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An object-centred reference frame for control of grasping: effects of grasping a distractor object on visuomotor control

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Abstract Previous evidence based on perceptual integration and arbitrary responses suggests extensive cross-modal links in attention across the various modalities. Attention typically shifts to a common location across the modalities, despite the vast differences in their initial coding of space. An issue that remains unclear is whether or not these effects of multisensory coding occur during more natural tasks, such as grasping and manipulating three-dimensional objects. Using kinematic measures, we found strong effects of the diameter of a grasped distractor object on the aperture used to grasp a target object at both coincident and non-coincident locations. These results suggest that interference effects can occur between proprioceptive and visuomotor signals in grasping. Unlike other interference effects in cross-modal attention, these effects do not depend on the spatial relation between target and distractor, but occur within an object-based frame of reference.

Keywords Kinematics · Reach to grasp · Multisensory information · Vision · Proprioception · Motor control

Introduction

The view that the senses are interrelated modalities rather than independent channels has been recently supported by several studies providing evidence for common neural and attentional mechanisms for processing of multisensory information (e.g., Driver and Spence 1999). In these studies, the emphasis was on cross-modal links between combinations of vision, audition and tactile inputs.

Most of the research conducted in humans on cross-modal integration has typically focused on perceptual integration, and has involved an arbitrary response, such as reaction time, to a sensory stimulus. However, the study of the effects of multisensory coding during more natural tasks, such as grasping and manipulating three-dimensional objects, is still in its infancy. This is perhaps surprising, given that these manual actions generally involve a complex interplay between vision, proprioception and touch (Castiello 2005). Nevertheless, recent research on multimodal issues shows that cross-modal links in motor control are substantial and numerous.

Distractor size was previously identified as a key parameter for distractor effects on grasping by Castiello (1996). Gentilucci et al. (1998) used distractor size to investigate cross-modal links between haptic information and visuomotor control when reaching to grasp a visual target. In their experiments, participants reached and grasped with one hand a visual target (sphere) presented with different sizes, while holding another unseen sphere (distractor) of different sizes on the other hand. These authors found that proprioceptively guided manipulation with the right hand influenced finger shaping of visuomotor grasping with the left hand when the two objects differed in size. They reported an interference effect only for an unseen small distractor object. Moreover, this effect was only seen for a distractor manipulated by the right hand while reaching to grasp an object with the left hand.

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In a subsequent study Patchay et al. (2003) confirmed and extended this result. They found that the kinematics of a hand reaching to grasp a visual target object were influenced by haptic and proprioceptive input from an unseen distractor manipulated in the other hand. Patchay et al. (2003) found that the maximum grip aperture of a visually guided reach-to-grasp was proportional to the diameter of the distractor object manipulated proprioceptively with the other hand. More importantly, this bimanual cross-modal interference effects occurred only when the distractor object was actively grasped. The effect was absent in a control condition where the non-reaching hand merely received tactile and proprioceptive stimulation, without grasping a distractor object. The effect seems to arise from cross-modal interference between two concurrent plans for object-oriented action. Interference between actions of the two hands has been reported previously for finger-tapping (Wing et al. 1989) and for reaching (Huer et al. 1998; Kelso et al. 1979). However, we believe that this is the first demonstration of a cross-modal interference effect linked specifically to interaction with objects.

Despite this increasing knowledge about cross-modal effects during more natural actions a crucial issue still remains unsolved. Does interference between object-oriented actions such as grasping show the same principles of spatial organisation as other psychomotor functions, such as selective attention and orienting responses? A classic finding from a number of cross-modal studies of selective attention is that responses were facilitated when the stimuli presented in different modalities were located in the same position rather than in different positions in external space (Driver and Spence 1999). These effects have been found for arbitrary responses (Spence and Driver 1996), and for orienting responses, such as saccades (Bell et al. 2005) and reaching (Pouget et al. 2002). A particularly striking effect in studies of visually guided reaching is the tendency for the hand path to curve away from a distractor location (Tipper et al. 1997). This behaviour has been attributed to a process of inhibiting distractor locations, and is thought to use an external frame of reference (Tipper et al. 1998). All the findings are consistent with a supramodal coding of either locations in external space, or of objects individuated by their location. The generality of location-based coding is shown by studies of temporal order judgement. Here, judgements about the time of two stimuli are improved when the signals come from different locations rather than the same location (Spence et al. 2003). This effect may be due to the redundancy of spatial separation enhancing temporal discrimination (Zampini et al. 2003).¹ Manipulating spatial location by crossing the hands produces an inversion of temporal order judgements (Yamamoto and

Kitazawa 2001). In the context of the present study, the literature on distractor effects in attention and action generally suggests a strong influence of the spatial discrepancy between target and distractor on the magnitude of distractor effects (Tipper et al. 1997).

Neurophysiological studies have suggested a basis for spatial modulation of such effects in bimodal neurons. Two spatially concordant sensory stimuli can produce response enhancement in several neural structures involved in action, including the putamen, parietal cortex and superior colliculus (Graziano and Gross 1993; Stein 1998). However, these results have been obtained with orienting responses, such as saccades and pointing movements. No representation of the target as an object is required for such responses. Therefore, it remains unclear whether object-oriented actions, such as grasping, are also organised according to an external spatial frame of reference. To summarise, interference in most cross-modal situations depends on the spatial coincidence between target and distractor. This view would predict large effects of a haptic distractor on visuomotor grasping when distractor and grasp target are located close to each other in space, and lesser distractor effects as the target–distractor distance increases. However, this hypothesis has not been fully tested for grasping actions.

