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Automatic adjustments toward unseen visual targets during grasping movements

Zhongting Chen¹ · Jeffrey A. Saunders¹ 

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Abstract We investigated whether control of hand movements can be driven by visual information that is not consciously perceived. Subjects performed reach-to-grasp movements toward 2D virtual objects that were projected onto a rigid surface. On perturbed trials, the target object was briefly presented at a different orientation ($\pm 20^\circ$ rotation) or different size ($\pm 20\%$ scaling) during movement. The perturbed objects were presented for 33 ms, followed by a 200-ms mask and reappearance of the original target object. Subjects perceived only the mask and were not aware of the preceding perturbed stimuli. Unperturbed trials were identical except that there was no change in the target object before the mask. Despite being unaware of the brief perturbed stimuli, subjects showed corrective adjustments to their movements: rotation of the grip axis in response to orientation perturbations, and scaling of grip aperture in response to size perturbations. Responses were detectable 250–300 ms after the perturbation onset and began to reduce 250–300 ms after the reappearance of the original target. Our results demonstrate that the visuomotor system can utilize visual information for control of grasping even when this information is not available for conscious perception. We suggest that this dissociation is due to different temporal resolution of visual processing mechanisms underlying conscious perception and control of actions.

Keywords Grasping · Online control · Consciousness · Action · Perception

✉ Jeffrey A. Saunders
jsaun@hku.hk

¹ Department of Psychology, University of Hong Kong, Hong Kong, Hong Kong SAR

Introduction

Although we have some degree of voluntary control of our motor actions, the sensorimotor processing that underlies control of actions may be largely automatic and unconscious. Many previous studies have demonstrated unconscious modulation of actions (see below), which suggests that conscious supervision is not necessary for continuous sensorimotor control. There is also some evidence for dissociation between conscious visual perception and use of visual information for control of actions (for review, see Milner 2012). This study investigates how control of grasping can be modulated by visual feedback about target properties that is not consciously perceived.

Modulation of actions without conscious awareness could arise due to separate visual processing streams for perception and action, as proposed by Milner and Goodale (1995, 2008). One line of evidence for visual processing by distinct streams comes from the functional impairments observed from visual agnosia and optic ataxia (Goodale et al. 1991, 1994). An agnosiac patient, DF, with lesions in the ventral stream is unable to make perceptual judgments of orientation and shape, yet is able to make appropriate goal-directed actions that depend on these properties. Patients with optic ataxia, which is associated with damage in dorsal areas, show the opposite pattern of impairment: deficits in reaching and grasping but preserve ability to judge orientation and shape. The double dissociation suggests that visual processing for control of actions involves different mechanisms than used for perceptual tasks like shape recognition. If visuomotor control involves distinct visual processing mechanisms, then actions could be affected by visual information that is not accessible to conscious perception.

A number of studies have demonstrated that subjects can make automatic online corrections to hand movements

in response to changes in the target even when unaware of the changes. For example, some studies have used saccadic suppression to mask perturbations in the location of the target of a reaching movement, and found that subjects made fast and accurate corrective adjustments despite the lack of conscious awareness (Bridgeman et al. 1979; Pélisson et al. 1986; Prablanc and Martin 1992). Other studies have observed corrective responses to perturbations that were not consciously perceived due to presentation of a masking image before the perturbed stimuli (Greenwald and Knill 2009a, b; van Mierlo et al. 2009). These results indicate that we can automatically modulate our actions in response to changes in the environment even when we are not consciously aware of the changes.

In these masked perturbation studies, however, the visual information required to correct movements remains consciously available. For example, if the target of a reaching movement is displaced during saccadic suppression, subjects are not aware of the change in location, but are still able to consciously perceive the new location of the target. Thus, the critical information required for feedback control—the position of the target relative to the hand—remains consciously available. If control of actions is largely based on unconscious visual processing, then this may not be necessary. Visuomotor adjustments could also potentially be driven by subliminal visual information that cannot be consciously perceived.

Some previous studies have demonstrated that unseen visual targets can influence movement planning. Binsted et al. (2007) used object substitution masking, which is a form of backward masking, to present unseen visual targets for pointing movements. They observed a normal Fitt's law relationship between the size of the unseen target and the speed of movement. Even though the masked targets were not consciously perceived, subjects appropriately modulated their movements to account for the size of the target. Heath et al. (2008) found that this effect persisted even with a substantial delay (2000 ms) between target presentation and movement. These results demonstrate that movement planning can be influenced by the characteristics of unseen visual stimuli.

The results of Cressman et al. (2007) further demonstrate that unseen masked stimuli can influence hand movements after the initiation of movement. Cressman et al. (2007) tested conditions in which subjects had to modify pointing movements in response to a cue, and found that task-irrelevant cues with similar shape affected movement trajectories even when these cues were not consciously perceived due to metacontrast masking. The cues were presented near the onset of movements, so responses occurred during the ongoing movement. Responses to the unseen cues were away from the intended movement goal, which suggests that they were due to automatic online control. A

follow-up study found that these responses were also unaffected by subjects' expectations (Cressman et al. 2013).

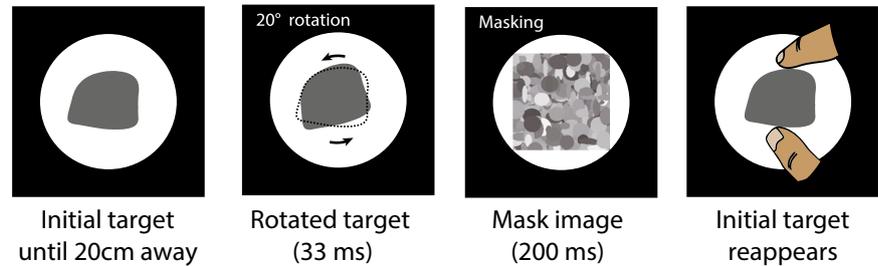
Some other recent studies have used continuous flash suppression to present invisible targets for hand movements. The results using this technique are mixed. Roseboom and Arnold (2011) found evidence for implicit visuomotor learning based on stimuli that were masked by CFS. In this study, subjects reached toward unseen oriented lines presented to the suppressed eye, and received visible feedback about target orientation only after the movement was completed. Over time, the orientation of the hand relative to the masked target became more precise, but there was no increase in ability to consciously detect the orientation of the masked target. However, another study by Ludwig et al. (2013) used a similar method and failed to replicate these findings. Ludwig et al. (2013) found no effects of CFS masked stimuli on either grip aperture or orientation, but did observe a reduction in detection thresholds with increased exposure. From these results, it is unclear whether visual information that is masked by CFS can contribute to control of the hand during grasping movements.

