The continuous updating of grasp in response to dynamic changes in object size, hand size and distractor proximity

Sophia Karok, Roger Newport*

School of Psychology, University of Nottingham, University Park, Nottingham NG7 2RD, UK

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ABSTRACT

Reaching out to pick up an object seems a trivial matter, but selecting the appropriate hand configuration requires a series of complex computations that process the object’s dimensions, orientation and environment. A current debate in motor control concerns how and when the motor system responds to unexpected changes in the visual and spatial properties of objects to be grasped. In the current experiment, visual manipulations that increased either target size, distractor proximity or hand size were applied gradually and continuously throughout reach to grasp movements. All manipulations were associated with early and continuous modifications of the grasping component, but only an increase in hand size affected transport characteristics. This suggests that visual information of both the object and the environment is continuously processed in movement computations, in keeping with models of motor control that posit high weighting for online sensory feedback.

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1. Introduction

Interaction with the environment through goal-directed action is a fundamental human skill and both vision and proprioception are essential for normal reaching and grasping behaviour. Successful grasping requires a series of computations devoted to analysing an object’s dimensions and its surroundings before selecting the appropriate movement path and hand configuration. Movement planning relies heavily on visual information, including estimates of object’s dimensions or properties, for example: using more fingers in the grasp if the object is perceived as heavy or slippery and executing the movement more slowly if the object is fragile (Fikes, Klatzky, & Lederman, 1994; Jeannerod, 1984; Marteniuk, Leavitt, MacKenzie, & Athenes, 1990). The extrinsic properties of an object (e.g., its location, orientation, etc.) are used in the planning of the transport of the hand towards the object and the intrinsic properties of the object (e.g., shape, size) are thought necessary to prepare the most appropriate hand configuration during execution of the grasp (Chieffi & Gentilucci, 1993; Jeannerod, 1981). However, such goal-directed movements are not always accurate and properties may change before the movement is complete; thus visual (and other sensory) information may also provide feedback after movement onset and guide necessary corrections (Hoff & Arbib, 1993; Wolpert, Ghahramani, & Jordan, 1995). Indeed, visual feedback plays an important role in acquiring and developing motor skills (e.g., Fayt, Minet, & Schepens, 1993; Sidaway, Yook, & Fairweather, 2001), and this particularly applies to grasping movements (Schenk, Mair, & Zihl, 2004).

Behavioural experiments have demonstrated that the human motor system can make rapid adjustments in response to sudden changes to a target object. For example, Castiello, Bennett, and Stelmach (1993) observed that participants switched between precision and whole hand grips, depending on which was most appropriate to the suddenly changed object size. Paulignan, MacKenzie, Marteniuk, and Jeannerod (1991) and Paulignan, Jeannerod, MacKenzie, and Marteniuk (1991) further showed that the precise grip aperture (distance between index finger and thumb) is matched to accommodate the visual change in object size. Grip aperture has also been found to be adapted when the haptic object does not match initial visual information (Weigelt & Bock, 2007), even when participants are not consciously aware of the discrepancy (Gentilucci, Daprati, Toni, Chieffi, & Saetti, 1995) and participants are much poorer at grasp control when visual information of target or hand is absent (Rand, Lemay, Squire, Shimansky, & Stelmach, 2007) or inconsistent (Whitwell & Goodale, 2009).

It has been argued that perturbations to the target location involve different neural mechanisms to perturbations in target size. Perturbations in target location generally elicit a detectable
kinematic adjustment (e.g. in velocity or hand path) around 100 ms following a sudden change in the target location (Day & Lyon, 2000; Paulignan, MacKenzie, et al., 1991), whereas size perturbations are associated with a measurable grip size adjustment that occurs much later, between 170 and 300 ms after perturbation onset (Castiello et al., 1993; Paulignan, Jeannerod, et al., 1991). However, because object-size change is more unnatural than a potential change in location, slower responses may simply represent the recalibration or replacement of the original motor plan. On the other hand, patients with optic ataxia (OA), a disorder associated with lesions to the parietal cortex, specifically the parieto-occipital-junction (Jackson et al., 2009; Karnath & Perenin, 2005), show dissociation for deficits related to reaching and grasping to suddenly altered targets. While OA patients, such as patient IG, can be impaired when adjusting to targets that suddenly jump to extra-foveal locations (e.g. Gréa et al., 2002), they are unimpaired when responding to changes in target size that occur in centrally foveated vision (Himmelbach, Karnath, Perenin, Franz, & Stockmeier, 2006). Thus, although patients with the non-foveal variant of optic ataxia might sometimes appear to have deficits in the on-line control of grasping, these deficits may instead be the result methodologies that expose a failure to simultaneously process the spatial properties of a new target presented suddenly in an extra-retinal location while executing a reach towards the original target location in central vision, rather than a grasping deficit per se (Himmelbach et al., 2006; Jackson et al., 2008).