The present study therefore aims to investigate how proprioceptive and haptic information from a distractor stimulus grasped in one hand can influence the grasping component of the other hand when reaching towards a visual target object. In particular, we assessed whether the interference depended on whether the positions of the target and distractor were coincident or not. The results should show whether any interference is simply due to actively grasping a distractor object, independent of its location, or alternatively, whether the location of the distractor grasp reduces as the distractor–target distance increases. The results should clarify the frame of reference within which object-oriented grasping is coordinated. If the former, location-independent pattern of interference is found, we would conclude that grasping may use a special frame of reference, different from the egocentric spatial frame used for reaching (Jeannerod 1981, 1984) and selective attention (Driver and Spence 1999). However, if the latter, location-dependent pattern of grasp interference is found, we would conclude that grasping uses the common visuo-spatial frame of reference reported for other cross-modal effects.

Methods

Participants

Eight right-handed participants (four males and four females, aged 18–29 years, mean age 23.1 ± 4.1) recruited from the university population took part in the study. All participants had normal or corrected-to-normal vision, and none of them had any known neuromuscular

¹On the other hand, this spatial redundancy effect seems to occur only when the stimuli to be discriminated are primarily represented in different cerebral hemispheres. Zampini et al. (2003) found that temporal order judgements do not depend on spatial separation when both are presented in one hemifield, while identical separations, which span the midline facilitate temporal order judgement.

disorder affecting the upper limbs. All were naïve as to the purpose of the experiment, and in compliance with the Royal Holloway University of London Ethical Committee regulations, written informed consent was obtained. Each participant attended one experimental session of 1-h duration.

Material and apparatus

The experimental setup (see Fig. 1) was displayed in a well-lit room. Participants were seated comfortably

facing the work surface (depth 44 cm, width 42 cm, and 100 cm from ground level). A starting switch was flush with the work surface, and was positioned 22 cm from the target's centre and 8 cm from the participant's thorax. The stimuli were two inflatable rubber bulbs (height 9 cm). The bulb mounted on the work surface served as the target, while the bulb mounted beneath served as distractor. The target had a constant diameter of 55 mm and was filled with an epoxy compound to render it unalterable when grasped. It could be positioned at the centre of the work surface, that is, at 22 cm from the starting switch (Fig. 1a, b), or on the right-hand side of