The contrasting findings from studies using backward masking techniques and continuous flash suppression may be due to how these methods affect dorsal and ventral visual processing streams. Continuous flash suppression involves resolution of binocular conflicts. Yuval-Greenberg and Heeger (2013) found that CFS suppressed the activity in the early visual processing area V1, which would limit the information available to both ventral and dorsal processing streams. In contrast, backward masking takes advantage of limited temporal resolution, which may selectively affect ventral visual areas. Kouider et al. (2009) found that brief (30- to 50-ms) masked stimuli produced a significant activation of the dorsal stream, but not the ventral stream. Activation of the ventral stream only emerged with longer exposure, which coincided with the threshold for conscious awareness. Other studies similarly found that backward masking selectively reduces activity in ventral visual areas (Bar et al. 2001; Grill-Spector et al. 2000; Noguchi and Kakigi 2005). These results suggest that backward masking, with sufficiently short delays, would effectively isolate dorsal visual processing, while CFS masking would have more generalized effects.

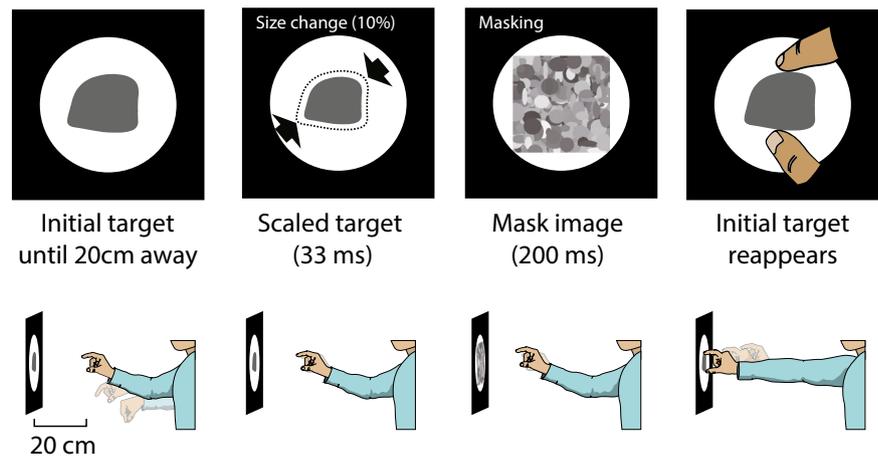
In these previous studies investigating subliminal influences on visuomotor control, the task demands encouraged responses to the subliminal stimuli. In Cressman et al. (2007, 2013), the unseen cue was task irrelevant, but subjects still had to attend to the location of the invisible cue and prepare to adjust their movement in response to a similar visible cue. In the other studies, subjects were required to direct their movement toward unseen target position (Binsted et al. 2007; Heath et al. 2008), or align their hand with the orientation of an unseen target (Roseboom and

Fig. 1 Illustration of the sequence of stimuli presented on perturbed trials. Subjects began movement when a grasping target was presented on the projection surface. The initial target remained visible until the hand reached a distance of 20 cm from the surface, which triggered the perturbation. The target was briefly presented (33 ms) at a different orientation (Experiment 1) or different size (Experiment 2), followed by a 200-ms mask. The mask prevented the subjects from being aware of the changes in the stimuli. After the mask, the original target reappeared and remained visible through the remainder of the trial. Unperturbed trials were identical except that the target was not rotated or scaled before the mask was presented

Experiment 1 - Masked orientation perturbations



Experiment 2 - Masked size perturbations



Arnold 2011; Ludwig et al. 2013). Although subjects could not consciously perceive the masked stimuli, they were explicitly trying to use this information to guide movement. If normal control of movements involves visual processing that is not consciously accessible, then unseen stimuli could affect performance even when not encouraged by task demands.

Present study

In this study, we test for subliminal influences on grasp point selection when reaching to grasp smooth random shapes like shown in Fig. 1. When presented with such objects, subjects automatically modulate their grip according to object size, and select appropriate contact points that allow a stable grasp (Kleinholdermann et al. 2013; Chen and Saunders 2015). Although grasp point selection is a complex function of object shape and orientation, it can be performed with little conscious effort.

Chen and Saunders (2015) investigated online selection of grasp points using a perturbation method, which is similar to the method used here. Subjects reached to grasp virtual objects that sometimes changed their orientation or shape during movement. We found that subjects quickly

adjusted their grip toward appropriate contact points for the perturbed targets, with a minimal effect on movement duration or optimality of grasp points. In the case of shape perturbations, grasp point selection required analysis of target shape during the ongoing movement. Corrective adjustments were detectable within 320 ms, suggesting that the visuomotor system has relatively fast shape-processing mechanisms for online control of grasping.