The types of perturbation applied in previous experiments may be described as obtrusive, using sudden or unexpected changes in the presentation of real (Gentilucci et al., 1995) or virtual objects (e.g. Bock & Jüngling, 1999; Himmelbach et al., 2006) or employing incongruent haptic and (not visual) feedback (e.g. Säfström & Edin, 2008; Weigelt & Bock, 2007). The manipulation of the object affordances in these cases was applied at, or shortly after, movement onset, which may not necessarily be the optimal method for determining the efficiency of the grasp component to adjust to unexpected changes. This is an important point as it has implications for the hierarchy of reaching over grasping (cf. Dubowski, Bock, Carnahan, & Jüngling, 2002; Gentilucci, Chieff, Scarpa, & Castiello, 1992). It could be argued that the kinematic details of grasping are transient (Ulloa & Bullock, 2003), rather than pre-planned, and are dependent on the reach component (Jeannerod, 1981). An alternative conception is that the current movement plan is continuously updated using sensory feedback loops, which uses internal models to integrate sensory feedback with motor output (e.g. Wolpert et al., 1995). By perturbing object affordances later in the movement, after prehension has been initiated, such an online mechanism may be exposed, resulting in fast online grasp adjustments in response to spatial parameters that are computed in real-time. The current study investigated this issue by manipulating object and bodily properties in real-time during movement execution.

The notion of online grasp control has been applied to changing object properties (such as object size, shape and clearance, e.g. (Saling, Alberts, Stelmach, & Bloedel, 1998)), but it is unclear how (if at all) the visuospatial features of the effector are incorporated in precision grip computations. Scaling of grip aperture to object size has been reported to remain relatively stable when vision of the hand is occluded (e.g. cf. Connolly & Goodale, 1999; Hesse & Franz, 2009; Winges, Weber, & Santello, 2003), suggesting that vision of the effector does not contribute significantly to the control of grasping. Nonetheless, merely comparing vision vs. no-vision of the hand does not rule out the use of proprioceptive information of the hand that can be used to compute the grasp margin. A more appropriate manipulation may involve changing, rather than removing, the visual properties of the hand (for example, changing the size) and to determine whether such changes are incorporated in computations of grasp. The only known study to investigate the effects of changing hand size on grasping was reported by Marino et al. (2009), who found a reduced grip aperture when the hand size was increased throughout a block of trials, and this effect carried over when visual feedback was removed. However, a habituation technique was employed and the various conditions were executed in blocks, thus not allowing further insight into online grasp control mechanisms that incorporate the dimensions of the effector.

At issue in the current study is how changing the visual properties of the target object and of the hand cause online adjustments in grasping behaviour. To date, most studies have imposed perturbations early in prehension, but this experiment applied gradual manipulations throughout the movement using a virtual feedback system in order to clearly discriminate the online movement system. In addition, most studies have introduced perturbations of object size or location, but not changes in the location of distractor items, even though the effects of distractor location on reach to grasp has been known for some time (e.g. Jackson, Jones, Newport, & Pritchard, 1997). In the current experiment, visual manipulations altered either the object size (object intrinsic property), the proximity of distractor objects (object extrinsic property) or hand size (bodily intrinsic property) on a trial-by-trial basis in a randomised manner. Online adjustments to both transport and grasp components in response to these changes were compared to a baseline condition in which no changes occurred. Verbal reports of subjects’ conscious awareness of the various manipulations were also noted.

In keeping with various models of movement control (e.g. Glover, 2004; Hoff & Arbrih, 1993; Ulloa & Bullock, 2003; Wolpert & Ghahramani, 2000) and the notion that proprioceptive recalibration may be induced by visual information, it was anticipated that appropriate adaptations in the fine grasping calibration would be made in all conditions, such as to avoid ‘collision’ or prevent ‘overestimation of grasp size. Because the manipulations occurred gradually throughout the reach it should be possible to determine whether adjustments to the grasping components are fast, smooth and continuous as a result of the utilisation of continuous sensory feedback, or large and wholesale (with associated lengthening of movement time) as a result of grasp reprogramming.

2. Method

2.1. Participants

Ten neurologically healthy volunteers from Nottingham University took part in the experiment (6 men, 4 women; mean age 21.6 years, SD 1.5). All subjects were right-handed and had normal or corrected-to-normal vision. All were naive as to the purpose of the experiment and gave informed consent to participate. The study was approved by the local ethics committee and conducted in accordance with the ethical standards as laid down in the Declaration of Helsinki.

2.2. Apparatus and stimuli

Participants were seated on a height-adjustable chair allowing them to comfortably view their hands and target objects via the MIRAGE VR system. Participants viewed real-time video images of their own hand (captured at 60 Hz) via a horizontal mirror placed 320 mm above the work surface. The mirror reflected the image of the hands and objects presented on a 28” computer screen positioned 320 mm above, and parallel to, the mirror. Thus the positioning of the mirror and cameras allowed for the display on the mirror to appear as direct visual feedback of actual movements (see Fig. 1). Captured images could be displayed raw, or manipulated using custom in-house software with a processing delay of under 2 ms and the overall delay between image capture and display was undetectable at less than 20 ms. Graspings were recorded using Polhemus Liberty motion tracking sensors (sampling at 60Hz) attached to the index finger and thumb of the reaching hand. Head movements were not restricted, but straight posture and adjustable seating height allowed for the viewing angle to be standardised as well as natural. The experimental session was conducted under ambient light level, but no external objects or edges were visible.