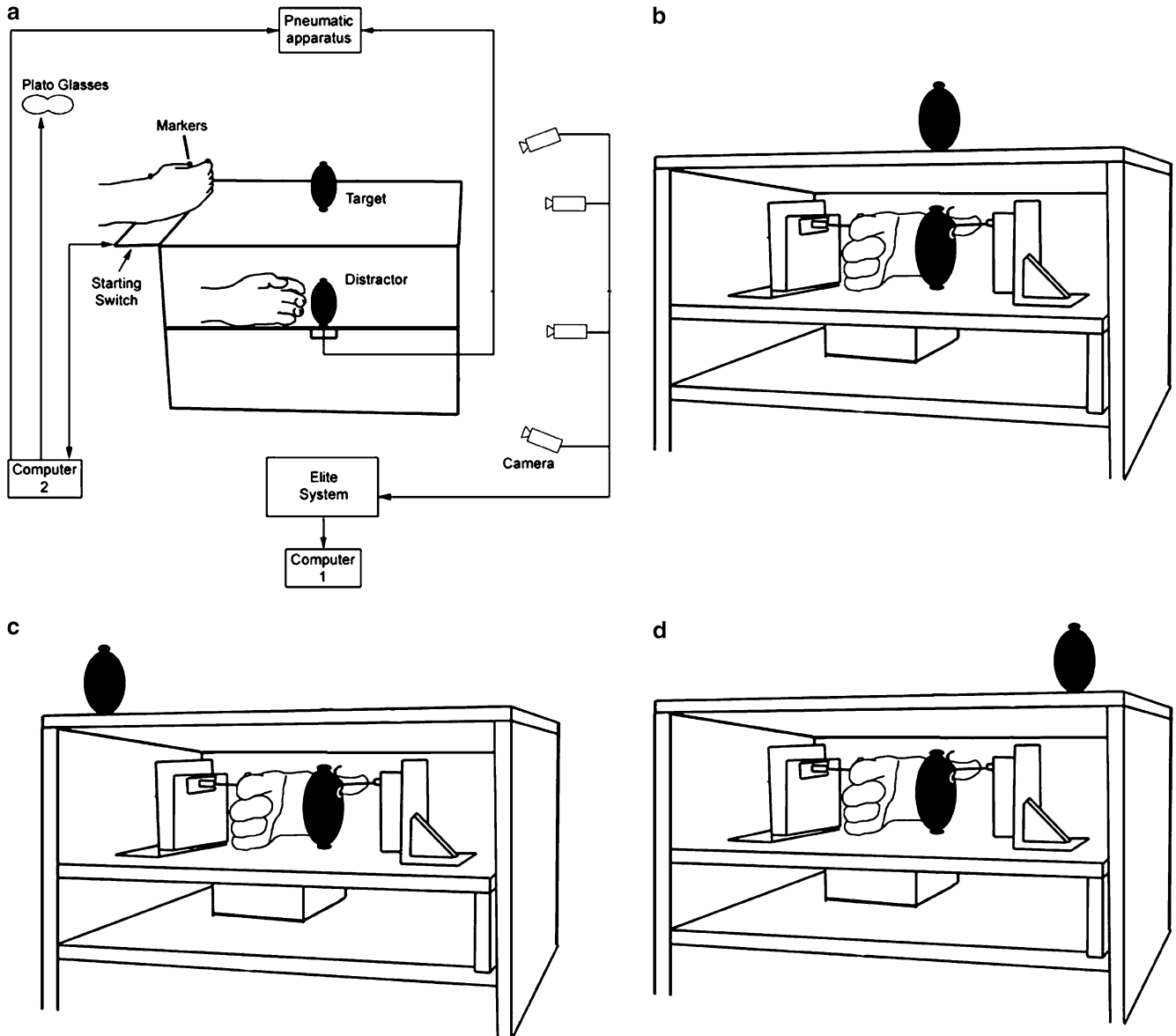


Fig. 1 Schematic representation of the experimental setup. *Panel A* represents the transverse view of the setup. It represents the two hands at rest before the trial starts. The grasping hand rests on a starting switch with index finger and thumb gently opposed. The distractor hand is open around the distractor object. *Panel B* shows the front view of the experimental setup. It shows the position of the 'distractor' hand. The *two small panels on the side* represents the two

adjustable starting block sensors mounted on contact microswitches positioned on the lateral and anterior sides of the distractor. This ensured that the participant's index finger and thumb were held in a consistent starting position (open grip) before the start of each trial. *Panels C and D* represent the front view of the experimental setup showing the spatially not coincident (*panel C and D*) locations of target and distractor. This figure is not in scale

the participant, at 18.5 cm from the centre of the work surface (Fig. 1c), or at 22 cm from the starting switch or on the left-hand side of the participant, at 18.5 cm from the centre of the work surface, and at 22 cm from the starting switch (Fig. 1d).

The other stimulus (the distractor) was always located in a position coincident with the central position of the target, underneath the work surface and at 86 cm from ground level in a compartment opened at both ends (see Fig. 1b). The distractor was inflated and deflated by computer-controlled pneumatic apparatus. Customised software regulated the passage of compressed air (maximum pressure 138 kPa) to the bulb. The airflow was appropriately timed to inflate the distractor stimulus to the required sizes. A one-way valve enabled air to be locked in the system with minimum leakage, thus maintaining the required size of the distractor constant throughout a trial. Another valve was activated to release the air and deflate the bulb. The participants could not see the distractor during the experiment.

The participant's hands were positioned as follows: the subject used the target hand (right or left depending on condition) to reach towards and grasp the target. The target hand rested on the starting switch with the index finger and thumb held in slight opposition, with the more ulnar digits flexed. The distractor hand (left or right depending on condition) was positioned so that the thumb and index finger rested in adjustable starting blocks, mounted on contact micro-switches positioned on the lateral and anterior sides of the distractor. This ensured that the participant's index finger and thumb were held in a consistent starting position (open grip) before the start of each trial. A light indicated to the experimenter the correct starting position of the distractor hand. During each trial, subjects grasped the distractor with the distractor hand. Furthermore, the distractor was connected to an oscillator. The oscillator was driven by a 16-Hz square wave signal fed through an amplifier at 5 V sufficient to provide a clearly suprathreshold vibrating signal. This computer-controlled non-noxious mechanical vibration was parallel to the vertical axis of the distractor, and was used in a vibrating distractor task in the study.

During the whole study, participants wore light-weight spectacles fitted with liquid crystal lenses (Plato Technologies Inc.) that rendered the target stimulus visually accessible by changing from blanked/translucent to clear. The same customised software operated the clearing of these lenses.

Data acquisition

Kinematics of the target hand were recorded with, and processed by a four cameras ELITE motion analysis system (BTSwin Milan, Italy). The system was used to collect 3D time-displacement data from three infrared-reflecting hemispherical passive markers (\varnothing 6 mm). The markers were positioned on the wrist (radial aspect of

the distal styloid process of the radius), the index finger (radial side of the nail) and on the thumb (ulnar side of the nail). The displacement of the markers was recorded with four 100-Hz video cameras. Two cameras were positioned 2.7 m in front of the participant at a 30° intra-camera angle, and the other two cameras were placed 1.5 m fronto-laterally on the right and left sides of the participant at a 90° intra-camera angle. The calibrated working space was 50-cm deep, 40-cm high and 30-cm wide, from which the spatial accuracy measured from stationary and moving stimuli was 0.03 mm.

Procedure

Three reaching and grasping tasks were administered. The three tasks differed only regarding the distractor conditions, and are described as follows:

Baseline condition In this baseline condition only the target was presented at the centre, right or left positions. There was no distractor. The participants had to reach and grasp the target with the index finger and thumb at normal speed, as soon as the lenses of the spectacles cleared. The lenses stayed clear for 3,000 ms. Participants were further instructed to keep holding the target for a little while before coming back to the starting position ready for the next trial. This baseline condition was administered first, so that the participants had no prior exposure to the conditions where the distractor stimulus was introduced. Each participant performed a set of ten reaches for each target position with each hand respectively; a short period of rest was included between each set.