If this capability were due to specialized visual processing mechanisms for control of actions, then the online adjustments observed in Chen and Saunders (2015) may not require conscious perception of the target shapes. The experiments reported here test whether online adjustments to grasp points can be also driven by targets that are not consciously perceived. We used backward masking to introduce brief subliminal perturbations in the target object during a reach-to-grasp movement, as illustrated in Fig. 2. A 200-ms masking stimulus was presented during virtual grasping movements, in which subjects were instructed to ignore. On some trials, the target object was briefly presented at either a different orientation ($\pm 20^\circ$, Experiment 1) or with a different size ($\pm 20\%$, Experiment 2), immediately before the mask. The delay between the perturbed stimuli and the mask was 33 ms, which is in the range that

Grasping performance on unperturbed trials

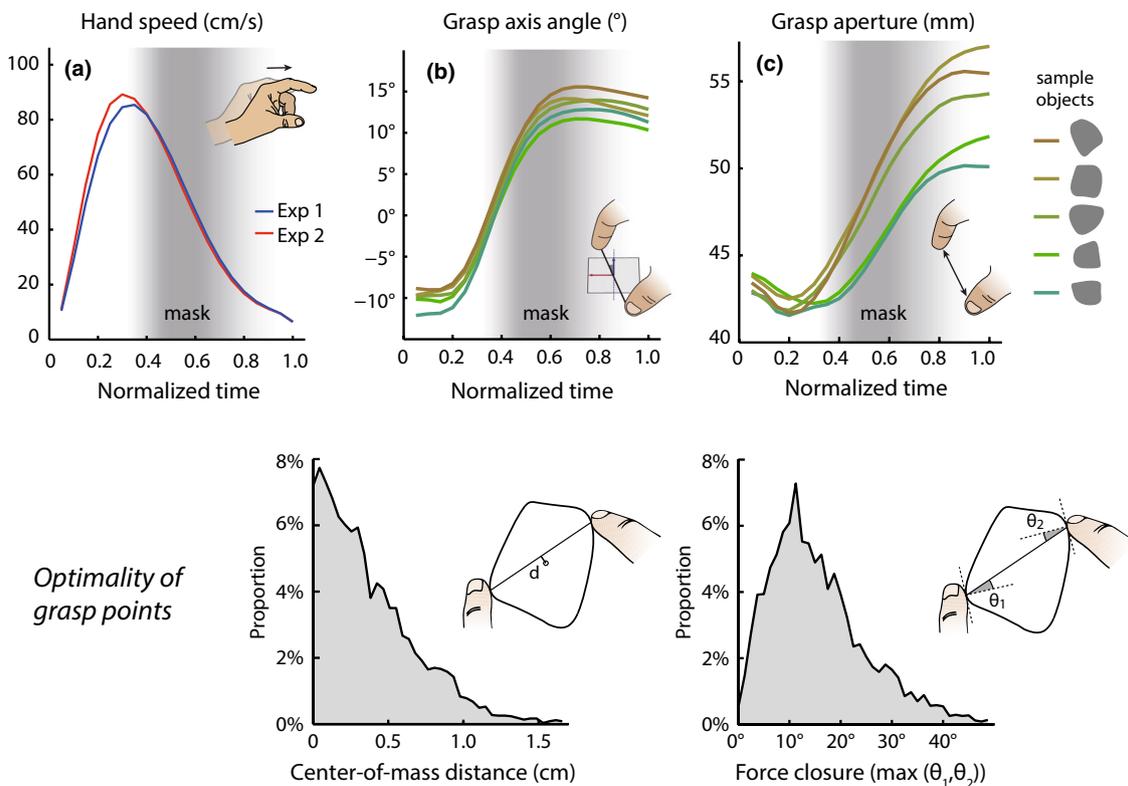


Fig. 2 Grasping kinematics and optimality of final grasp points on unperturbed trials. The *top left graph a* plots the average speed of the hand as a function of normalized time, measured from movement onset to contact with the surface. The *gray regions* depict the average interval when the mask was visible. The *top middle and right*

graphs plot the average grip aperture (**b**) and grip axis orientation (**c**) as a function of normalized time for some sample objects. The *bottom graphs* show the distribution of the distance from the grip axis to center of mass distance (**d**) and the angular error in force closure errors (**e**) across the entire set of unperturbed trials

would be expected to selectively interfere with ventral processing. We found that this delay was sufficiently brief to prevent conscious awareness of the perturbations. On both perturbed and unperturbed trials, subjects perceived only the masking stimulus.

If the visual masking is due to the lower temporal sensitivity of ventral processing, then the brief perturbed stimuli might still be available to dorsal visual processing mechanisms involved with planning and control of grasping movements. One would then expect normal corrective adjustments in response to the subliminal perturbations, similar to responses to visible perturbations of the target. We compared hand movements in conditions with and without the brief perturbations to test for such responses. Specifically, we expected that subjects would rotate their grip axis to follow the orientation change of the objects (Experiment 1) and adjust the size of the grip aperture to match the expanded or shrunk objects (Experiment 2).

In these conditions, there was no incentive for subjects to adjust their planned movement in response to the brief

perturbations. Subjects were not expecting the target to change, even transiently, and were not consciously aware of the brief changes to the target during grasping trials (with a few exceptions—see results). The initial and final target objects were the same, so they could successfully complete the task by moving their fingers to pre-planned grasp points. This contrasts with the task demands in previous studies investigating subliminal influences on visuomotor control, in which subjects were required to direct their movement toward unseen targets, or be prepared to adjust their ongoing movement in response to a cue. In contrast, our task could be performed in a natural manner using only the consciously perceived target, and there was no explicit or implicit incentive to deviate from a pre-planned movement. If perturbations influence hand movements in this situation, it would suggest that responses are due to online control processes used in normal grasping movements, which automatically adjust the grip in response to visual information about the target regardless of conscious awareness.

Methods

Subjects

Twenty-six subjects (10 males and 16 females) participated in Experiment 1, and fifteen subjects (3 males and 12 females) participated in Experiment 2. For Experiment 1, we initially ran 16 subjects. Because a large proportion of subjects were able to discriminate the orientation perturbations in the post-test, we increased the sample size in Experiment 1 to obtain a larger subset of subjects that could not discriminate the perturbations. The qualitative findings were the same for the initial and full samples, and the increased sample size did not change the outcomes of any significance tests. All subjects were right-handed and had with normal or corrected-to-normal vision. Subjects were recruited from the University of Hong Kong and were paid for their participation. The procedures were reviewed and approved by the University's Human Research Ethics Committee for Non-Clinical Faculties.