The target object was always one of three wooden blocks, only differing in their volumetric dimensions: 30 mm × 15 mm × 30 mm (small), 30 mm × 30 mm × 30 mm (medium) and 30 mm × 60 mm × 30 mm (large). The blocks were thus identical in depth, were used one at a time (depending on
condition) and were placed 25 cm anterior to the starting position. Two flanker blocks (30 mm × 60 mm × 15 mm), acting as distractors, were always placed 5 cm away at either side of the target block, perpendicular to reach direction.

2.3. Design and procedure

At the start of each trial, subjects rested their thumb and index finger of the right hand on a small protrusion at the starting location. Subjects were instructed to reach towards, grasp with a precision grip, and lift the centre object in front of them after hearing a beep. This signal coincided with the visual appearance of the target area and free-view was extinguished when the transport phase ended (5 mm before object contact). The task required lifting the target object, even after vision extinguished. Subjects were instructed to carry out a natural grasp, but were not allowed to grasp the object over the top. No instructions were given as to where to fixate. Practice trials were carried out under a no-manipulation free-view condition until they felt comfortable with the task (approx. 4 trials).

Participants performed the grasping task under four experimental conditions: hand bigger (HB), object bigger (OB), distractors move (DM) and a no change (NC) control condition. Fig. 2 illustrates a schematic representation of the manipulations in each condition. Manipulations were always initiated at movement onset (when movement velocity exceeded 50 mm/s) and progressively increased in magnitude in-flight and attained final perturbation intensity at the end of the reach. Perturbations were displacement-dependent; that is, the size of the perturbation increased linearly with hand transport in the forward direction. Each condition was carried out with two of the possible three target objects. In the HB condition, the participant’s right hand increased laterally in size and attained up to a 100% greater width (increased hand size was used in this experiment because it was expected that an increase was more likely to elicit an effect than a decrease) (de Vignemont, Ehrsson, & Haggard, 2005; Marino et al., 2009; Mauguere & Courjon, 1978; Pavani & Zampini, 2007). This condition was performed with the small and the medium-sized blocks as target objects. In the OB condition, the visual size of the target object increased from small-to-medium and medium-to-large block size (100% increases); the actual physical object always corresponded to the eventual block size to allow for haptic congruency (i.e. the initial size viewed was half of the actual size and the final viewed size was the same as the actual size). In the DM condition, the distractors moved towards the target object; this condition was also performed with the small and medium-sized object (the distractors were always present, but did not move in any other condition). The increase in approximation of the distractors was 100%, so that the actual 5 cm distance between middle and distractor block eventually appeared as 2.5 cm. The final real position of the distractors was 2.5 cm from the target so that collision with the physical objects was still possible. The NC (no change) control condition served as a baseline and means of comparison against the other conditions; no perturbations took place in this condition; NC condition was carried out using the small and medium-sized blocks as target objects. The large target block was only used so that haptic congruency could be achieved where necessary.
In all, there were four conditions, with two variants of target object size each, which were presented in blocks of eight and the block was repeated 16 times, comprising a total of 128 grasping trials. The order of trials within each block was counterbalanced and randomised, so habituation to any of the manipulations was highly unlikely. Using the excuse of potential technical difficulties, participant was asked if they had noticed anything “strange” that may have happened during trials at the end of every block, since the experimenter could supposedly not see what the participants could see; participants were not informed about the exact manipulations that would take place and inexplicit questioning about what was noticed was to avoid paying too much attention to the potential changes and thus to ensure a natural grasp. After every block, it was noted whether the participant noticed changes in object size, hand size, clearance or other.

2.4. Data analysis

All grasping trials were individually analysed in order to extract the necessary kinematic markers. Movement onset and offset were defined by velocity criteria: the first frame in which the index finger or thumb exceeded a velocity threshold of 50 mm/s was taken as movement onset and movement offset was signalled when velocity fell below 100 mm/s. Movement time (MT) was defined as the time between movement onset and offset. Aperture profiles (direct distance between thumb and index finger) were analysed using various parameters: Maximum grip aperture (MGA) refers to the maximum thumb to index finger distance achieved during the reach, and the relative time to reach MGA was expressed as a percentage of MT (%TTMGA). Final grip aperture (FGA) was defined as the finger to thumb separation at the moment that vision was occluded. Grip stability (GS) was indexed by the changes in grip aperture by calculating the number of times the first derivative of grip aperture (rate of change of grip) crossed zero. If a standard grip aperture profile opens and then closes once, the rate of change will be positive during opening and negative during closing and thus the first derivative will cross zero only once. A less stable grip, with many adjustments, will record a zero crossing each time it changes from opening to closing, or vice versa. The transport component of the movement was calculated using peak velocity (PV), and relative deceleration phase (time after PV) expressed as a percentage of MT (%DP).

