Grasping after a Delay Shifts Size-Scaling from Absolute to Relative Metrics

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Abstract

■ We carried out three experiments designed to compare the effects of relative and absolute size on manual prehension and manual estimates of perceived size. In each experiment, right-handed subjects were presented with two different-sized 3-D objects in a virtual display and were instructed to pick up or estimate the size of one of them. In Experiment 1, subjects were requested to pick up the smaller one of two virtual objects under one condition and the larger one under the other condition. In fact, the target object was identical on all trials; it was simply paired with a smaller object on some trials and a larger object on others. To provide veridical haptic feedback, a real object was positioned beneath a mirror at the same location as the virtual target object. In Experiment 2, one of the virtual objects was marked with a red dot on its top surface. From trial to trial, the marked object was paired with a larger, smaller, or same-sized object. Subjects were instructed to always pick up the marked object on each trial. In both Experiment 1 and 2, half the subjects were tested in delayed grasping with a 5-sec delay between viewing the objects and initiating the grasp, and half in real-time grasping without a delay. Using the same display of virtual objects as in Experiment 2, subjects in Experiment 3 were requested to estimate the size of the marked object using their index finger and thumb (i.e., they showed us how big the object looked to them). After estimating the target object's size, they picked it up. All subjects gave their estimates either immediately or after a delay. Recording of hand movements revealed that when subjects in Experiments 1 and 2 picked up the target object in real time, their grip aperture in flight was not significantly affected whether the object was accompanied by a larger object or a smaller one. When subjects picked up the target object after a delay, however, their grip aperture in flight was larger when the target object was accompanied by a smaller object than when it was accompanied by a larger object. A similar size-contrast effect was also observed in Experiment 3 in which subjects gave manual estimates of the perceived size of the target object. This perceptual effect was observed both when the estimates were given immediately and when they were given after a 5-sec delay. These results suggest that normal (real-time) visuomotor control relies on absolute metrics, whereas delayed grasping utilizes the same relative metrics used by conscious perception. ■

INTRODUCTION

Vision provides us with a rich array of information about our surroundings—information that allows us to think about the world and guide our actions. Although it seems self-evident that our actions are directed by our conscious[1] perception of objects, recent evidence from a broad range of studies on neurological patients and normal observers suggests otherwise. On the basis of this work and complementary studies in the monkey, Goodale and Milner (1992) have proposed that the visual perception of objects is mediated by neural processes that are functionally and anatomically distinct from those mediating the visual control of actions directed at those objects. In particular, they have proposed that the dorsal stream of visual processing, which projects from primary visual cortex to the posterior parietal cortex, transforms visual information for the control of skilled motor actions; whereas the ventral stream of visual processing, which arises also from primary visual cortex but projects to inferotemporal cortex, transforms visual information for perceptual representation. Of course, vision for action and vision for perception work together in controlling our behavior as we live our complex lives. But they play separate but complementary roles in the production of adaptive behavior.

Vision for action and vision for perception differ both with respect to the metrics and frames of reference that each system uses and with respect to the time-scale over which each system operates. To be able to grasp and/or manipulate an object, for example, it is essential to 'compute' the absolute[2] size of the object and its orientation and position with respect to the observer. This information is critical to the formation of the anticipatory posture of the hand and fingers as we reach towards the object (Jeannerod, 1988). Moreover, the programming and control of such an action require that the metrical information about the location and disposition of the object be computed in egocentric frames of reference—in other words, in frames of reference that take into the position of the arm, hand, and fingers (Graziano & Gross, 1994; Soechting & Flanders, 1992). In addition, this computation must be done on the basis of the position of the object and the position and posture of the relevant effectors (e.g., hand) at the precise moment that the action is initiated. Observers and target objects rarely stay in a static relationship with one another and, as a consequence, the egocentric coordinates of a target object can often change dramatically from moment to moment. It makes sense, therefore, to compute the required coordinates for action immediately before the movements are initiated and it makes little sense to store these coordinates (or the resulting motor programs) for more than a few milliseconds before executing that action. Indeed, there is evidence that the motor program begins to change or decay almost immediately if it is not used—in less than 800 msec for saccades (Gnadt, Bracewell, & Andersen, 1991) and in less than 2 sec for manual aiming movements and grasping (Goodale, Jakobson, & Keillor, 1994; Elliot & Madalena, 1987). Thus, actions directed to remembered objects (objects that were present in the visual array, but are no longer there after a delay) look quite different from actions directed to objects that remain visible (Hu, Eagleson, & Goodale, 1999; Bridgeman, Peery, & Anand, 1997). In short, visual information about a goal object for an intended action reflects the absolute size of objects and their egocentric location with respect to the initial position of the relevant effector. Moreover, these values must be computed in 'real time'.

The situation is quite different for conscious perception, however. Vision for perception appears not to rely on changes in the absolute size of objects and their egocentric locations—a fact that explains why we have no difficulty watching television, a medium in which there are no absolute metrics at all. Instead of using absolute metrics and egocentric frames of reference, our perceptual system computes the size, location, shape, and orientation of an object primarily in relation to other objects and surfaces in the scene. This kind of visual information appears to be critical for object recognition and memory (McCarthy, 1993; Feigenbaum & Rolls, 1991). In the case of conscious perception, it is the identity and meaning of the object that we are concerned with—not its precise metrical size or its location with respect to the observer. In other words, the metric of visual perception is relative to other objects in the world. Encoding an object in a scene-based frame of reference (sometimes called an *allocentric* frame of reference, particularly with respect to the object's spatial location) permits a perceptual representation of the object that preserves the relations between the object parts and its surroundings without requiring precise information about the absolute size of the object or its exact position with respect to the observer. In other words, the metric of conscious perception is often relative, not absolute. Moreover, perception operates over a much longer time-scale than that used in the control of action. We can recognize objects we have seen minutes, hours, days—or even years before. The time-scale for visual perception is several orders of magnitude larger than the time-scale for the visual control of action in real time.