Apparatus and stimuli

The stimuli were computed-generated images of 2D shapes back-projected on a semi-transparent acrylic surface by BenQ 710ST DLP projector with a resolution of 1920×1080 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 sub-pixel resolution. Subjects were seated at a table and allowed free movement of their head. The projection surface was fronto-parallel relative to the line of sight, at a viewing distance of approximately 50 cm. A black board with circular aperture was placed over the surface to create a 14.6-cm-diameter window, which was centered in front of the subjects. The projection surface was rigid and attached to the table, so that subjects could make firm contact without moving or distorting the surface. The hand started at a marked location on the table and was visible throughout trials.

The index finger and thumb of a subject's right hand during movements were tracked at 240 Hz with a 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 or 80 mm. Each pair of calibration points was presented twice and the procedure was repeated if the RMS error between measurements was greater than 4.5 mm. The separation of sensors was compared to the separation of the calibration targets to compute

an additive correction that was applied when estimating grip aperture during the experimental trials. The small offsets between the sensors and the fingertips would have little effect on the orientation of the grip axis, so the raw sensor positions were used to compute grip axis angles. The calibration data were also used to estimate a mapping from the sensors to the position of the fingertips relative to the object at the moment of contact, in order to calculate the optimality of final grasp points.

The grasping targets were smooth, random 2D shapes rendered in gray on a dark background. Shapes were generated by computing the convex hull of 5–7 random vertices and then by applying Gaussian blur to the radial function ($\sigma = 17^\circ$). The shapes had an average radius of 2.37 (± 0.223) cm and an average area of 18.09 (± 3.39) cm² across objects. Twelve unique base shapes were used for both experiments. These shapes were a subset of the shape set used previously in Chen and Saunders (2015). Each object could appear in one of two orientations within the image plane, which differed by a 20° rotation. The base orientation was arbitrarily chosen, and the same pairs of orientations were used in both experiments.

Procedure

The main task in two experiments was to reach and touch a projected object in the way that they would if they were grasping the object. At the start of each trial, subjects had their right-hand index finger and thumb together on a starting location on a desk, which was approximately 40 cm away from the projection surface. The target shape for grasping was presented, which cued the subject to begin their movement. Subjects reached to touch the object and held their fingers on the surface until the stimulus disappeared, which occurred 210 ms after contact with the surface was detected. The positions of the index finger and thumb were recorded throughout the trial. There was no speed requirement, but subjects were encouraged to move immediately after stimulus presentation and avoid explicitly thinking about their movement. They were instructed to try to do the task as if they were grasping an object in daily life.

On both unperturbed and perturbed trials, a mask stimulus that occluded the object was presented for 200 ms during the hand movement (Fig. 1). On perturbed trials, the target was briefly presented with either a different orientation (Experiment 1) or a different size (Experiment 2) just before the onset of the mask. The perturbations were triggered when the index finger was 20 cm from the target in the depth direction, and the mask appeared 33 ms (two display frames) after the perturbation onset. In Experiment 1, the brief perturbation was a 20° clockwise or 20° counter-clockwise rotation within the image plane. In Experiment

2, the brief perturbation was a 20 % increase or decrease in size. On unperturbed trials, the mask was presented with the same timing, 33 ms after the index finger was 20 cm away, but there was no preceding perturbation of the object. Subjects were not told about the perturbations in advance and were instructed to ignore the mask and reach to the target as they would normally. The object presented after the mask was always the same as the original object, for both perturbed and unperturbed trials, so the task did not require subjects to react to either the mask or the brief changes on perturbed trials.

Due to a technical problem, the perturbed stimuli in the grasping trials of Experiment 2 were sometimes presented for three frames (50 ms) rather than two frames (33 ms). This occurred on 11.56 % of perturbed trials. Although this could have potentially made the perturbations more noticeable, subjects remained unaware of the perturbations. We removed these trials from analysis of grasping performance, so that the results were based solely on trials where the perturbation was presented for 33 ms.

The trial sequence was the same in both Experiments 1 and 2. Subjects first performed 10 practice trials with no perturbations to familiarize themselves with the grasping task. After the practice, subjects performed a block of 432 grasping trials, with breaks provided after every 32 trials. Each of the 24 combinations of object and orientation was presented 18 times, of which 1/3 had no perturbations, 1/3 had positive perturbations (+20° rotation or +20 % scaling), and 1/3 had negative perturbations (−20° rotation or −20 % scaling). Order of conditions was randomized across the session. Subjects typically completed the grasping trials in 40 min. After the grasping trials, subjects were asked whether they noticed any changes in the objects during the trials. With the exception of three subjects (two in Experiment 1; one in Experiment 2), whose grasping data were excluded, none of the subjects reported noticing any changes in the target object.

After finishing the grasping trials, subjects performed another block of forced-choice discrimination trials to test whether they were capable of perceiving the backward-masked stimuli used in the perturbed conditions. We explained to subjects that the object would briefly change before the mask, and asked them to try to identify the change. Subjects were presented with a sequence of stimuli that was closely matched to the stimuli experienced on grasping trials with perturbations. An initial target object was presented for between 900 and 1100 ms, with duration randomly varied across trials, and then a perturbed target was presented for 33 ms followed by a 200-ms mask. After these stimuli, a pair of objects was presented with different orientations (Experiment 1) or different sizes (Experiment 2), and subjects judged which of these objects had been briefly presented before the mask. Perturbations

were present on all trials, and the response options always included the correct perturbed object. Subjects made no hand movements during the stimulus presentation on discrimination trials; their task was only to discriminate the briefly presented objects by pointing one of two options. Responses were forced choice, and they were encouraged to guess the answer even if they felt that they had not seen the perturbed object. Subjects performed 8 practice trials to familiarize themselves with the discrimination task, and then 96 experimental trials. The target objects were randomly chosen from the same set used on grasping trials. The direction of perturbations and the position of the correct response option were randomized across trials.