Vibrating distractor condition A vibrating distractor condition was presented in the second task. For this task the size of both the target and the distractor was 55 mm in diameter. The target was presented at the centre, right or left positions. Participants were instructed to hold the distractor with one hand throughout the trials without squeezing it in order to feel the vibration. The other hand reached and grasped the target each time the lenses cleared. Each participant completed a set of ten reaches for each target position with each hand respectively; a short period of rest was included between each set. The purpose of this task was to give the participant a continuous and passive tactile/kinaesthetic input to be compared with the distractor task where the distractor varied in size (described in the following). This condition allows to control for possible distractor effects, which are independent from distractor size. Comparing the vibrating distractor condition to conditions involving an active grasp of the distractor should show whether any interference is due to the distractor providing tactile/kinaesthetic input to the hand, or due to the representation of a concurrent object-oriented grasping action on the distractor.

Distractor task In this task, one hand grasped the distractor while the other hand reached and grasped the

target. Four main conditions were administered. These conditions were labelled as follows: (1) the no-distractor control condition, in which the target alone (diameter 55 mm) was presented. This was similar to the baseline condition; (2) the small distractor condition, in which the distractor diameter was 43 mm and the target diameter was 55 mm; (3) the same-size distractor condition, in which the diameter of both the target and the distractor was 55 mm; (4) the larger distractor condition, in which the distractor diameter was 75 mm and the target diameter was 55 mm. In all these four conditions the target was presented either to the centre, right or left positions. These conditions occurred in random order, and were presented in equal numbers within each set of trials. For these conditions the sequence of events was the following. The experimenter triggered each trial from the computer keyboard. On pressing a key the distractor was inflated according to the condition. On hearing a tone (1,000 Hz, 500 ms) delivered 1,000 ms after the lenses turned opaque, the participant had to close the hand on the distractor. Then the lenses cleared at irregular intervals between 1,000 and 2,000 ms after the tone and the participant was instructed to reach and grasp the target at normal speed as soon as the lenses cleared, and to remain holding the target for a little while. In the no-distractor condition no tone was delivered, when the lenses cleared the participant only had to reach and grasp the target while keeping the index finger and thumb of the distractor hand on the starting blocks. After the prehension movement was completed, the starting position for each hand was resumed for the next trial. Contact with the distractor was maintained until the end of every trial. Each participant first completed four sets of 16 trials with one hand and then performed the same number of trials with the other hand.

Note that, therefore, the spatial discrepancy between the distractor and the target in our design is given by the two-way interaction of target location (right, central or left to reaching hand) and reaching hand (left, right). Practice trials were performed before the experiment, and a short period of rest was allowed after each set of trials.

Data processing

The BTSwin software package was used to construct the 3D coordinates of the markers from the images. A morphological model of the hand (grip) was used to reconstruct the location of the markers and their links. The resulting x , y and z -axis displacement data were then smoothed using a low pass finite impulse response linear filter with an automated cut-off frequency (D'Amico and Ferrigno 1992).

The statistical analyses have been largely confined to the dependent variable that was thought to be specifically relevant to the scientific hypothesis under test. This

variable was the amplitude of maximum grip aperture. The amplitude of maximum grip aperture refers to the maximum distance between the two markers positioned on the index finger and thumb. Grip profiles were characterised by a single peak reached at approximately 70% of movement duration (see Fig. 2).

This variable was chosen because consistent results within the reach-to-grasp literature have shown that the amplitude of maximum grip aperture is precisely and almost linearly related to object size (e.g. Jakobson and Goodale 1991). Thus, if the results show a smaller or larger maximum grip aperture according to distractor size, this would suggest effects of distractor size on the kinematics of the grasp for the target object. Given the nature of the task to be performed upon the distractor, it is predicted that chiefly this dependent measure concerned with the grasp component will be affected by the experimental manipulations. To assess whether distractor size manipulations also affected hand transport control, the maximum tangential velocity of the wrist marker in the plane of the work surface, a conventional and sensitive index of hand transport was also calculated (Gentilucci et al. 1991; Jakobson and Goodale 1991).

Data analysis

The baseline condition, the vibrating distractor condition, and the no-distractor condition were analysed separately in a $2 \times 3 \times 3$ repeated measures analysis of variance (ANOVA) with hand (right or left), location (left, centre or right) and condition (baseline, vibrating or no distractor) as within subjects factors. These conditions are referred to as control conditions. The remaining experimental conditions were concerned with the parametric influence of distractor size on the reach-for-grasp task. Two separate ANOVAs were performed on the maximum grip aperture and maximum transport velocity measures of the experimental conditions. Each ANOVA used a $2 \times 3 \times 3$ repeated measures design with hand (right and left), distractor condition (small distractor, same-size distractor or large distractor) and target location (coincident, right or left) as within subjects' factors. Whenever sphericity was violated, the Greenhouse-Geisser corrected significance values of the degrees of freedom are reported in the results. The corresponding post-hoc test was employed to test for significant differences between factor means when relevant. Bonferroni adjustments were used when necessary. The significance level was set at $P=0.05$ for all tests.

Results

We first report the results of analyses investigating control conditions, and then report the effects of distractor size and spatial location on hand aperture and hand transport measures.