Several lines of evidence provide support for the idea that vision for action uses egocentric frames of reference whereas vision for perception uses allocentric frames of reference. Wong and Mack (1981) carried out an experiment in which subjects fixated a small target that was presented within a surrounding frame in an otherwise dark room. After a 500-msec blank period, the frame and target re-appeared but the frame was displaced a few degrees to the left or right. The target itself stayed at the same location as before. Nevertheless, subjects consciously perceived the target as having moved in a direction opposite to that of the actual displacement of the frame, instead of perceiving the frame as having changed position. This illusory perception was sustained even when, after the blanking period, the target was displaced in the same direction as the frame but by only one third of the distance. In this case, the perceived and actual changes of target position were in opposite directions. Yet, despite the presence of this strong illusory displacement of the target, subjects consistently directed their saccades to the true location of the target. Similar dissociations between perception and action have been observed in studies using aiming movements. Bridgeman, Kirch, & Sperling (1981), for example, found that even though a fixed visual target surrounded by a moving frame appeared to drift in a direction opposite to that of the frame, subjects persisted in pointing to the veridical location of the target. In short, conscious perception of the location of a visual stimulus is computed in allocentric frames of reference whereas visuomotor output to the same target is computed in egocentric frames of reference.

There is evidence, however, that conscious perception in allocentric frames of reference *can* affect motor performance when the actions are not initiated immediately but only after a delay. For example, in the Wong and Mack (1981) experiment described earlier, saccades made to a remembered visual target were made to the consciously perceived target position rather than to the true location where it had appeared. In other words, the trajectory of the memory-driven saccade was determined by the location of the target with respect to the frame, whereas the trajectory of the target-driven saccade was determined by the location of the target in oculocentric coordinates, without the influence of the frame. Recently, Bridgeman et al. (1997) examined this interaction using an induced Roelofs effect, in which the position of a target inside an off-center frame appears to be biased opposite the direction of the frame. The effect always influences the conscious perception of the target's location immediately after viewing the target and frame. The same effect, however, appeared in manual pointing—but only when the movement was executed after a 4-sec delay between viewing the target and initiating the movement. In real time, of course, the pointing movement was directed at the target. In a similar vein, Creem and Proffitt (1998) studied verbal judgments and motor adjustments of geographical slant perception. When subjects viewed a hill, their verbal judgements of the incline of the hill were greatly overestimated compared to their motor adjustments. Yet after a delay, when the hill was no longer visible, their motor adjustments were similar to their exaggerated verbal judgements. Creem and Proffitt argued that actions after a delay are guided by an explicit stored representation of visual information. Thus, if motor actions are driven by stored representations that are derived from conscious perception of object location, then they will use the same allocentric frames of reference as the original perception.

Just as the frames of reference mediating the conscious perception of object location differ from those underlying the visuospatial control of action, so do the metrics underlying the conscious perception of object size. In our daily life, we rarely make judgements of the absolute size of an object, but instead make judgements based on the relative size of objects in the visual scene. These relative judgements can nevertheless be quite subtle and precise. There is a long history of work with pictorial illusions showing that our conscious perception of object can be fooled by visual displays in which targets are surrounded by similar visual stimuli with much smaller or larger size than the targets. A prototypical size-contrast illusion is the Ebbinghaus Illusion (or Titchener Circles Illusion): two target circles of equal size, each surrounded by a circular array of either smaller or larger circles, are presented side by side. Subjects typically report that the target circle surrounded by the array of smaller circles appears larger than the one surrounded by the array of larger circles, presumably because of the difference in the contrast in size between the target circles and the surrounding circles. In another version of the illusion, the target circles can be made to appear identical in size by increasing the actual size of the target circle surrounded by the larger circles. Although our perceptual judgements are clearly affected by these manipulations of the stimulus array, there is good reason to believe that the calibration of size-dependent motor outputs, such as grip aperture during grasping, would not be. When we reach out to pick up an object, we must compute its real size if we are to pick it up efficiently. It is not enough to know that it is larger or smaller than surrounding objects. One might expect, therefore, that grip scaling would be insensitive to size-contrast illusions. Such a result was recently found in two experiments that used a three-dimensional version of the Ebbinghaus illusion in which two thin 'poker-chip' disks were arranged as pairs on a standard annular circle display (Haffenden & Goodale, 1998a, b; Aglioti, DeSouza, & Goodale, 1995). Trials in which the two disks appeared perceptually identical but were physically different in size were randomly alternated with trials in which the disks appeared perceptually different but were physically identical. Even though subjects showed robust perceptual illusions—even in a matching task in which they opened their index finger and thumb to match the perceived diameter of one of the disks—their grip aperture was correlated with the real size of the disk when they reached out to pick it up. The dissociation between perceptual judgements and the calibration of grasping is not limited to the Ebbinghaus Illusion. The vertical–horizontal illusion is one in which a vertical line that bisects a horizontal line appears longer than the horizontal line even though both lines are in fact the same length. Vishton and Cutting (1995) demonstrated that even though subjects show the usual perceptual bias in their judgements of line length, they did not show a bias when they attempted to reach out and 'grasp' the lines. The relative insensitivity of reaching and grasping to pictorial illusions has also been demonstrated for the Müller–Lyer illusion (Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996) and the Ponzo illusion (Brenner & Smeets, 1996). Most recently, Creem, Wraga, and Proffitt (1998) demonstrated a similar dissociation between verbal judgements and locomotor accuracy using a large-scale Müller–Lyer illusion.

But skilled motor actions are not entirely immune to the influences of conscious perception. Thus, as described earlier, stored visual information about an object's location, which was acquired through conscious perception of its position in allocentric frames of reference, did influence actions when those actions were not initiated immediately after seeing the target but rather after a short delay. However, what about grasping? Will the scaling of grip aperture also move into relative metrics if a delay is interposed between viewing the goal object and initiating the grasp? Certainly, there is evidence that the kinematics of grasping movements are affected by such a delay (Hu et al., 1999; Goodale et al., 1994). The question remains, however, would grip scaling after a delay show evidence of relative-size judgments? We attempted to answer these questions by performing a series of experiments in which we compared grasping movements directed at objects in real time with grasping initiated to the same objects but after a 5-sec delay. In addition, we examined the metrics used by subjects when they were asked to estimate the size of these objects.

