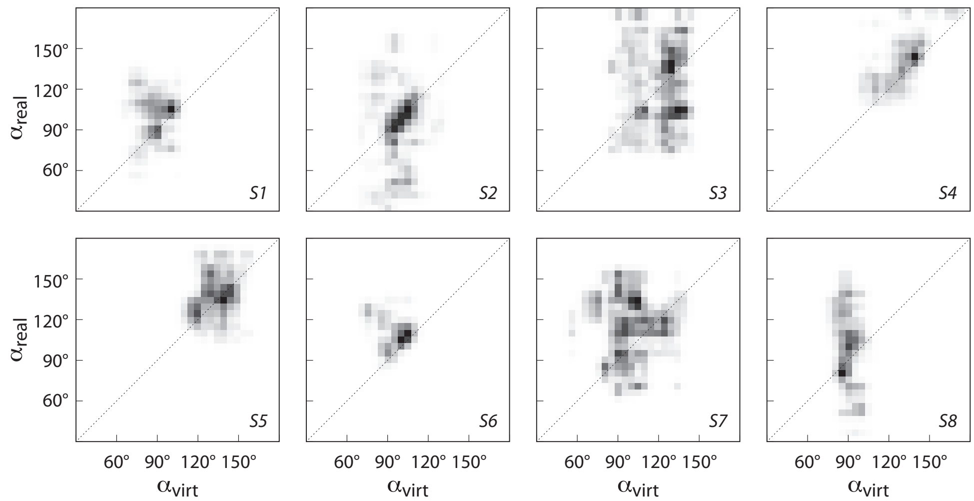

Figure A3. Joint likelihood distributions of observed grip axis angles from virtual and real grasping of targets with the same shape, analyzed separately for the eight individual subjects. The density indicates the relative frequency of observing grip angles of virtual and real on a randomly selected pair of virtual and real grasping trials with the same object shape.

direction of the contour at contact points. The angular deviation was computed at both the index finger and the thumb, and the maximum of these deviation angles was used for analysis.

Figure A4a shows the histograms of the COM measure for the two tasks. One can see that the overall distributions of COM deviation from the two tasks were similar. We computed a measure of COM deviation for each subject and task by taking the median across the set of trials. The mean COM deviation across subjects was 4.44 mm ($\pm$1.13 *SD*) for the task of grasping real target and 3.81 mm ($\pm$1.08 *SD*) for the virtual grasping one, which were not significantly different, $t(7) = 1.31$, $p = .230$.

Figure A4b shows histograms of force closure deviation for the two tasks. The mean angular deviations were 21.21° ($\pm$7.99° *SD*) for the real grasping task and 20.68° ($\pm$4.21° *SD*) for virtual

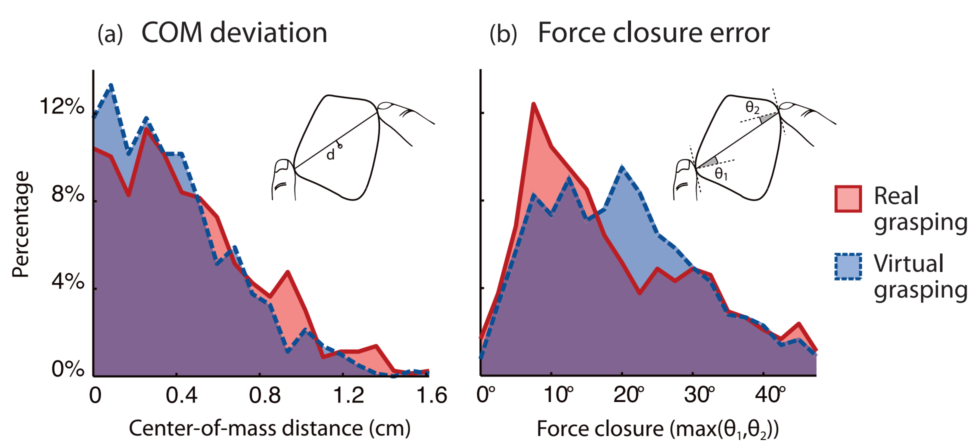

Figure A4. Histograms of center of mass (COM) and force closure measures of optimality in grasp point selection. (a) The COM deviation is the distance from the grasp axis to the center of mass of the object. (b) The force closure error is the maximum angular deviation between the grasp axis and the surface normal directions. Solid red and blue dashed curves show results for real grasping and virtual grasping respectively. See the online article for the color version of this figure.