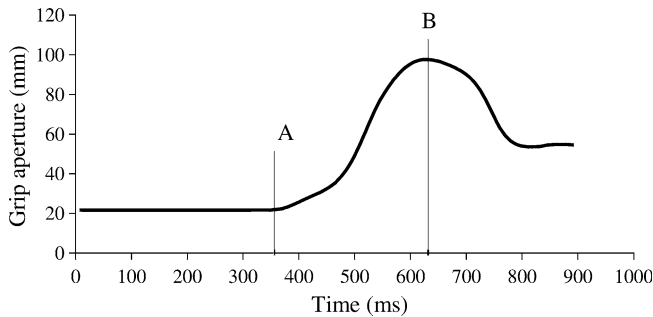


Fig. 2 Example of a graphical representation of grip aperture (distance between index and thumb) as a function of time, in one participant in a trial with the right hand in the control condition (without distractor) with target located on the *left*. The vertical line *A* represents the opening of the grip aperture from an initial resting posture (21.7 mm, 350 ms) and the vertical line *B* represents the maximum grip aperture (97.6 mm, 630 ms)

When the control conditions (baseline, vibrating and no distractor) were compared separately, there was no significant main effect of hand [$F(1,14) = 0.003$, $P > 0.05$], condition [$F(1.12,15.69) = 1.22$, $P > 0.05$] or of target location [$F(2,28) = 1.25$, $P > 0.05$]. Moreover, no significant hand \times condition [$F(1.12,15.69) = 0.23$, $P > 0.05$], hand \times location [$F(2,28) = 1.32$, $P > 0.05$], condition \times location [$F(2.62,36.73) = 1.58$, $P > 0.05$] and hand \times condition \times location [$F(2.62,36.73) = 2.55$, $P > 0.05$] interactions were revealed. In sum, the results of control conditions suggest first that experience of the distractor on preceding trials did not per se alter grip kinematics for an individual trial on which no distractor was signalled. We found no difference was found between the condition in which the distractor was never experienced (baseline condition) and the condition in which the distractor was not present (no distractor condition) but it was intermingled with distractor conditions (small distractor, same-size distractor, large distractor). Second, the results suggest that it is the action of grasping the distractor, rather than the tactile input or posture of having the other hand open that produces the distractor effect. Passive experience of the distractor as a tactile and proprioceptive stimulus (vibrating distractor condition) does not produce significant changes in the grip aperture of the hand reaching towards the target. This is demonstrated by the fact that no differences were found between the vibrating distractor condition and conditions in which no distractor was present.

We turn now to effects of active grasping of different sizes of distractor in the experimental conditions. The data for maximum grip aperture and maximum transport velocity are shown in Table 1.

Our analyses focussed on a number of specific predictions. First, distractor size was expected to influence grasp size but not transport velocity (Patchay et al. 2003). Second, the investigation of the prediction from the attentional literature that distractor size effects on both grasping and transport measures should be greater when target and distractor are coincident than when they are not. As regards the first prediction, a significant

main effect of distractor condition on grasp aperture was found [$F(1.37,19.12) = 70.1$, $P < 0.001$; see Fig. 3]. Post-hoc contrasts showed significant differences in grip aperture for all pairwise contrasts of distractor size condition. A significant main effect of location was also found [$F(1.15,16.08) = 11.82$, $P < 0.05$]. Post-hoc comparisons revealed significantly smaller maximum grip apertures when the target was not coincident with the distractor than when the target was in the central location, coincident with the distractor (all $P < 0.05$). However, grip aperture was not significantly different between the right and left target locations ($P > 0.05$). The main factor hand [$F(1,14) = 0.27$, $P > 0.05$] and the interaction between hand and condition [$F(1.37,19.12) = 0.01$, $P > 0.05$] were not significant. Importantly and crucial for the second prediction, the interactions location \times condition [$F(2.30,32.11) = 1.57$, $P > 0.05$], location \times hand [$F(1.15,16.08) = 1.05$, $P > 0.05$] and location \times condition \times hand [$F(2.30,32.11) = 1.75$, $P > 0.05$] were also not significant. Note that in the design, the second prediction regarding the modulation of distractor size effects by spatial location, is carried by the three-way interaction between location, distractor condition and hand. That is, there was no tendency found for the influence of distractor size on grip aperture to vary with the discrepancy between distractor and target spatial locations. Inspection of Fig. 4 shows that this is not just a problem of statistical power, with a genuine attentional effect failing to achieve significance because of a small number of subjects. In fact, the numerical effect runs in the opposite direction to the attentional prediction: the effect of distractor size was rather smaller for the central target location (target and distractor coincident) than for the average of the left and right target locations. In sum, these results suggest that the cross-modal grasp interference effect is not modulated by spatial coincidence.

Then a similar ANOVA was performed on the maximum hand transport velocity. This showed a highly significant main effect of target location [$F(2,14) = 22.89$, $P < 0.0001$], and significant effects of reaching hand [$F(1,7) = 9.50$, $P = 0.0178$] and distractor diameter [$F(2,14) = 5.82$, $P = 0.0308$]. The interaction between target location and hand was significant [$F(2,14) = 50.51$, $P < 0.001$]. No other effects achieved significance.

The hypotheses focussed on the role of spatial coincidence between target and distractor on grip and transport parameters. Univariate ANOVA showed that distractor effects in grasping are independent of spatial coincidence. Since this is a null statistical result, great care is needed in interpretation. It is considered important to show that the consistency of distractor size effects across spatial locations was not simply due to the choice of measures, or insufficient spatial separations in the setup. Therefore both grasp and transport measures were analysed simultaneously using multivariate methods (MANOVA). This analysis compares the sensitivities of each component to the factors of the design, rather than looking for statistical significance in either

Table 1 Mean grip aperture and mean maximum velocity for the three experimental conditions

| Experimental conditions | Mean grip aperture (mm) | Mean maximum velocity (mm/s) |
|-------------------------|-------------------------|------------------------------|
| Small-size distractor | 88 (1.9) | 926 (27) |
| Same-size distractor | 93 (1.9) | 899 (28) |
| Large-size distractor | 94 (1.8) | 904 (23) |

mm millimetres; *mm/s* millimetres by second
Standard error across subjects in parentheses