Results

Awareness of perturbations during grasping trials

To assess whether the backward masking was successful at preventing conscious awareness of the perturbations, we debriefed the subjects after they completed the grasping trials. We first asked them a general question about whether they noticed anything unusual, and then specifically asked whether they noticed that the objects had briefly rotated or changed size before the mask on some trials. A large majority of subjects, 24 of 26 in Experiment 1 and 14 of 15 in Experiment 2, reported no awareness of the perturbations and were generally surprised to learn that the target object had often changed. Three subjects did report noticing non-specific changes in the target on some trials. The data from these subjects were excluded from our analysis of grasping performance. Except for these three subjects, backward masking effectively prevented awareness of the perturbations.

Grasping movements on unperturbed trials

Subjects easily understood the virtual grasping task and appeared to perform movements in a natural manner. There was no indication of any delay in movement initiation or increase in movement duration compared to typical reaching movements. The reaction time between presentation of a target and detection of hand movement (>5 % of peak speed) averaged 375 ms (± 130 ms SD) in Experiment 1 and 360 ms (± 67 ms SD) in Experiment 2. The duration between movement onset and contact with the projection surface averaged 1027 ms (± 185 ms SD) in Experiment 1 and 972 ms (± 157 ms SD) in Experiment 2. For both experiments, there was no significant difference between the movement durations in unperturbed and perturbed trials (Experiment 1: $t(23) = 1.21$, $p = .238$; Experiment 2: $t(13) = 1.75$, $p = .103$). The reaction times and movement

durations are comparable to those observed in Chen and Saunders (2015) using a virtual grasping task, and results from an unpublished pilot study that tested grasping of physical objects under similar conditions.

The kinematics of hand movements and grip adjustments are also generally consistent with normal grasping movements. Figure 2a plots the average speed of the hand as a function of normalized time, measured from onset of movement until contact with the projection surface. The interval when the mask was visible is shown in gray. The speed profile is typical of grasping movements, with no indications of a discontinuity at the appearance or disappearance of the mask. Figure 2b, c plots mean grip orientation and grip aperture as a function of normalized time for some sample objects. The orientation of the grip axis was quantified by the angular deviations from the sagittal plane. We determined the plane spanned by the grip axis and the horizontal direction (i.e., plane with vertical tilt), and computed the angle within this plane between the grip axis and the central vertical line. The orientation of the grip axis at the end of movement varied across the objects, and one can see gradual adjustment over the course of movement toward the different final grip axes. Grip aperture showed a typical pattern of increasing to a maximum and then decreasing during the final portion of the movement, with maximum grip aperture co-varying with the final grip aperture. The ratio of the maximum grip aperture to the final grip aperture was 1.17–1.23, which is somewhat lower than has been observed for grasping real objects with similar size, $MGA/FGA = 1.4\text{--}1.7$ (e.g., Westwood et al. 2002; Eloka and Franz 2011; Voudouris et al. 2013). Otherwise, the kinematics appeared similar to normal grasping.

We further analyzed the optimality of the final grasp points on unperturbed trials to test whether subjects touched the virtual objects at contact points that were appropriate for an object's shape and orientation. One measure was the distance of the grip axis from the center of mass of the object. Figure 2d plots the distribution of center of mass distances from unperturbed trials in the two experiments. The observed grip axes tended to be close to the center of mass, with average distance of only .34 cm ($\pm .10$ cm SD). Another measure was the angular deviations from force closure at the contact points. Force closure was computed by comparing the orientation of the final grasp axis to the surface normal directions at each contact point, and then taking the maximum angular deviation. Figure 2e plots the distribution of force closure angles from unperturbed trials. The average error was 15.2° ($\pm 3.7^\circ$ SD), which would be sufficient for a stable grip for most common surfaces. For comparison, we also computed the force closure that would result if the same grip axis were used for a different, randomly chosen target object. The errors in force closure were significantly lower than if the observed

grip axes were compared to a different random target [$F(1,36) = 83.3, p < .001$]. This demonstrates that grasp points were more optimal than would be expected due to chance, confirming that subjects reached toward contact points that were appropriate for the shape and orientation of the target object.

Responses to masked orientation perturbations

To analyze the effect of masked orientation perturbations on hand movement, we compared the grip axis angles over the course of movement across perturbations conditions. Grip axis angles were computed as deviations from the sagittal plane. We determined the plane spanned by the grip axis and the horizontal direction (i.e., plane with vertical tilt), and computed the angle within this plane between the grip axis and the central vertical line. Figure 3a plots the mean grip axis angles as a function of time for the unperturbed condition (black) and the conditions with positive (blue) and negative (red) perturbations before the mask. For this analysis, trials were aligned at the moment when the hand was 20 cm from the target, which was the trigger for object rotations on perturbed trials. One can see that the grip axis angles on perturbed and unperturbed trials begin to diverge about 250 ms after the perturbation onset. The direction of this effect corresponds to the direction of object rotation: Brief presentation of objects rotated by 20° in a clockwise direction produced a small clockwise rotation of the average grip axes, and vice versa.

We used the difference between the mean grip axis angles in the positive and negative perturbation conditions as a measure of the perturbation effect. Figure 3b plots the mean perturbation effect, averaged across subjects, for 50-ms windows of time after perturbation. The perturbation effect was significantly greater than zero after a delay of 250 ms [$t(23) = 2.85, p = .009$] and reached a maximum of 2.21° ($\pm .48^\circ$ SE) after a delay of 450 ms relative to the perturbation onset. The perturbation effect reduced during the final portion of movement when the original target was visible, but remained significant up to the moment where the fingers made contact with the surface [$1.48^\circ \pm .42^\circ$ SE; $t(23) = 3.57, p = .002$]. Note that the original target reappeared 233 ms after the perturbation onset, so the reduction in perturbation effect began about 250–300 ms after the mask was removed and the original target became visible again. The pattern of results suggests that subjects responded to both the appearance of the rotated object and the reappearance the original target, with similar response latency.