EXPERIMENT 1

In the first experiment, subjects were required to make an explicit comparison between the sizes of two objects before picking up one of them. In one condition, subjects were asked to pick up the larger one of two objects; in the other condition, they were asked to pick up the smaller one. In fact, as Figure 1 shows, in both conditions they were picking up the same target objects, each of which had been paired with a corresponding smaller or larger object.

As illustrated in Figure 2, subjects were presented with two objects in a virtual display in which the 3-D virtual image of each object was located below a mirror. A robot arm was used to place a real object in a location beneath the mirror corresponding to the position of the virtual image of the computer-rendered target object. This arrangement ensured that the subject experienced veridical haptic feedback that corresponded to the visual information from the virtual image. Using such a virtual display gave us complete control over the visual appearance of the target objects and the time-period during which they were visible. One group of subjects was required to pick up the target object (the larger or the smaller one) as soon as the two objects came into view. A second group of subjects was required to pick up the target object after a 5-sec delay during which the two objects were no longer in view. In both cases, the actual grasping movement was made in visual open loop and neither the objects nor the moving hand was visible during the hand movement.

We anticipated that those subjects who grasped the target object immediately in 'real time' would not be influenced by the difference in size between the target object and its companion. In other words, we predicted that maximum grip aperture, a kinematic parameter that has been shown to be highly correlated with object size (Jakobson & Goodale, 1991; Jeannerod, 1988), would not be influenced by this relative-size information. The reason for this prediction is clear. Although the subjects' choice of target object (the smaller one or the larger one) would be mediated by the conscious perception of the visual array, the actual grasping movement itself would be programmed on the basis of the actual size of the target object—not its relative size with respect to the other object. In other words, we expected that the scaling of maximum grip aperture would reflect the absolute size of the target object rather than its relative size with respect to the smaller or larger object with which it had been paired. In the case of the delayed grasping movements, however, we expected that the maximum grip aperture would be influenced by the relative difference in size between the two objects. In this case, any real-time visuomotor program that might have been formed would have decayed over the 5-sec delay period, and the grasp instead would have to be programmed on the basis of stored information about object size. We expected that this stored information would have been formed on the basis of earlier perceptual processing of the visual array, and thus would have incorporated the relative size of the two objects. In other words, we expected that after a delay subjects would open their fingers wider for a target object paired with a smaller object than they would for the same object when it was paired with a larger object.

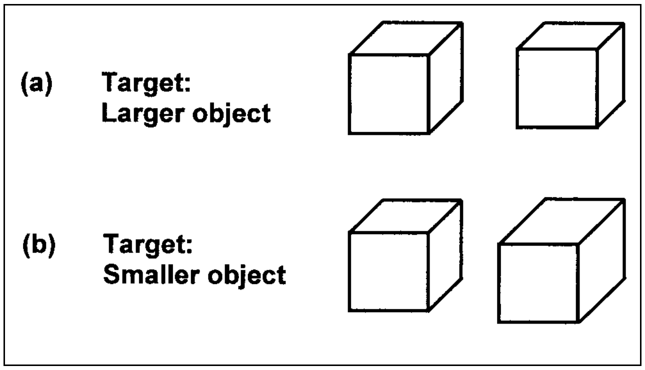

Figure 1. The 3-D virtual objects used in Experiment 1. Subjects were instructed to grasp the larger object in display (a) and the smaller object in display (b). In fact, the target objects in (a) and (b) were identical in size.

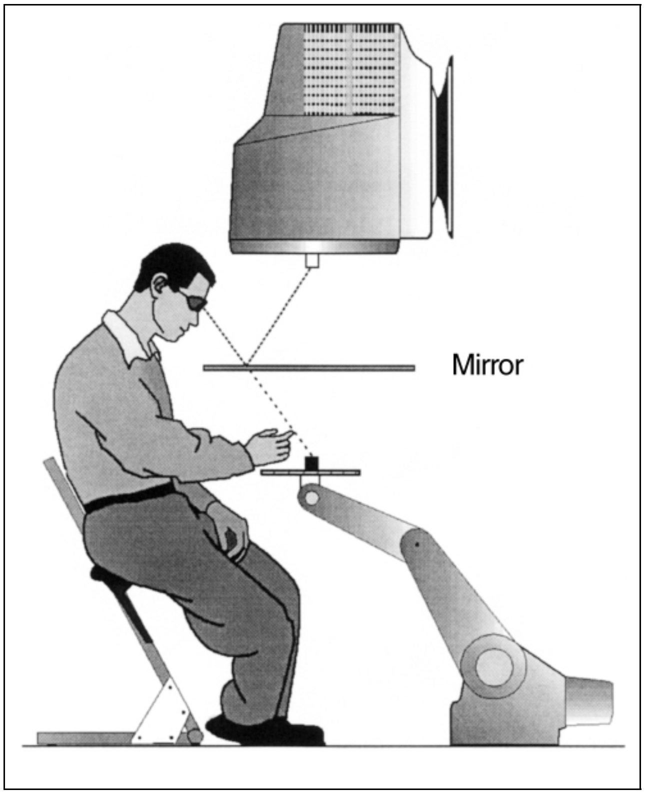

Figure 2. Simple illustration of the experimental setup showing the relationship between the virtual and real objects.

Results and Discussion

As predicted, the scaling of the grasping movement produced by subjects who reached out immediately to