Fig. 3 Mean values of amplitude of maximum grip aperture (in mm) for the six experimental conditions. Within-subject standard errors are indicated by the vertical bars

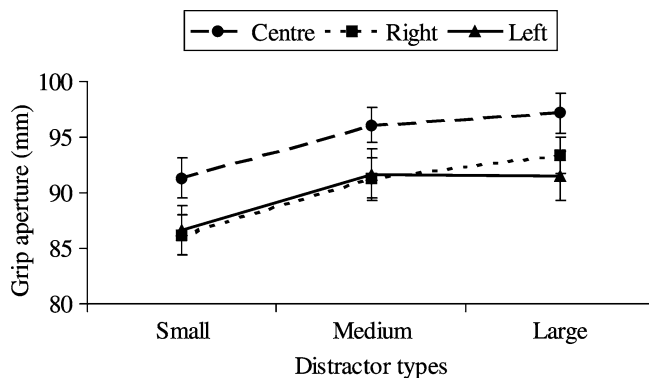
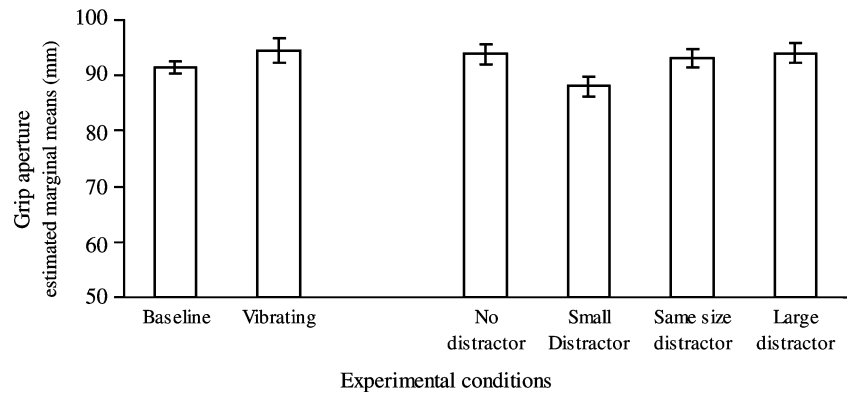


Fig. 4 Graphic representation of the interaction condition × location. This figure shows that the distractor size effect was almost unchanged across the three target locations. Centre (*circles*): coincident target and distractor; right (*squares*): target on right-hand side of participant; left (*triangles*): target on left-hand side of participant. Within-subject standard errors are indicated by the vertical bars

component individually. The main effect of distractor condition was considered. This was highly significant (Wilks' Lambda=0.1117, approximated by $F(4,26)=12.94$, $P<0.0001$). That is, some linear combination of the transport and grasp measures was sensitive to the distractor size. Inspection of standardised canonical coefficients (SCCs) from the MANOVA shows to what extent grasp aperture and transport velocity each contributed to this effect. The SCCs were 2.30 and -1.21 , respectively. That is, the grasp component was more affected by the distractor diameter than was the transport component. Moreover, the directions of the effects were different: increasing distractor size

tended to boost grasp apertures, but reduce transport velocity.

Next the effects of the spatial relation between target and distractor were investigated in the same way. In the design, this is given by the interaction between target location and reaching hand. This was highly significant (Wilks' Lambda=0.1057, approximated by $F(4,26)=13.49$, $P<0.001$). Now, however, the SCCs showed the inverse pattern (grasp aperture -0.40 , transport velocity 1.63). This shows that the measure of hand transport was over four times more sensitive to spatial location than the measure of grasp, and confirms that the design was well able to capture the standard spatial effects. Whereas the distractor effect was largely confined to the grasp component, and the spatial coincidence effect was effectively confined to the transport component.

However, the crucial test comes from the interaction between the two preceding effects, defined as the three-way interaction in the design between distractor size, reaching hand and target location. This tests whether the distractor effect and the spatial effect might interact, and also shows whether this interaction primarily affects the transport or the grasp component. The MANOVA interaction was significant (Wilks' Lambda=0.1417, approximated by $F(8,54)=11.18$, $P<0.001$). The SCCs were -1.08 for grasp aperture, and 4.19 for transport velocity. That is, the tendency for distractor effects to vary with spatial location was largely confined to the hand transport measure. The grasp aperture measure showed diameter effects, which were relatively independent of spatial location.

It is believed that this analysis lends some support to the claims regarding an object-based reference frame for

grasping. First, it was shown that appropriate variables for the grasp and transport components of the movement were differentially sensitive to the distractor width and spatial location factors of the design, respectively. Distractor size effects influence grasp only, independent of spatial location, while spatial location effects influence transport only, independent of distractor size. The strong dissociation between distractor size effects on grasping and distractor location effects on transport recalls the original hypothesis of independent visuomotor channels for these two components of prehension (Jeannerod 1981).

Discussion

In this study we investigated how kinematics of a hand reaching to a visual target are influenced by haptic and proprioceptive input from an unseen distractor manipulated in the non-reaching hand presented in a location either coincident or not coincident with the reach target.

These results confirm selective interference effects of the distractor on the grasping component of the reaching hand (Gentilucci et al. 1998; Patchay et al. 2003). When the distractor was smaller or bigger than the target, the amplitude of maximum grip aperture was respectively smaller or bigger, than in the conditions where the size of the distractor was not taken into account (baseline condition, vibrating distractor condition) nor altered (no distractor condition).