Detection of masked orientation perturbations

In addition to asking whether subjects were aware of perturbations during grasping trials, we also conducted a

Experiment 1: responses to masked orientation perturbations

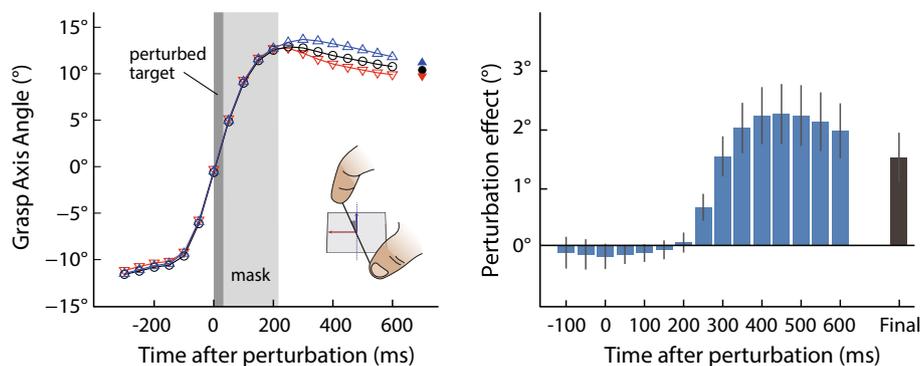


Fig. 3 Responses to masked perturbations of target orientation in Experiment 1. The *left panel* plots the mean angles of the grasp axis, averaged across subjects, as a function of time after perturbation onset. The *three lines* plot results from conditions where the target was briefly rotated by $+20^\circ$ (blue), -20° (red), or remained constant (black). The *dark gray* region depicts the interval of time when the perturbed target was presented, and the *light gray* regions shows the interval of time with the mask. The divergence between the per-

turbed conditions corresponds to a small rotation of the grasp axis in the direction of the target rotation, which reduces by the end of the trial (*solid points*). The right panel plots difference between the mean grasp axes from the positive and negative perturbation conditions for 50-ms windows of time. *Error bars* depict ± 1 standard error. A significant perturbation effect was detected after 250 ms, and the effect reached a maximum 450 ms after perturbation onset (color figure online)

post-test to test whether subjects were capable of perceiving the masked perturbations with conscious attention. The stimuli were the same as in the grasping experiment, but subjects were instructed to look for the briefly presented stimuli and identify whether the rotations were leftward or rightward. For each subject, we computed sensitivity (d') and criterion measures from the discrimination judgments. Subjects showed some individual differences in response bias, with criterion measures averaging $.41 \pm .47$ SD, but there was no systematic tendency to respond leftward or rightward [$t(25) = 1.51, p = .14$]. For any given response bias, one can compute a 95 % CI for the sensitivity measure that would be expected from random binomial trials.

Subjects were classified as performing above chance when their sensitivity was outside the range expected due to chance (e.g., $d' > .53$ for criterion = 0). Of the 24 subjects that were not aware of the perturbations during grasping, 8 were unable to discriminate the perturbations at a rate above chance even when attending to this task. The other 16 subjects showed an ability to discriminate the changes, with average percent correct of 87.4 % (± 11.7 % SD) and average d' of 2.79 (± 1.25 SD). These results indicate that the perturbations were difficult to perceive even when directing attention to this task, but that some subjects were able to discriminate at a level above chance. We suspect that the discrimination ability was based on the detection of rotational motion before the mask, which would allow the direction of rotation to be distinguished even if the perturbed stimuli were not clearly perceived.

Subjects who were able to discriminate the direction of rotation might have had some level of awareness of the

perturbations on grasping trials, which could account for their perturbation responses. To test whether this could explain our results, we compared discrimination and grasping performance across individual subjects. Figure 4a plots the magnitude of the perturbation effect on grasping as a function of sensitivity on the discrimination trials. There was no significant correlation between these measures [$r(23) = .031, p = .887$]. We also compared the average perturbation effect (merging time windows of 400–500 ms) for the subset of subjects that showed chance performance (circles) and above-chance performance (squares) on the discrimination task. The results are shown in Fig. 4b. A significant perturbation effect was observed even for the subjects that could not reliably discriminate the perturbations [$t(7) = 5.39, p = .001$], and there was no difference in the magnitude of the perturbation effect compared to the subjects who were able to discriminate the perturbations [$t(22) = .747, p = .463$]. Thus, the observed perturbation responses were not solely due to a subset of subjects who could potentially discriminate the perturbations. Even if these subjects were excluded, there is still an observable effect of the rotational perturbations on grip orientation during reaching.

Responses to masked size perturbations

To analyze the effect of the brief size perturbations in Experiment 2, we measured the size of the grip aperture as a function of time, shown in Fig. 5a. The black line shows the average grip aperture on unperturbed trials, and the blue and red lines show the average grip aperture on perturbed

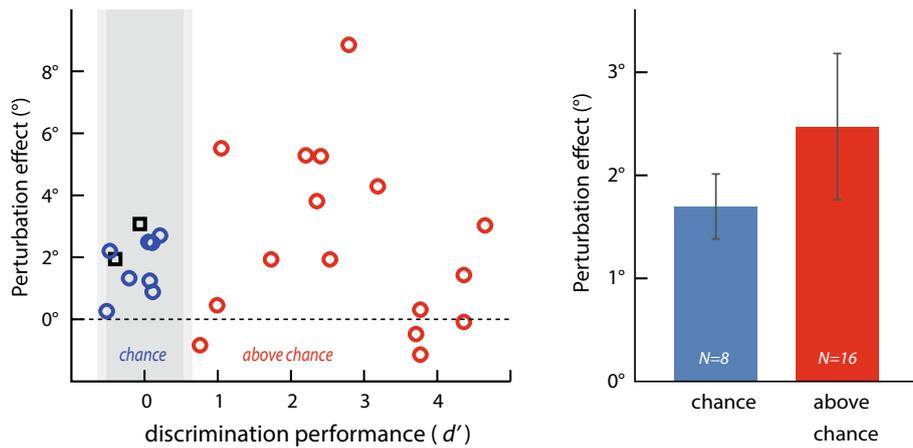


Fig. 4 Results from post-test discrimination trials in Experiment 1 compared to the effect of perturbations on grasping. As a measure of the perturbation effect for each subject, we computed the average difference between the grasp axes in positive and negative perturbation conditions for the time interval 400–500 ms after perturbation onset. The *left panel* plots the perturbation effect for individual subjects as a function of their performance on discrimination trials (d'). There was no correlation between discrimination and grasping performance. The *gray regions* depict the 95 % confidence intervals for d' if dis-

crimination judgments were random with response criterion equal to 0 (*inner*) or 1 (*outer*). The *right panel* plots the mean perturbation effects for the subset of subjects that could reliably discriminate the perturbations (*red*) and the subset that performed at chance (*blue*). Grasp axes were affected by perturbations even for subjects who were not able to discriminate the perturbations in the post-test, and there was no difference in the average perturbation effect compared to subjects that were able to discriminate the perturbations (color figure online)