Data were analysed by entering mean data for each participant in 1-way repeated-measures analyses of variance (ANOVA) for each dependent measure. Planned comparisons were conducted to directly compare each of the three experimental conditions against the baseline no change (NC) condition (i.e. NC vs. OB, NC vs. HB and NC vs. DM). Differences between the other conditions were of no theoretical interest.

3. Results

Of the 1280 grasping trials, 80 (6.25%) had to be excluded from analysis due to recording or movement errors. Data were collapsed across object size for each condition and the means (and standard deviations) are shown in Table 1. The ANOVAs showed significant main effects for MT ($F(3,27) = 14.74$, $p < 0.0001$), PV ($F(3,27) = 39.06$, $p < 0.0001$), MGA ($F(3,27) = 103.98$, $p < 0.0001$), %TTMGA ($F(3,27) = 16.60$, $p < 0.0001$), FGA ($F(3,27) = 171.05$, $p < 0.0001$) and GS ($F(3,27) = 8.20$, $p < 0.001$). Only the main effect for deceleration phase was not (or marginally) significant ($F(3,27) = 2.88$, $p = 0.054$).

Planned comparisons revealed that, compared to the NC control condition, OB reached had larger and later maximum grip apertures, larger final grip apertures and more stable grip profiles. In contrast, both DM and HB reaches had smaller maximum grip apertures. DM reaches also exhibited smaller final grip apertures whereas HB reaches showed additional effects on transport, with shorter movement times and higher peak velocities (see Table 1 for details). Fig. 3 illustrates the average velocity and grip aperture profiles for each condition. It is important to note that the profiles shown in Fig. 3 are not an artefact produced by data averaging. That is, secondary movements were not masked by averaging across reaches in order to create the mean profile. Fig. 4 shows all the reaches performed by a representative participant and clearly indicates that each reach was performed in the same smooth manner.

Table 1

<table>
<thead>
<tr>
<th>Measure</th>
<th>NC</th>
<th>OB</th>
<th>DM</th>
<th>HB</th>
</tr>
</thead>
<tbody>
<tr>
<td>MT (ms)</td>
<td>688.85 (126.16)</td>
<td>616.17* (90.15)</td>
<td>680.98 (121.39)</td>
<td>673.66 (135.04)</td>
</tr>
<tr>
<td>PV (ms)</td>
<td>801.07 (133.76)</td>
<td>880.20* (116.66)</td>
<td>815.98 (121.91)</td>
<td>807.19 (139.81)</td>
</tr>
<tr>
<td>MGA (mm)</td>
<td>41.52 (5.24)</td>
<td>43.71 (3.60)</td>
<td>42.63 (3.81)</td>
<td>42.71 (5.38)</td>
</tr>
<tr>
<td>%TTMGA (%MT)</td>
<td>72.47 (9.24)</td>
<td>75.09 (7.20)</td>
<td>95.21* (7.87)</td>
<td>78.13 (7.56)</td>
</tr>
<tr>
<td>%TTMGA (3,27) = 14.74, $p &lt; 0.0001$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>%DP (%MT)</td>
<td>75.58 (8.78)</td>
<td>77.64 (8.34)</td>
<td>87.36* (4.68)</td>
<td>77.35 (6.16)</td>
</tr>
<tr>
<td>%DP (7.20) = 68.97 (5.64)</td>
<td>90.70* (5.58)</td>
<td>69.59 (5.64)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FGA (mm)</td>
<td>66.12 (6.57)</td>
<td>68.97 (5.64)</td>
<td>90.70* (5.58)</td>
<td>69.59 (5.64)</td>
</tr>
<tr>
<td>%TTMGA (%MT)</td>
<td>1.44 (0.43)</td>
<td>1.20 (0.23)</td>
<td>0.99* (0.34)</td>
<td>1.34 (0.33)</td>
</tr>
<tr>
<td>%TTMGA (5.58) = 1.44 (0.43)</td>
<td>1.20 (0.23)</td>
<td>0.99* (0.34)</td>
<td>1.34 (0.33)</td>
<td></td>
</tr>
</tbody>
</table>

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

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All subjects reported object and distractor changes (and some reported other changes such as supposed increased frequency of the beep sound or object visibility time), but only two noticed the changes in hand size (of which only one participant noticed it during early trials). There were no noticeable differences in any measure between those subjects who noticed the hand size change and those who did not.

3.1. Summary of results

Overall, these results indicate that adjustments to grip aperture were made in response to all perturbations types (see Fig. 3b). When the distractors moved closer to the target object (DM) or the hand grew larger (HB), participants reduced their grip aperture accordingly. When the target object increased in size (OB), participants increased their grip and reached maximum grip aperture later and made fewer aperture adjustments. For the condition in which the width of the hand increased (HB) additional early changes in the transport of the hand were also observed, with faster reaches being executed, even though most participants failed to notice the increase in hand size.

4. Discussion

All three types of perturbation resulted in modifications to grasp formation when applied throughout the movement. Increases in hand or object size and approximation of distractor objects were associated with early modifications of the grasp component, whereas an increase in hand size was also associated with early modifications to the reach profile. These results indicate an online visual control system, in which corrections are achieved in a closed-loop manner using continuous feedback mechanisms.