The main issue at stake in the present study was to test whether the coincident locations of distractor and target stimuli could account for the pattern of results described previously. To this end we presented target and distractor at coincident and non-coincident locations. Importantly, we found that the cross-modal grasp aperture effect we previously described (Patchay et al. 2003) was independent of the spatial coincidence between target and distractor. That is, the cross-modal interference effect in grasping occurred effectively independently of whether the target and the distractor were in coincident or non-coincident positions. While care must be taken in interpreting this null result, a MANOVA-based sensitivity result showed that the design was sufficiently sensitive to reveal such effects. Thus, a measure of the transport component (peak wrist velocity) was significantly modulated by the spatial relation between distractor and target, but not by distractor size. This was exactly the inverse of the pattern found for grasp aperture. This suggests a clear double dissociation between the susceptibility of transport and grasp components to grasp distractor effects. The transport component is influenced by the spatial location of the distractor but not by its size, while the grasp component is influenced by the size of the distractor, and not by its spatial location. In this sense, the study suggests that the transport and grasp channels of prehension are independent with respect to susceptibility to distractor spatial properties (Jeannerod

1981), though their execution is clearly linked (Haggard and Wing 1995). Furthermore, the present results confirm that distractor effects and object representation are dissociable. For example, in an attempt to target specifically the grasping component Castiello (1999) asked participants to reach-and-grasp a target presented in conjunction with a distractor of a different size, but similar in colour and positioned roughly in the same position as the target. It was found that the subjects' amplitude of peak grip aperture while enroute to the target was influenced by the size of the distractor. If the target was small, the amplitude of peak grip aperture was greater when the distractor was large than when no distractor was present. Conversely, the amplitude of peak grip aperture for the grasp of a large target was less when the distractor was small than when there was no distractor. Little evidence for changes at the level of the reaching component was found. In contrast, Tipper (for a review see Tipper et al. 1998; see also Welsh and Elliott 2004) specifically targeted the reaching component. Subjects were required to initiate the reach as quickly as possible after a visual cue (either blue or green in colour) had appeared followed by the presentation of two stimuli, a target (either a blue or green block) and a distractor (a red block), both similar in size but separately positioned at one of the four different locations. Prior to the start of the experiment the subjects had been instructed only to move (i.e. reach-and-grasp the target) if the cue matched the target's colour. In such situations distractors appear to compete for the control of action. These effects were evident from subsequent analyses of the reaching component. Distractor effects were found for movement duration, peak velocity and spatial trajectories. No evidence of distractor interference effects at the level of the grasping component was found. The contrast between these studies suggests that a visual scene can evoke parallel motor processes, that parallel activation of multiple motor representations triggers mutual interference, and that visual spatial attention may bias the competition between representations that leads to interference.

A tenet from previous selective attention studies is that shifts of attention in one modality tend to be accompanied by corresponding shifts in other modalities. Attention appears to be distributed across a single supramodal representation of external space. That is, the correspondence between the modalities is due to a common focus of attention with respect to external space (for review see Driver and Spence 1999). Interference from an irrelevant distractor modality increases when the target is close to the distractor (Spence et al. 2003). Further, when a target is expected on a particular side in just one modality, discrimination in other modalities also improves on that side. This suggests a tendency for common spatial attention shifts across the modalities, due to a common, supramodal representation of external space. For example, in one experiment a flash in the left visual field leads to faster tactile dis-

criminations with the left rather than the right hand shortly after the flash; whereas a right flash gave an advantage to the right hand (Spence et al. 1998).

In the present study it was hypothesised that the interference deriving from a distractor in one modality (tactile/proprioceptive) would affect an action towards a visual target. Further, the extent of such interference was used as an index to investigate whether the location of the target with respect to the distractor plays a role in the interference process. Assuming that in the present study vision is the primary modality, then one would have expected interference effects to be larger when the distractor is located in the same position of the target where visual attention is directed. Equally, if the target is strongly expected in a specific location in one modality, but distractor stimuli associated with other modalities occur at a different modality, then interference should be reduced. This reduction would be explained by observing that the distractor falls outside a multisensory action space dominated by the target modality.

In contrast to this prediction it was found that interference effects were present both when the target and the distractor were presented at coincident locations and also when they were presented at different locations. In attentional terms this may be explained by suggesting that the link between distractor and target representations, which generates the observed interference, involves a different organising principle of attention from that involved in orienting in external space. Note that our task and measures seem to be sensitive to the organisation of reaching space (as shown by the sensitivity of transport velocity to the target-distractor separation).

It is therefore suggested that grasping actions may rely on an object-based rather than a location-based frame of reference. The MANOVA analysis suggests the coexistence of two apparently independent forms of spatial organisation or visuomotor frames of reference. These are a location-based organisation influencing the transport component but not the grasp component, and an organisation based on object geometric properties, which influences the grasp component but not the transport component. Object-based representations have long been important in theories of vision (Marr 1982). They have recently been proposed also in visuomotor grasping (Jeannerod and Frak 1999; Castiello 1999; Westwood and Goodale 2003).