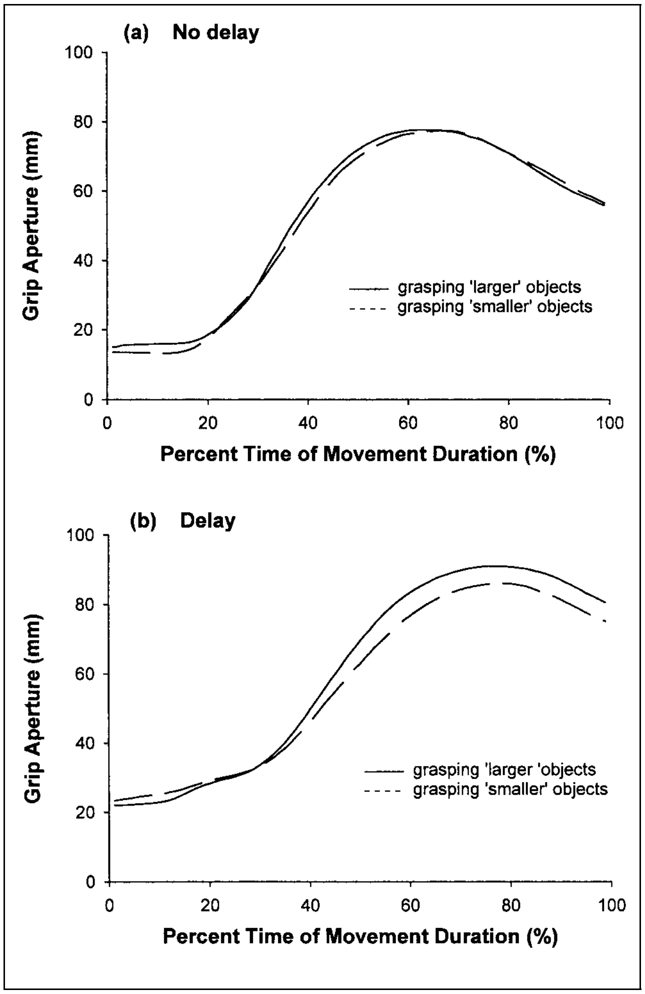

Figure 3. Representative traces of grip aperture in Experiment 1 for grasps directed at the smaller and the larger of two objects. In fact, the target object was the same size in both cases; it was simply accompanied by a larger object in one case and a smaller object in the other. (a) No delay, (b) delay. (Movements were normalized for movement duration).

pick up the target object was not affected by the presence of another larger or smaller object—even though the subjects had been asked to make an explicit comparison between the size of the two objects in the array. As Figure 3a illustrates, maximum grip aperture was the same for a given target object whether that object was accompanied by a larger object or a smaller one. In fact, as the group data summarized in Figure 4 indicate, there was no significant difference in grip aperture between the two conditions [65.14 vs. 64.38 mm for 'larger' vs. 'smaller'; $F(1, 12) = 0.535$, n.s.]. It is also important to point out that subjects were still scaling for the real width of the object as shown in Figure 5. Thus, the larger the target object was, the wider they opened their hand.

The picture was quite different for the subjects who reached out to pick up the object after a 5-sec delay. As Figure 3b illustrates, their maximum grip aperture was larger when the target object was accompanied by a smaller object than when it was accompanied by a larger object. Overall, as the graph in Figure 4 shows, subjects opened their fingers significantly wider when they were required to pick up the larger of the two objects than when they were required to pick up the smaller one [68.40 vs. 66.61 mm for 'larger' vs. 'smaller'; $F(1, 12) = 6.060, p < .05$], even though the target object was in fact the same one in both conditions. Of course, as shown in Figure 5, superimposed on this relative-size effect was the effect of the real width of the object: the wider the target object, the wider they opened their hand.

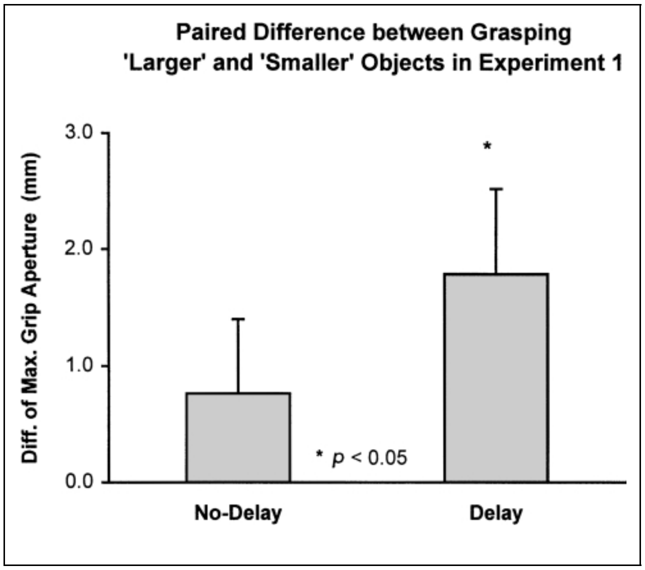

Figure 4. Mean values of the difference in maximum grip aperture between grasping the 'larger' and 'smaller' objects in Experiment 1. In fact, the target object was the same size in both cases; it was simply accompanied by a larger object in one case and a smaller object in the other (error bars represent the standard error of the mean difference).

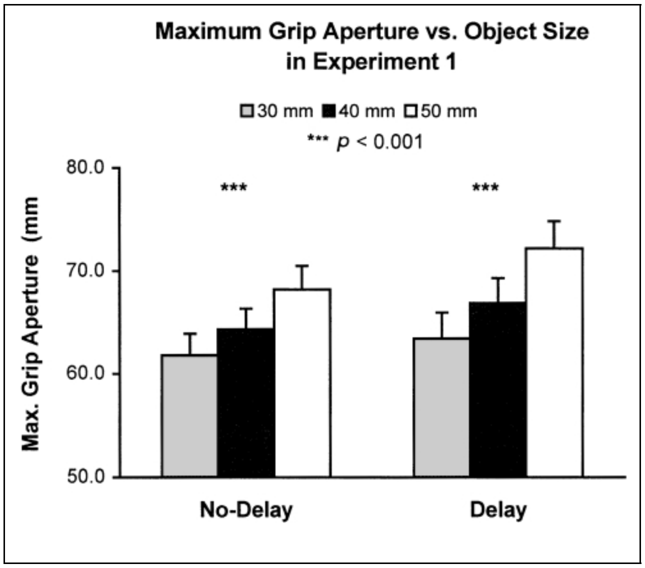

Figure 5. Mean values of maximum grip aperture as a function of real object size in Experiment 1 (error bars represent the standard error).

The fact that grip scaling becomes sensitive to the relative size of an object after a delay reflects a shift in motor programming from absolute to relative metrics. It appears that even a delay as short as 5 sec forces the subject to rely, not on the real-time visuomotor transformations that would normally be used to program an object-directed grasping movement, but on stored perceptual memories of the target object and the array in which it was embedded. Because conscious perception uses relative metrics, as reviewed in the Introduction, the relative size of the two objects in the array stored in memory can influence the scaling of the grasp when the object is no longer in view.