4.1. Responding to object size

The considerable increase in maximum grip aperture in the OB condition is in line with the results from many previous studies (Castiello, Bennett, & Paulignan, 1992, 1993; Hesse & Franz, 2009; Paulignan, Jeannerod, et al., 1991; Roy, Paulignan, Meunier, & Boussaoud, 2006; van de Kamp, Bongers, & Zaal, 2009). The increase in aperture (being strongly correlated with object size (Smeets & Brenner, 1999; Ulloa & Bullock, 2003)), the later peak in MGA and the apparent increase in grip stability can all be explained by an ever-increasing grip, as opposed to the decrease in grip aperture normally observed after peak aperture when reaching towards stable targets (Jeannerod, 1984). In other words, as participants noticed the increase in size, the initial aperture was no longer sufficient to avoid underspecification of the grip size (and potential collision) and so the grip opening was increased further. Because the size continued to grow as the movement unfolded, so the grip aperture also continuously increased.

Most studies using size perturbation paradigms have attempted to reveal the time course of corrective grasping which is supposed to be indicative of the hierarchy of the components of prehension (e.g. Dubowski et al., 2002; Gentiliucci, 2002; van de Kamp et al., 2009). A faster adjustment in the reach component following changes in object size or location has been interpreted as the grip component adjusting to fit in with the dynamics of transportation (Castiello et al., 1993; Jeannerod, 1981; Paulignan, MacKenzie, et al., 1991; Paulignan, Jeannerod, et al., 1991). However, this contention does not explain more recent findings: Timman, Stelmach, and Bloedel (1996), for example, forced a reopening of the grip aperture to a second maximum and this produced a deceleration in the transport component and it has also been found that adjustments of grip size to fit a new object size can be made as quickly as responses to location changes (about 120 ms; Roy et al., 2006; van de Kamp et al., 2009). Smeets and Brenner (1999) review the evi-
dence and propose a model of the visuomotor control of grasping that suggests that the two ‘channels’ of prehension are holistic and not independent of each other (cf. Dubowski et al., 2002).

However, the precise moment of grasp adjustment can vary depending on the type of experimental setup, procedure or method of analysis and the current study was not concerned with the absolute speed of grip adjustment, so much as whether the motor system can make smooth and continuous online adjustments in response to continuous changes in intrinsic and extrinsic object properties. By applying the perturbation after movement onset (becoming more pronounced as the movement progressed), and bearing in mind that total movement time was generally less than 700 ms, any significant adjustments can be interpreted as resulting from online corrections. Particularly, since the perturbations increased in magnitude with the movement, a successful grasp required continuous visual guidance and continuous corrections. Grasp reorganisation following object size perturbation were independent from more general aspects of the movement (e.g. MT, deceleration phase), which suggests that the corrections were perturbation-specific, occurred in-flight and did not require a secondary, corrective motor plan.

These results show a smooth grasp adjustment to object-size perturbations, which indicates that the size change was processed early and grip aperture increased linearly with the progressive object size increase. That is, the size increase was adapted to-flight, before the eventual object size was attained. There has been an ongoing debate within motor control as to whether movements are entirely preplanned (Plamondon, 1995), continuously regulated by afferent information (e.g. Ulloa & Bullock, 2003) or a combination of the two (i.e. an ‘integrative hybrid’; Desmurget & Grafton, 2000). On the basis of finding double-peak aperture profiles (see above) and prolonged movement times in conditions of object size change, some researchers (e.g. Bennett & Castiello, 1995; Castiello et al., 1993; Paulignan, Jeannerod, et al., 1991) argued for a superimposition of the current movement strategy and that the motor programme cannot be adjusted smoothly. Similar conclusions were reported in size-perturbation studies that did not find the double-peak pattern (e.g. Bock & Jüngling, 1999; Hesse & Franz, 2009) and posit an open-loop feedforward mechanism in which possible discrepancies are adjusted only at the very end of the trajectory via internal feedback loops (e.g. Milner, 1992). The observation, in the current experiment, that grip apertures were smoothly and continuously adjusted in response to changes in object size argues strongly for a model in which on-line motor control utilises continuously regulated computations such as that proposed by Ulloa and Bullock (2003).

4.2. Responding to distractor object

Grip aperture was also continuously adjusted in response to changes in the approximation of non-target flanker objects. The present study further confirms and extends findings regarding obstacle avoidance in grasping in that subjects decreased their maximum grip aperture when the obstacles approached closer (Mon-Williams et al., 2001; Saling et al., 1998; Tresilian, 1998), suggesting that the grip is adjusted in order to reduce potential threat of collision with distractor objects. In the current paradigm, the obstacles were always present as a matter of control, which may explain the lack of a significant increase in the temporal component in this condition compared to NC (no change) baseline trials. Nonetheless, the novel methodology allowed the manipulation the target object clearance so that the opening around the target object became progressively narrower. As a result, any adjustments made in this condition can be inferred to have occurred early: the increasing magnitude of virtual perturbations applied in this experiment was dependent on the point in the trajectory that the hand is away from the objects; thus, bearing in mind the time to peak velocity, the most significant change in distractor distance occurred early in the acceleration phase. This is reflected in the grip profiles for the DM condition in that subjects reached their adjusted grip apertures relatively early and maintained it for the latter half of the movement (see Fig. 3b).