For example, Westwood and Goodale (2003) asked participants to grasp a target object within a size-contrast display following an auditory cue. The peak grip aperture was unaffected by the perceptual size illusion when the target array was visible between the response cue and movement onset. However, peak grip aperture was affected by the illusion when the target array was occluded from view at the time the auditory cue was presented. The authors suggest that dedicated, real time visuomotor mechanisms are engaged for the control of action only after the response is cued and only if the target is visible. These visuomotor mechanisms compute

the absolute metrics of the target object and therefore resist size-contrast illusion. However when the target is no longer visible, a perceptual representation of the target object can be used for action planning. Unlike the real-time visuomotor mechanisms, perception-based movement planning makes use of relational metrics, and it is therefore sensitive to size-contrast illusions. Their views partially fit with the present results. In this study, subjects experienced (proprioceptively) the metrics of the distractor. They then retained that information, which automatically affected their later action towards the target. When the previously experienced distractor was different in size from the target, then conflicting perceptual object representations may have determined interference.

Previous grasping studies have not focussed on distinguishing object-centred representations from external space representations, as is done here. The concept of independent visuomotor channels for reaching and grasping has dominated the study of prehension since its beginning (Jeannerod 1981). The balance of recent evidence suggests that the reaching and the grasping channels are not executed independently within the motor system. In contrast, the results suggest that the underlying representations of space used by the transport and grasp channels may indeed be independent. It is believed that these results present the first clear dissociation between an external visuospatial reference frame for the reach component and an object-based reference frame for the grasp component.

One possible rejoinder to the absence of spatial modulation effects in the study comes from a new interpretation of spatial effects by Zampini et al. (2003). They found that spatial separation between sensory sources influenced temporal order judgements between these sources only when each sensory source projected primarily to a different cerebral hemisphere. In their designs, this corresponded to positioning the sources on opposite signs of the body midline: equivalent separations within one hemisphere were less effective. They suggest that apparently spatial effects should really be considered as hemispheric effects. In the setup (Fig. 1), the distractor was always located on the midline. Therefore, on a strict view, distractor and target were always in the same hemisphere, irrespective of target location. Thus, we may have failed to find spatial modulations of our effects because, like Zampini et al. (2003) Experiment 5, our stimuli did not span the midline. In future experiments, the distractor location as well as the target location might be manipulated independently to explicitly test this explanation. In the meantime, however, we think that our data do not lend themselves easily to the strict hemispheric interpretation of Zampini et al. (2003). First, in this design, distractor and target were always associated with opposite hands. Their somatomotor representations, if not their visual representations, were thus always associated with opposite hemispheres. It is not directly clear how the Zampini et al. (2003) hemispheric account of temporal

discrimination would transfer to a hemispheric account of spatial action effects. As we understand it, however, between hemisphere situations should show less interference than a same-hemisphere situations. We nevertheless found clear interference between distractor and target hand. Nevertheless, we cannot exclude the possibility that visual target representation and somatomotor representation of the distractor might always be co-represented in a single hemisphere. However, we found distractor effects on visuomotor measures of hand transport, suggesting that between-location and within-hemisphere interference does exist for skilled actions, if not for temporal order judgements. Further research on the influences of location, hemisphere and task on principles of spatial organisation will be necessary to clarify this point.

Our results also clarify the concept of “object-based attention” (Duncan 1984; Scholl 2001). Previous studies have used the term to explain the fact that a visual distractor at a fixed position relative to a target is more effective when the target and distractor fall within a visual object than when they do not (for review see Scholl 2001). Such results show that object boundaries modulate the spatial representations within which selection occurs. The results, support a stronger claim that selecting objects for action involves an object-centred representation quite independent from external space. Whereas the location factor does not produce changes in the cross-modal distractor effect, significantly larger maximum grip apertures were found when the target was coincident with the distractor than when they were not coincident. It is suspected that the main effect of location arises because the distractor may be processed as a physical obstacle in the coincident location, even though it is in a different vertical plane from the target. An increased grip aperture is a common finding in several conditions where the difficulty of the reaching component of the task is increased (Wing et al. 1986). A further aspect of the results was that the maximum grip aperture was approximately the same when the distractor was bigger than the target or equal to it in size. Maintaining a high grip aperture involves a motoric cost, and is in any case limited by the musculoskeletal constraints of the finger joints. This may explain why the large distractor did not cause a proportionate increase in grasp aperture.

Finally, a vibrating distractor task was also included in this study to separate passive from active grasping. Interference effects were obtained only when the distractor was actively grasped. This excludes the possibility that continuous and passive proprioceptive input was responsible for the reported interference effects. The cross-modal interference seen here occurs at the level of action representations, and not at the sensory level.

All in all, the present results suggest that the grasp interference effect is not modulated by spatial location and that this effect may occur within an object-based frame of reference dictated by the type of action and task adopted. This frame of reference differs from the external visuo-spatial frame of reference used in reach-

ing. Making a coordinated prehension movement requires coordination of reaching and grasping components. However, the results suggest that the two components may have quite different principles of spatial organisation.

A final point is concerned with whether the present experiment allows speculations in terms of multisensory integration or whether these results could be simply understood in terms of the influence of one hand posture on the other. In other words, does the proprioception/tactile input from the distractor hand influence the visual, the proprioceptive or the motor aspects of the grasp? The control conditions required subjects to maintain the distractor hand in the same posture as for the distractor conditions, and also controlled for the level of tactile stimulation, yet did not modulate grasp aperture. This suggests that it is the change in the proprioceptive tactile input from actively grasping the distractor object that influences the aperture of the visuomotor grasping task. The interference appears to occur at the level of object-oriented actions, not at the level of postures or sensory inputs.

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