EXPERIMENT 2

In Experiment 1, subjects were tested in two blocks of trials: one block in which they were verbally instructed to grasp the larger of two objects and another block in which they were instructed to grasp the smaller of two objects. The verbal instructions made it quite explicit that the subjects were to make a comparison between the size of the two objects. It is possible, of course, that these instructions could have primed the subjects to store the relative size of the two objects in memory. Alternatively, the very language, ‘larger’ or ‘smaller’, could have led to the use of a larger or smaller grasp when subjects were working ‘off-line’ after a delay, and were recalling what it was they had seen 5 sec earlier.

To eliminate these possibilities, we carried out a second experiment in which subjects were not required to make a size discrimination. In this experiment, one of the objects was marked with a red dot and subjects were simply instructed to pick up the marked object. On randomized trials, the object with the dot was paired with a smaller object, a larger object, or an object of the same size (see Figure 6). One group of subjects was required to pick up the marked object immediately; the other group, after a 5-sec delay. Although there was no explicit instruction to pick up the larger or smaller object, we still expected that subjects who initiated their grasp after a delay would continue to show the same effect we observed in Experiment 1: namely, that their hand would open wider in flight when the marked object was paired with a smaller object than when the same object was paired with a larger object. Again we expected that the subjects who grasped the marked object immediately would not be affected by the presence of a larger or smaller object.

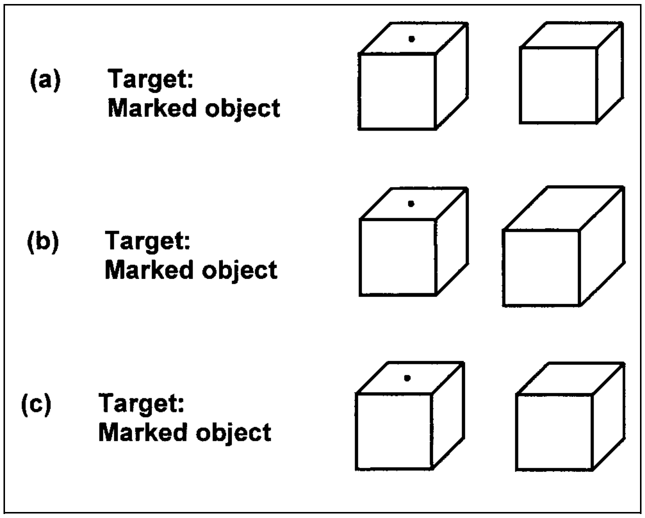

Figure 6. The 3-D virtual objects used in Experiments 2 and 3. The target object was marked with a red dot. (a) The marked object was the larger object; (b) the marked object was the smaller object. (c) The marked object was the same size as the other. The marked objects in (a), (b) and (c) were actually identical in size.

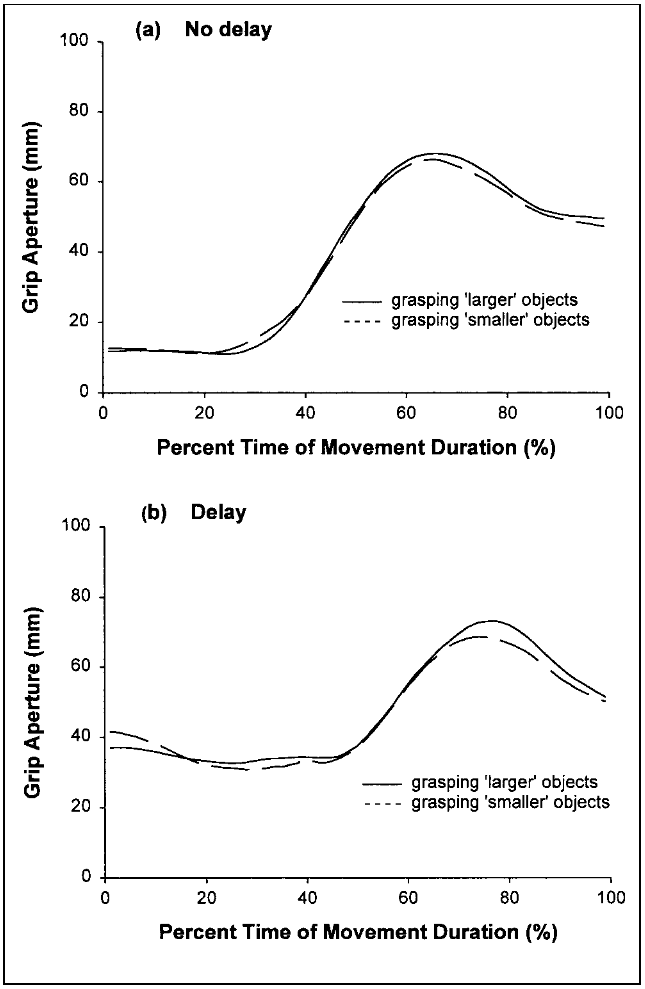

Figure 7. Representative traces of grip aperture in Experiment 2 for grasps directed at the smaller and the larger of two objects. In fact, the target object was the same size in both cases; it was simply accompanied by a larger object in one case and a smaller object in the other. (a) No delay, (b) delay (movements were normalized for movement duration).

Results and Discussion

Our predictions were borne out by the data in Experiment 2. Subjects who picked up the marked object in 'real time' were not affected by the presence of another larger or smaller object. As Figure 7a illustrates, maximum grip aperture was the same for a given target object whether that object was larger or the smaller of the two objects in the array. Moreover, as the group data summarized in Figure 8 indicate, there was no significant difference in grip aperture between the two kinds of trials [67.8 vs. 67.7 mm for larger vs. smaller, $F(1, 13) = 0.031$, n.s.]. Just as was the case in Experiment 1, however, the subjects' grip aperture was sensitive to the actual width of the object (see Figure 9).