(*Appendix continues*)

grasping, which were not significantly different, $t(7) = .22$, $p = .823$. However, the distribution for real grasping appears to be concentrated at lower angles, suggesting that there was some improvement in optimality that is not captured by the mean deviations. We speculate that this may be related to the wider range of grip angles observed in real grasping for some subjects. In virtual grasping, when there is no consequence to grasping at sub-optimal locations, they have been more likely to choose grip axes with comfortable hand orientation at the cost of slightly lower optimality. The overall similarity of the force closure distributions suggests that any reduction in optimality for virtual grasping was either small or occurred on a limited portion of trials.

Grip Aperture

The means of final grip aperture size (FGA) were similar for real and virtual grasping (real grasping: 59.07 ± 3.98 mm; virtual grasping: 57.27 ± 4.04 mm), and there was no significant difference, $t(7) = 1.29$, $p = .239$.

While the final grip apertures were equivalent for real and virtual grasping, the dynamics of grip aperture differed. The maximum grip aperture sizes (MGA) were significantly larger for real grasping (71.55 ± 7.76 mm) than for virtual grasping (61.57 ± 5.16 mm); $t(7) = 5.95$, $p < .001$. There was also a significant difference between the MGA/FGA ratios for the two tasks (real grasping: 1.27 ± .09; virtual grasping: 1.08 ± .04); $t(7) = 9.07$, $p < .001$. The larger MGA in real grasping is likely because force has to be directed inward when contacting the physical objects, which is not needed when touching the screen in virtual grasping.

Dynamics of Hand Movement

The duration of hand movements was compared across tasks. On each trial, duration was measured from when subject initialized their movement (reached 5% of the peak velocity) to when the hand touched the target or the projection surface. The mean movement duration was 948.7 ms (±121.5 *SD*) for real grasping and 946.0 ms (±189.2 *SD*) for virtual grasping, respectively, which were not significantly different, $t(7) = .053$, $p = .959$.

The speed of hand movement as a function of normalized time was also compared. Figure A5 shows hand movement speed in the direction of sagittal plane as a function of normalized time, averaged across subjects. There was no significant difference between the peak velocity in the two tasks, $t(7) = 1.75$, $p = .124$, but peak velocity occurred earlier for virtual grasping than real grasping, $t(7) = 2.65$, $p = .033$. Thus, in addition to the different dynamics of grip control, there were also some differences in the dynamics of hand transport between two tasks.

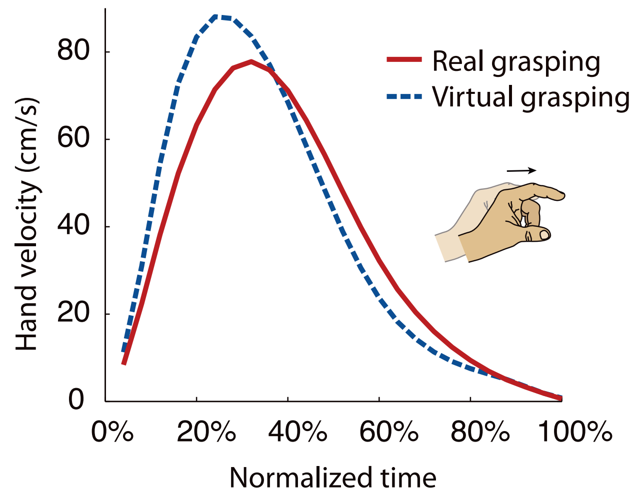

Figure A5. Mean hand movement speed as a function of normalized time for real grasping (red line) and virtual grasping (blue dashed). See the online article for the color version of this figure.

Summary and Conclusions

The results of this experiment indicate that the physical constraints and haptic feedback, which are missing from virtual grasping, have limited effects on grasp point selection for this class of objects. The dynamics of grip control and hand transport were different for real and virtual grasping, and we also observed some differences in the distribution of grip axes for the two tasks. However, the grip axes were correlated across real and virtual grasping, and the optimality of grip axes compared with the shapes was similar. This suggests that virtual grasping involves the same grasp point selection mechanisms that are used for real grasping.

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