In all conditions, but most clearly in the DM and OB conditions, noticeable adjustments to grip aperture began within 300 ms of movement onset. When inspecting the aperture profiles in Fig. 3, one has to consider the grip adjustments in relation to the velocity profiles: perturbations were movement-dependent, gradually increasing in magnitude and peaking in salience during the early period of acceleration, eventually reaching a 100% perturbation at the end of the movement. Thus, the corrections in grip aperture are fast and online, bearing in mind that the delay needed for a noticeable visual or proprioceptive signal to influence an ongoing movement is around 80–100 ms (Paillard, 1996). The early corrections made in response to changes in object properties neatly fit in with the idea that an on-line control mechanism relies on continuous visual feedback, which challenges the notion that movement control is heavily reliant on motor output and that discrepancies are adjusted for only at the very end of movement.

4.3. Responding to hand size

The current results illustrate that the grasp component can respond quickly and smoothly to changes to the properties of objects to be grasped and to non-target objects in their immediate proximity, but to further strengthen the notion that visual information is recruited early in the course of the movement, the current experiment also manipulated properties of the hand. It has previously been argued that the dimensions of the effector are not incorporated when computing grip margins. The most common approach to investigating the importance of visual feedback for the execution of grasping movements is to remove visual feedback-field of the hand at particular moments and observing possible changes in movement kinematics. A number of studies report that not seeing the hand during prehension had no effect on grasping or reaching kinematics (e.g. Prablanc & Martin, 1992; Winges et al., 2003), while the majority found an increased MGA and MT and reduced peak velocity (e.g. Berthier, Clifton, Gullapalli, McCaffi, & Robin, 1996; Churchill, Hopkins, Ronnqvist, & Vogt, 2000; Hesse & Franz, 2009), but this was explained in terms of programming the movement with a larger safety margin due to the increased uncertainty. Rand et al. (2007) further suggest that changes in the transport component can be attributed to visibility of the target and Churchill et al. (2000) also found that 50% of the difference in MT can be explained by the lack of environmental cues. According to these findings, then, the role of visual feedback of then hand is, at most, marginal and circumscribed to the very end of the trajectory.

Nevertheless, Connolly and Goodale (1999) identified the problem of controlling for constant light levels, enabling subjects to view the target object while occluding the view of their reaching arm, and it was found that total MT increased, but the aperture profile remained unchanged. They interpreted their results in that the hand posture can be programmed on the basis of visual information of the target object and proprioceptive feed-back from the hand. It could thus be argued that the apparent unimportance of visual feedback of the hand may be explained by an overreliance on proprioceptive information as a compensatory strategy (hence the increased MT), and so an online control system may be at work nonetheless. Indeed, Saunders and Knill (2003), in a reaching study using virtual feedback of hand position, found that subjects corrected perturbed trials early in the acceler-

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ation phase and also that early perturbations were corrected more accurately than later perturbations. This mirrors findings from late-onset object size changes in grasping experiments (Hesse & Franz, 2009; van de Kamp et al., 2009), in which late-onset perturbations resulted in greater grip overshoot. An early supervision may thus be functionally advantageous, making it logically more pragmatic.

The present study directly addressed whether visual information of the moving hand and its surrounding are continuously integrated throughout the course of a goal-directed movement. Because visual deprivation studies are not conclusive about how visual information may be used, the other option is to alter the visual feedback of the hand, which was made possible with the current methodology. Participants responded to an increase in hand size with changes to the kinematic profile of the transport of the hand towards the target object. Moreover, these adjustments were gradual and smooth, as shown by the same, low number of grip adjustments (zero-crossings in the rate of change of grip aperture) as the NC no change control condition. Figure 4 shows all velocity and grip aperture profiles from the NC and HB conditions for a typical participant. Clearly, these profiles are smooth and represent efficient, unitary movements.

Although the reduction in grip aperture is not as great as might be expected from a hand that finished the movement twice its real width, the reduction in grip aperture nevertheless ties in with the idea that participants executed the movement as though they really had a physically larger hand, having to proportionally adjust the opening of their grip. Marino et al. (2009) reported the same finding after habituating subjects to an increased hand size over the course of a block of trials. This habituation paradigm, however, merely demonstrates that subjects can adapt to a larger hand size, which is made evident in their grasping, but the present results further highlight that the dimensions of the effector are incorporated in the online coordination of prehensile actions. Furthermore, in the Marino experiment, participants saw their hand in central vision at the end of each movement and thus may have processed the change in hand size independently of the reach to grasp action. In the current study, the hand was only visible during the reach itself. Thus, incorporation of the effector dimensions appears to be automatic and independent of conscious processing, since the majority of the subjects did not report noticing the increase in hand size throughout the task, or when they were explicitly asked afterwards. This automatic updating is a consistent finding in motor control (e.g. Binsted, Brownell, Vorontsova, Heath, & Saucier, 2007; Gréa et al., 2002; Heath, Maraj, Godbolt, & Binsted, 2008; Ro, 2008; Saunders & Knill, 2003; Schen, Schindler, McIntosh, & Milner, 2005) and indicates that a conscious visual percept is not necessary to support motor output and update the movement plan.