As expected, the picture was quite different for the subjects who reached out to pick up the marked object after a 5-sec delay. As can be seen in the individual data illustrated in Figure 7b as well as in the group data summarized in Figure 8, subjects opened their fingers significantly wider when the marked object was the larger of the two objects than when it was the smaller one [67.3 vs. 65.9 mm for larger vs. smaller; $F(1,13) = 7.175$, $p < .05$]—even though the marked object was the same size in both kinds of trials. Again, as Figure 9 illustrates, superimposed on this relative-size effect was the effect of the real width of the object: the wider the target object, the wider the subjects opened their hand.

The results of Experiment 2 confirm those already seen in Experiment 1. In addition, they show that the shift from an absolute to a relative metric for grip scaling is not dependent on some sort of instructional or verbal mediation. Instead, it appears that stored perceptual memories of the objects that are used to program a delayed response are indeed organized in relative metrics.

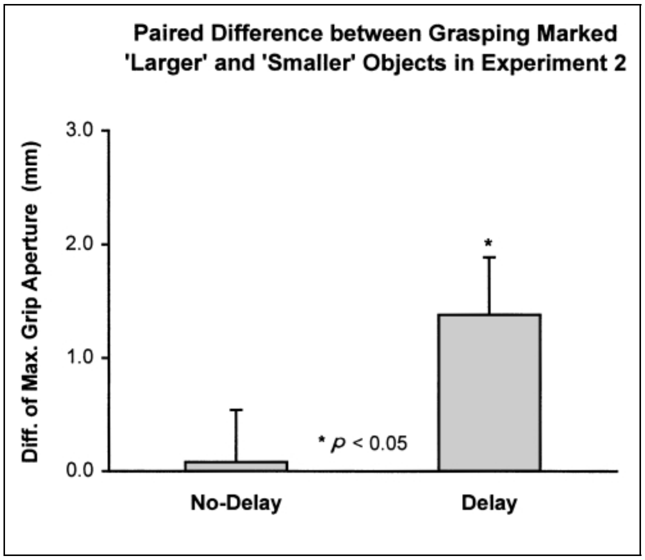

Figure 8. Mean values of the difference in maximum grip aperture in Experiment 2 between grasping the marked objects accompanied by a larger object and the marked objects accompanied by a smaller object (error bars represent the standard error of the mean difference).

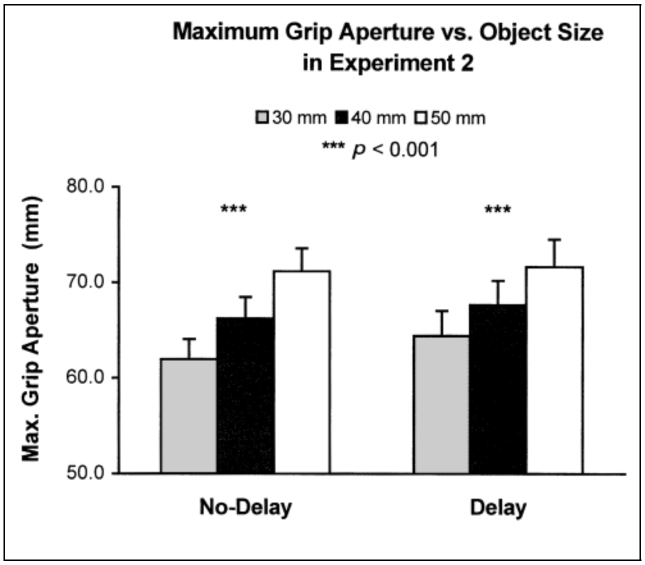

Figure 9. Mean values of maximum grip aperture as a function of object size in Experiment 2 (error bars represent the standard error).

EXPERIMENT 3

In both Experiments 1 and 2, subjects were tested for the scaling of grasping movements. When subjects picked up a target object immediately, it did not matter which object it was paired with: the grasp was scaled to the real size of the target object and was not affected by the presence of the other object. When subjects picked up the target object after a 5-sec delay, however, a significantly larger grip aperture was observed when the target object was paired with a smaller object than when the same target object was paired with a larger object. These findings suggest that motor actions in real time rely on absolute metrics whereas delayed grasping reflects the influence of the relative visual information. Since conscious perception, as argued in the Introduction, processes visual information in relative metrics, it is inevitable to ask whether conscious judgements of size would demonstrate the same pattern as observed in delayed grasping.

To examine this hypothesis, we conducted a third experiment in which subjects were requested to make conscious perceptual estimations of the size of a target object. In this experiment, the visual array was identical to that used in Experiment 2; that is, one of the virtual objects was marked with a red dot. Subjects were instructed to estimate the width of the marked object by opening their thumb and index finger a matching amount while keeping their hand on the start platform. Once they had given their manual estimate, they were to reach out

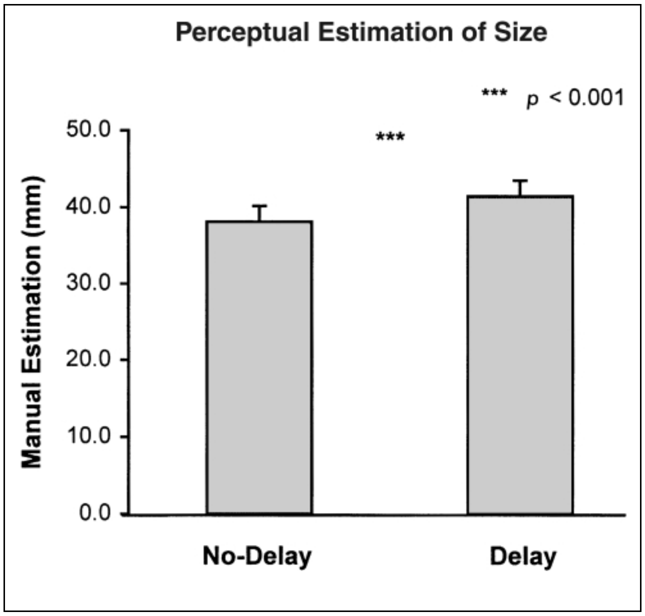

Figure 10. Mean values of perceptual estimates of object size under no-delay and delay conditions in Experiment 3 (error bars represent the standard error).

and pick up the object. In this experiment, subjects were tested in both a no-delay and a 5-sec delay condition.