Experiment 2: responses to masked size perturbations

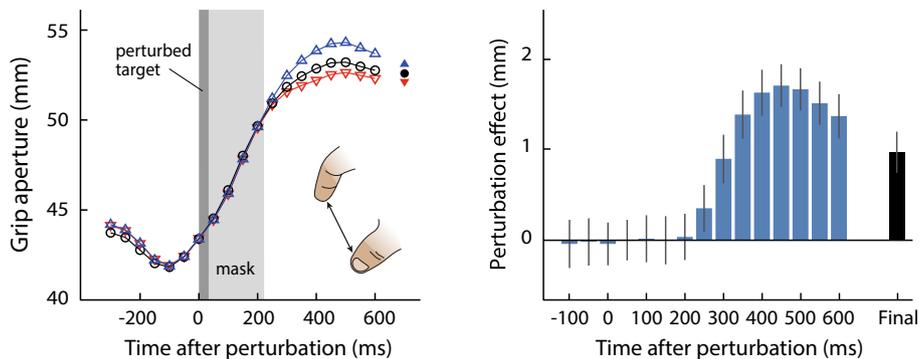


Fig. 5 Responses to masked perturbations of target size in Experiment 2. The *left panel* plots the mean grip apertures, averaged across subjects, as a function of time after perturbation onset. The *three lines* plot results from conditions where the target was briefly increased in size by 20 % (*blue*), decreased in size by 20 % (*red*), or remained constant (*black*). The *dark gray region* depicts the interval of time when the perturbed target was presented, and the *light gray regions* shows the interval of time with the mask. The divergence between the

perturbed conditions corresponds to a change in grip aperture in the direction of the change in target size, which reduces by the end of the trial (*solid points*). The *right panel* plots difference between the mean grip apertures from the positive and negative perturbation conditions for 50-ms windows of time. *Error bars* depict ± 1 standard error. A significant perturbation effect was detected after 300 ms, and the effect reached a maximum 450 ms after perturbation onset (color figure online)

trials where the stimuli were briefly increased or decreased in size by 20 %. We excluded the data from one subject that reported noticing some changes before the mask. Trials were aligned based on the frame where the index finger was 20 cm from the target, which was the trigger for the size change and mask. One can see a divergence in the size of the grip aperture for the two perturbation conditions, in

a direction consistent with the size of the briefly presented objects.

Figure 5b plots the mean difference between the grip apertures in two perturbed conditions as a function of time after perturbation, for 50-ms windows of time. A significant perturbation effect was detectable after a delay of 300 ms [$t(13) = 3.37, p = .005$]. The maximum perturbation

online control. Performance on discrimination trials revealed that many subjects could not perceive the perturbations even when trying, and there was no difference in grasping performance compared to subjects that could discriminate the perturbations with directed attention.

Discussion

Our results demonstrate that adjustments to the grip during reaching movements can be driven by subliminal visual information. Subjects made appropriate adjustments in response to brief rotation or scaling of the target, despite the fact that they were not aware of the backward-masked stimuli and no response was required to successfully complete the task. It is well established that subjects can make corrections to movement in response to perturbations without being aware of the perturbations (e.g., Greenwald and Knill 2009a, b; Pélişson et al. 1986; Prablanc and Martin 1992; van Mierlo et al. 2009). In these previous studies, however, the visual information required to determine corrective responses was available after the perturbations. Our results further demonstrate that the visual information that is inaccessible to consciousness can drive the motor responses. Subjects were able to make automatic adjustments toward stimuli that were not seen at all.

The perturbation responses in our conditions were detectable, but relatively small in magnitude. The average change of the orientation of the grip axis in response to perturbations in Experiment 1 corresponded to 5.53 % (± 5.93 % SD) of the amount of rotation applied to the perturbed stimuli, and the average change in grip aperture in Experiment 2 corresponded to 8.06 % (± 4.43 % SD) of the amount of scaling applied to the perturbed stimuli. Small responses may be due to the fact that grip orientation and size are adjusted gradually over the course of movement. Chen and Saunders (2015) tested responses to shape perturbations that persisted until grasping, but were otherwise similar to the conditions here, and found that much of the overall correction occurred late in the movements. In the present study, the perturbed stimuli were presented only briefly, followed by reappearance of the original target, so a limited amount of correction would be expected.

The dynamics of perturbation responses were similar in the two experiments and generally consistent with previous findings. For both orientation and size perturbations, responses emerged between 250 and 300 ms after perturbation onset and began to reduce about 250 ms after the original target had reappeared. These results suggest that it takes about 250–300 ms to make detectable adjustments to the hand in response to visual feedback about the grasping target. Previous studies testing perturbations of target size and orientation have observed comparable latencies. For

perturbations of target size, estimates of response latencies range from 214 to 440 ms (Bock and Jüngling 1999; Castiello et al. 1993; Dubrowski et al. 2002; Hesse and Franz 2009; Paulignan et al. 1991). For perturbations of target orientation, Voudouris et al. (2013) observed fast corrections of grip axis with average latency of 120 ms, while other studies have observed slower responses with latencies ranging from 200 to 320 ms (Desmurget and Prablanc 1997; Fan et al. 2006; Chen and Saunders 2015). The 250- to 300-ms latencies observed here are in the general range that would be expected from previous studies that tested visible perturbations, suggesting that the unseen visual perturbations were processed in a similar manner.