That the movement was executed in significantly less time in the HB condition makes it that all the more remarkable that a visually induced proprioceptive adjustment took place. This confirms that the body schema is composed of highly dynamic representations of the body parts that can be used for sensorimotor action (Buxbaum, Giovannetti, & Libon, 2000; Cardinali, Brozzoli, & Farne, 2009). In an ingenious experiment, Brozzoli, Cardinali, Pavan, and Farnè (2010) asked subjects to discriminate touches to their grasping hand during the course of the movement and found that perception of tactile stimuli was more strongly modulated by visual information of the target object at the initiation of the action, compared to the static condition. Taken together, it appears that the hand can be remapped early in a goal-directed movement, as shown by tactile perception (Brozzoli et al.) and influence on grasping parameters (the current study).

It is interesting to note that the remapping of body size did not seem to affect perception of object size. Because the hand was wider than in reality, this might have been expected to give the impression that the target object was smaller than in reality and smaller objects usually produce longer movement times, longer deceleration phases and smaller maximum grip apertures. That this did not happen suggests that the object was not perceived by the motor system as being smaller than its veridical size, despite the hand being larger than normal and reach to grasp parameters being adjusted accordingly. However, it should be noted that a rightward shift of around 50 mm was found in the movement trajectory of the HB condition relative to the NC condition. The peak of this shift coincided with the time to peak velocity and, with the shift being greater for the thumb than the finger, the difference between the finger and thumb shift also tallies well with the difference in MGA. Bearing in mind that the motor system is more concerned with hand position in conjunction to object position (Haggard & Wing, 1997; Smeets & Brenner, 2001), this adds weight to the notion of driving the effector to the object within a common reference frame. Moreover, this finding also suggests that the transport and the grasp components are more closely coupled than was originally assumed. On the other hand, it might also be argued that only the lateral position of the thumb was being processed, rather than the overall size of the hand.

The main finding from the HB condition is that vision of the hand is indeed important and is incorporated in the coordination of prehensile actions. In just over half a second, subjects took into account the changing properties of the hand and successfully grasped the target object by reducing their grip opening and moving their hand closer to the target object sooner. Indeed, this happened in a quick and automatic fashion, so that subjects generally did not report noticing the manipulation. This is unique and strong evidence for a continuous visual control signal from the moving hand, in keeping with models of motor control that posit high weighting for online sensory feedback without the need for conscious perception.

4.4. Implications for the neural mechanisms of grasping

It is interesting to note that the time-course of the divergence of grip apertures from those observed in the no change control condition were remarkably similar for the HB and DM conditions (see Figure 3) with observable differences between the mean grasp profiles appearing at around 280–300 ms for both. While this might suggest the recruitment of the same neural networks for the processing of target grasping and non-target obstacle avoidance, evidence from neuropsychology indicates otherwise. Optic ataxia is most often described as a disorder of visually guided reaching, often including an inability to scale or orient grasp appropriately, although this common conception has recently been questioned (e.g. Cavina-Pratesi, Letswaart, Humphreys, Lestou, & Milner, 2010; Jackson et al., 2009). Obstacle avoidance tends to be abolished in those with optic ataxia (Schindler et al., 2004) and preserved in most neglect patients (McIntosh, McClements, Dijkerman, Birchall, & Milner, 2004) with OA being associated with superior parietal damage and neglect with more inferior parietal pathways. Furthermore, obstacle avoidance does not appear to require conscious awareness of object type or location, as shown in patients with visual agnosia and extinction respectively (McIntosh, McClements, Schindler, et al., 2004; Rice, McIntosh, et al., 2006), suggesting that action-related dorsal structures are required for the on-line processing of non-target objects. The control of single target grasping, on the other hand, is preserved in optic ataxia when the target is presented in central vision. Himmelbach et al. (2006) demonstrated that while OA patient IC, who had previously been shown to be unable to smoothly adjust grip aperture and reach direction in response to a target that suddenly jumped from central to peripheral vision, was nevertheless no different to controls when reaching to a cen-
trally presented target that suddenly changed in size. Furthermore, Cavina-Pratesi et al. (2010) tested OA patient MH, who only presented with inaccurate grasping when reaching for distal targets in peripheral vision (right handed in right space) and whose grasping of proximal objects, that required no transport of the arm, was normal. They suggested that grasping impairments observed in typical OA patients might be a secondary result of inaccurate reach direction – forcing a widening of grip aperture in order to encompass the target – rather than a deficit specific to grasp formation. It is interesting that MH was also impaired at obstacle avoidance, failing to take proper account of extra-foveal obstacles in his right visual field when reaching with his right hand (Rice et al., 2008).