Results and Discussion

As Figure 10 shows, overall, subjects estimated the size of the marked object to be significantly larger in the delay condition than in the no-delay condition [41.5 vs. 38.1 mm for delay vs. no-delay; $F(1, 9) = 22.598$, $p < .001$]. It is not clear why the delay produced this tendency to overestimate the size of the object. There is evidence, however, that small objects in the scene are typically remembered as larger than they really were (for review, see Intraub, 1997). Nevertheless, the size estimates of the marked object were influenced by the other object in scene, no matter whether subjects gave the estimates immediately or after a 5-sec delay. As Figure 11 illustrates, in both delay and no-delay conditions, subjects opened their fingers significantly wider when the marked object was the larger of the two objects than when it was the smaller one [Delay condition: 42.7 vs. 40.2 mm for 'larger' vs. 'smaller'; $F(1, 9) = 18.167$, $p < .005$; No-delay condition: 39.2 vs. 37.1 mm for 'larger' vs. 'smaller'; $F(1, 9) = 37.034$, $p < .001$]—even though the marked object was the same size in both kinds of trials. Again, superimposed on this relative-size effect was the effect of the real width of the object: in all conditions, the wider the target object, the wider the subjects opened their fingers in manual estimations (see Figure 12). The results of Experiment 3 show that even in real time our conscious perception is influenced by the relative size of objects in the visual scene. Moreover the order of magnitude of the difference in estimation that we observed in this experiment is similar to that seen in grip scaling after a delay.

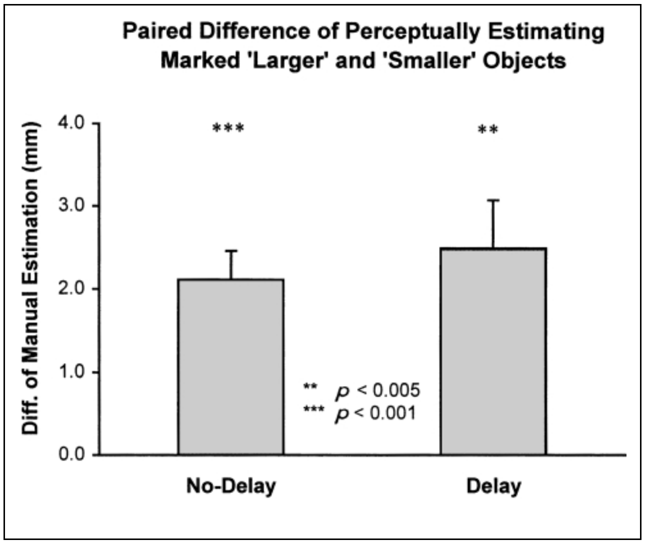

Figure 11. Mean values of the difference in perceptual estimates in Experiment 3 between estimating the marked objects accompanied by a larger object and the marked objects accompanied by a smaller object (error bars represent the standard error of the mean difference).

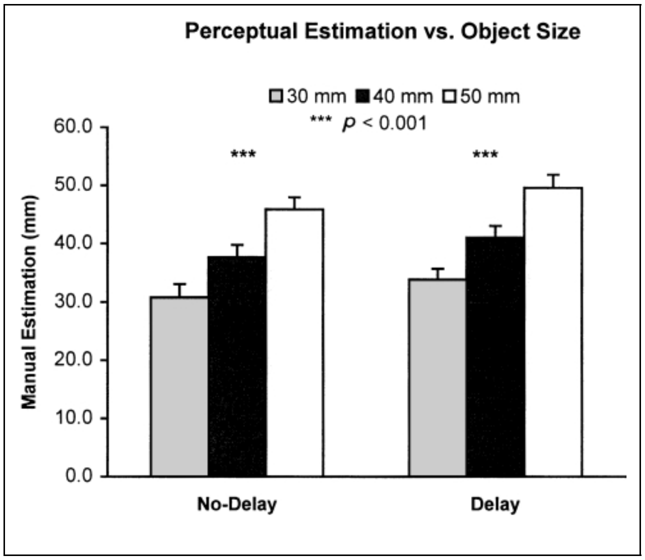

Figure 12. Mean values of perceptual estimates as a function of object size in Experiment 3 (error bars represent the standard error).

GENERAL DISCUSSION

Taken together, the results of the three experiments described above provide convincing evidence for a dissociation between the metrics used by the visual mechanisms mediating perception and those used by the visual mechanisms mediating the control of action. Even though perceptual judgments of an object's size are influenced by the presence of other objects in the visual array—resulting in a size-contrast effect—the scaling of real-time grasping movements directed at those objects reflects the absolute, not the relative, size of the target. These findings are similar to those of earlier studies showing that pictorial illusions that fool our perception of object size do not affect significantly the real-time scaling of object-directed actions (Jackson & Shaw, 2000; Haffenden & Goodale, 1998a, b; Brenner & Smeets, 1996; Gentilucci et al., 1996; Aglioti et al., 1995; Vishton & Cutting, 1995). It is important to note, however, that the stimulus array that we used in the present experiments was not so much a contrived illusion, as it was an example of a situation in our daily life when we are confronted with two or more possible goal objects. Yet, even in the two-object display, we found a clear difference between the scaling of grasping movements made in real time and the manual estimates; the former (vision for action) was based on absolute size while the latter (vision for perception) was based on relative size.

Because the haptic feedback in the real-time grasping task was always experienced right after subjects had glimpsed the target object, it could be argued that this immediate feedback provided a better calibration of the subjects' hand opening than the more delayed feedback they experienced in the other tasks, including the delayed grasping task and the two perceptual tasks. While it is certainly true that haptic feedback is critical for tuning the grasp, as shown in experiments in which the correlation between visual information and haptic feedback has been deliberately manipulated (e.g., Gentilucci, Daprati, Toni, Chieffi, & Saetti, 1995), what is remarkable is that the resulting recalibration of grip scaling has no effect on perceptual judgements of object size—even when such judgements are made manually. Additional evidence that immediate haptic feedback has no effect on perceptual judgments comes from earlier experiments on pictorial illusions that were carried out in our laboratory (Haffenden & Goodale, 1998a, b; Aglioti et al., 1995). In these experiments, subjects picked up the target objects over and over again—and thus received veridical haptic feedback for many trials. Nevertheless, this feedback had absolutely no effect on their perception of object size, and they continued to choose the target for their grasp on the basis of its apparent not its real size. Finally, there is some evidence that the recalibration of perceptual judgements of object size can occur without affecting the scaling of grasping movements directed at those same objects (Haffenden & Goodale, 1998a, b). In short, it appears that the visual control of action and visual perception are mediated by rather different processes—and that haptic feedback plays an essential role in the scaling of grasp but not in the 'scaling' of perception.