The automatic responses observed here suggest that continuous online control is used to guide the hand throughout reach-to-grasp movements. We observed unconscious adjustment of the grip orientation and size in response to brief presentation of a masked target, and then reduction of these effects after the reappearance of the original target, both with similar latency. In previous studies that have tested perturbations of grasping, adjustments were required to complete the task, which might encourage an unnatural strategy. In contrast, our conditions required no perturbation responses. The final target object was always the same as the initial target, so subjects could potentially continue their movement toward pre-planned grasp points. The fact that subjects still showed perturbation responses in these conditions suggests that continuous adjustment based on visual information is part of the normal process of controlling grasping movements.

The fact that some subjects were able to discriminate the perturbations in the post-test may appear to contradict our claim that the perturbations were unconscious. Self-reports indicate that very few subjects detected the perturbations during the initial grasping trials (3 of 41), but a substantial number were able to discriminate the perturbations in the post-test (16 in Experiment 1 and 4 in Experiment 2). However, these results are not actually contradictory. During grasping trials, subjects were not expecting any change in the stimuli, while during the post-test, subjects were explicitly looking for the changes. It is not surprising that subjects would be better able to detect the perturbations when attending to this task. The ability of some subjects to discriminate the perturbations when attending to this task does not imply that these subjects saw the perturbations while performing the grasping trials. Rather, it shows that these subjects were capable of perceiving the perturbations. It is quite plausible that they were unaware of the perturbations during the grasping task, as reported, but became able to see the perturbations with focused attention.

For our conclusions, the more important finding from the post-test results is that many subjects were *not* capable of discriminating the perturbations, yet still showed

measurable effects on grasping performance. For these subjects, discrimination performance provides validation for their self-reports. If a subject was unable to perceive the perturbations even with attention, then we can safely conclude that they did not perceive the perturbations during grasping trials when they were not looking for changes in the stimuli. To be conservative, we could consider only the results from subjects that could not discriminate the perturbations, and exclude the other subjects. This would not change our findings: Significant perturbation effects were observed for these subsets in both experiments. Thus, even self-reports were not reliable, our results still provide evidence that unseen stimuli can elicit adjustments to hand movements.

Some previous studies have similarly found that stimuli that are not consciously perceived due to backward masking can affect planning and control of movements. [Binsted et al. \(2007\)](#) and [Heath et al. \(2008\)](#) found that the speed of pointing movements was modulated by the size of unseen targets, and [Cressman et al. \(2007, 2013\)](#) found that an unseen cue could influence online control of pointing movements. Our results extend these findings, demonstrating that an unseen grasping target can elicit automatic corrective adjustments to the size and orientation of the grip during online control of hand movements. Taken together, these results indicate that masked stimuli can be used in various ways to guide actions, despite a lack of conscious awareness.

Our results may appear to conflict with those of some other recent studies that tested the effect of stimuli masked by continuous flash suppression on hand movements. [Roseboom and Arnold \(2011\)](#) observed an influence of CFS masked stimuli on the orientation of the hand during reaching movements, but this effect was relatively small and emerged only over time with training. [Ludwig et al. \(2013\)](#) failed to replicate the findings of [Roseboom and Arnold](#), and suggest that their learning effect could have been due to improved detection of the masked stimuli. In contrast, we observed clear effects of masked stimuli on movements without extensive training, in a situation where subjects were not trying to make any correction and were not even aware that perturbations might occur. This difference may be due to the manner in which stimuli were rendered invisible, as discussed in the Introduction. Neurophysiological evidence suggests that CFS masking affects early visual processing ([Yuval-Greenberg and Heeger 2013](#)), while backward masking selectively blocks input to ventral visual areas ([Bar et al. 2001](#); [Grill-Spector et al. 2000](#); [Noguchi and Kakigi 2005](#); [Kouider et al. 2009](#)). Thus, there is reason to think that the backward masking would have less effect on the visual information available for visuomotor control compared to CFS masking. This could explain the stronger influence of unseen stimuli found in our experiments and

other studies that used forms of backward masking ([Binsted et al. 2007](#); [Heath et al. 2008](#); [Cressman et al. 2007, 2013](#)).

One limitation of our method is that we used a virtual grasping task. Real grasping of physical objects imposes additional constraints on movements that are not present for our task. For example, picking up an object requires that the fingers apply inward force at the moment of contact, while in our conditions the force could remain directed forward until fingers made contact with the projection surface. This difference likely explains the relatively small ratio of maximum grip aperture to final grip aperture observed in our results. [Westwood et al. \(2002\)](#) compared real and virtual grasping and observed smaller MGA/FGA ratios for virtual grasping, which would be consistent with our results. Thus, there are clearly some differences between virtual grasping and real grasping. On the other hand, aspects of our task make it more natural than pantomimed movements. Movements were directed toward a target on a physical surface that remained visible throughout movement, and the hand could be compared to the target in a normal manner. Our results also suggest that grasp point selection was consistent with normal grasping. Grasp points varied depending on the shape and orientation of the virtual objects as would be expected for a stable grip. In a pilot experiment, we tested real and virtual grasping of random 2D shapes like used here, and observed similar optimality. While our virtual grasping task is a limited approximation of actual reach-to-grasp movements, there is reason to think that it involves similar visuomotor processing.

Conclusion

In this study, we tested whether reach-to-grasp movements could be modulated by visual stimuli that are not consciously perceived. During hand movements, we briefly presented objects with perturbed orientation or size, and used backward masking to prevent awareness. Even though subjects were not aware of the perturbations, we observed automatic corrective adjustments in response to both orientation and size perturbations. The time course of the responses, and the fact that the adjustments were actually disadvantageous for the task, suggests that the responses were due to automatic online control processes. Control experiments found that many subjects were not able to discriminate the perturbations even with attention, yet these subjects still showed significant effects of perturbations on grasping. The observed effects for these subjects cannot be explained by some unreported awareness of the perturbations. Our results demonstrate that visual information can be used for online control of grasping movements even when it is not accessible to conscious perception.

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