The distinction between impaired peripheral grasping (possibly as a result of inaccurate reaching), impaired obstacle avoidance and preserved central grasping is that the former two require the processing of multiple spatial locations, one being central (whether a target is present or not) and the other peripheral. Peripheral and central processing are thought to involve different neural mechanisms (Prado et al., 2005), with peripheral processing involving the medial aspect of the superior parietal lobule—specifically the parietal-occipital junction (POJ). A direct prediction from the above, for the current experiment, is that optic ataxia patients with POJ lesions should have a preserved ability to adjust to changes in centrally presented object size, but fail to compensate for changes to simultaneously presented peripheral distractor items. The response of OA patients to changes in hand size on this task is uncertain, but would provide valuable insight into the likely mechanisms for the processing of hand properties during reach to grasp. Such mechanisms are likely to rely heavily on parietal areas involving the integration of visual and proprioceptive information, as well as the processing of information from the visual periphery.

In addition to superior parietal areas involved in the on-line control of reaching, it is important to consider the potential role of the anterior intraparietal sulcus (aIPS) in this task as this area has been specifically implicated in the execution of grasping. Rice, Tunik and Grafton (2006) applied TMS over anterior, middle and caudal IPS either immediately before or during a grasping action towards an oblong bar that could unexpectedly be rotated through 90 degrees in order to increase the required grip size along the vertical dimension. Only stimulation to aIPS disrupted grasping behaviour, and then only during execution of the movement, regardless of whether the bar had been perturbed. In 2008, Tunik et al. noted the differential involvement of aIPS and the superior parietal lobe (SPL) during sudden perturbations to object size (Tunik, Ortigue, Adamovich, & Grafton, 2008). SPL was recruited later than aIPS with activation of SPL coinciding with the time required to detect, reprogramme and initiate an on-line response to a target perturbation (~186 ms). The authors surmised that aIPS is involved in the early internal representations of the task goal, comparing the desired and actual states of the hand. They hypothesised that the period of aIPS activation would be prolonged under perturbed grasping conditions when the task goal needed to be updated, but that when there sufficient error between the desired and actual states existed, SPL would further be recruited in order to mediate on-line corrections. In the current experimental arrangement, perturbations were smooth and gradual, rather than sudden as in the Tunik experiment. Given the smooth and continuous adjustment of grip aperture, it is possible that the discrepancy between the desired and actual states of the limb never reached sufficient levels to initiate recruitment of the SPL and that the involvement of aIPS would have continued until the termination of the grasp. A direct prediction of this would be that TMS to SPL would impair grasp formation to sudden perturbation, but not to gradual ones.

4.5. Experimental considerations

In this experiment hand and object size only increased and object clearance only ever decreased, but it would have been equally possible to have the hand and object decrease and the object clearance increase. Apart from the practical aspect of keeping the experiment to a manageable size, the primary reason for choosing the current arrangement was that there is evidence to suggest that enlarged hands are more readily accepted than reduced hands (Pavani & Zampini, 2007). In addition, increasing object clearance may not necessarily have required an adjustment to grip aperture, given that the aperture programmed was already sufficient to avoid the distractor objects. In relation to decreasing hand and object sizes, however, we would speculate that grip aperture would gradually increase and decrease respectively in a similar, constant manner to that observed for increasing hands and objects.

While this experiment has demonstrated the ability of the motor system to smoothly adjust to gradual changes in the properties of the object and effector, previous experiments have primarily observed wholesale reprogramming of grasp in response to changes in object size. The motor system is very adept at adjusting to task demands, however, and it may be that the most efficient way for the motor system to deal with sudden or large perturbation is to reconstruct the entire motor programme rather than to attempt a smooth and gradual change.

It is perhaps notable that the majority of effects were observed for grasp parameters rather than those related to the transport of the hand. Although such findings might be taken to suggest separate or hierarchic control mechanisms for reach and grasp, it must also be remembered that in all conditions here, the target was always presented centrally and did not change location; thus changes in the transport component ofprehension would have been kept to a minimum. Future experiments should involve gradually moving targets as well as moving distractors. If optic ataxia patients can adjust to the changing size of centrally presented targets, then they should also be able to track a moving object that does not suddenly move out of central to peripheral vision.

5. Conclusions

The present results provide strong and direct evidence for continuous, online visual control of grip aperture also confirms and extends findings of online grip scaling beyond more obtrusive paradigms and visual deprivation studies. Increases in object size, approximation of distractor objects and an increase in hand size were associated with early modifications of the grasping component, and only an increase in hand size also affected the general movement profile.

The contention of continuous feedback mechanisms in motor control does not fit well with classic feedforward models, which hold that the motor command is defined before onset of the movement and that feedback loops are engaged towards the end of the movement trajectory, if at all. Participants in the present study, however, responded to all visual perturbations in an automatic fashion. Corrections in grip aperture were fast and online and in light of these findings, it can be proposed that the a priori motor plan is crude rather than predefined and that a sensory feedback loop is powerful and continuously active.

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