Why should there be these differences between vision for action and vision for perception? By using relative rather than absolute metrics, the perception can construct a rich and detailed representation of the different objects in a scene and their relations with one another, without having to compute the absolute size of every object in the array and its location with respect to the observer. A goal-directed action, however, must be programmed with respect to the absolute size of the target and its location in egocentric space to be successful. To carry out the required computations in these two different domains, separate visual pathways have evolved for the visual perception on the one hand and the visual control of actions on the other (Milner & Goodale, 1995).

Although the visual control of actions depends largely on real world metrics that are focussed almost entirely on the target of the action, the results of the present study show that the scaling of actions made after a delay can be influenced by the presence of other objects in the visual array. The scaling of grasping movements made after a delay, like perceptual judgements, are based on the relative, not the absolute, size of the target object. This suggests that the motor program for these delayed actions uses stored perceptual information—and in doing so incorporates the relative metrics of perception into the programming of grip aperture.

This demonstration of a shift from on-line visuomotor metrics to stored perceptual metrics may help explain some otherwise puzzling observations in neurological patients. Consider, for example, the patient DF, a young woman who developed visual form agnosia as a result of anoxia from carbon monoxide poisoning (Milner et al., 1991). Even though DF is unable to indicate the size, shape, and orientation of an object, either verbally or manually, she shows normal preshaping and rotation of her hand when reaching out to grasp it (Goodale, Milner, Jakobson, & Carey, 1991). According to Goodale and Milner (1992), the cortical visual pathways mediating visual perception in DF are compromised while the cortical visual pathways mediating the visual control of action are relatively intact. Nevertheless, DF's accurate scaling of grasping movements was lost totally when she was required to initiate her hand movements following a 2-sec delay after viewing the object (Goodale et al., 1994). Now there was no correlation at all between the size of the object and the aperture of her grasp in flight. Presumably, DF—unlike the normal subjects in the present experiment—could not use a visual memory of the objects that were presented earlier to program her delayed grasping movements, because DF did not perceive those objects in the first place.

A converse example is the patient AT, who suffered damage to her cortical visuomotor systems and is unable to scale her grasp for unfamiliar 'neutral' targets, whose size and shape have to be computed directly on-line. Surprisingly, when presented with familiar objects of the same size, AT showed much better scaling (Jeannerod, Decety, & Michel, 1994), probably because she was able to invoke stored perceptual memories of those objects and use those memories to program her actions. It would be interesting in this context to see what would happen if AT were asked to delay her grasping to neutral objects. One might expect to see an improvement in performance with delay since now she would be forced to rely on perceptual memories of what she had just seen rather than on the more 'automatic' visuomotor computations that are clearly not working properly.

It is interesting to speculate about the neural substrates that might mediate the 'perceptual' control of motor actions. One area that may play an important role in the integration and transformation of conscious perception and motor actions is the prefrontal cortex, which has long been considered as an area where diverse signals are integrated to serve higher-order cognitive functions. The ventrolateral and dorsolateral prefrontal regions have not only rich connections with the ventral and dorsal visual pathways, respectively (Baizer, Ungerleider, & Desimone, 1991; Cavada & Goldman-Rakic, 1989), but are also reciprocally connected with each other and other cortical areas that receive input from both regions (Watanabe-Sawagushi, Kubota, & Arikuni, 1991; Barbas & Pandya, 1989). In delay tasks, in which visual information must be remembered for several seconds, neurons in the parts of the lateral prefrontal region are highly active during the delay (Rao, Rainer, & Miller, 1998; Funahashi, Chafee, & Goldman-Rakic, 1993). It is reasonable to speculate that such neurons could be part of a circuit that transforms stored perceptual information about an object into the required parameters for the production of motor actions. In this regard, it would be interesting to test whether the information about object location and structure that is stored in these neurons is coded in relative metrics (and allocentric frames of reference) or in absolute metrics (and egocentric frames of reference). If indeed these neurons are coding information about objects based on perceptual input (from the ventral stream), then we would predict that this information would be coded in relative metrics.

The idea that conscious perception influences motor actions does not contradict the claim made by Goodale and Milner (1992) that the visual mechanisms underlying conscious perception are distinct from those underlying the control of skilled actions. There are many situations where perception can influence action. When we reach out to pick up a fork, for example, the posture of our hand will vary depending on whether we intend to put the fork away or whether we wish to use it to eat a meal (for a discussion of this issue, see Milner & Goodale, 1995). In other words, our hand posture anticipates the purpose of our action and the function of a target object. But even here, semantic information about the object must be integrated with accurate metrical information about its absolute size and its location and orientation with respect to our hand. Of course, we can also rely to some degree on our memory to control even the metrical scaling of our grasp and its trajectory. But here, as the present study indicates, we must rely entirely on our perceptual memories of the object.

In summary, our study has shown that the same relative visual information, as conscious perception retains, influences the scaling of skilled grasping movements after a 5-sec delay between viewing target objects and initiating a grasp—even if no such influence occurs in the scaling of real-time grasping.

METHOD

The experiments were carried out at the University of Western Ontario in compliance with the Social Sciences and Humanities Research Council (Canada) Guidelines (1981).

Experiment 1

Subjects

The 26 subjects (mean age = 22.8 years) tested in this experiment were strongly right-handed, as determined by a modified version of the Edinburgh handedness inventory (Oldfield, 1971). All subjects had normal or corrected-to-normal vision, with a stereoacuity of at least 40″ of arc as determined by the Randot Stereotest (Stereo Optical, Chicago, USA). These subjects were students at the University of Western Ontario and were paid for their participation.

Apparatus

Figure 2 shows a simplified representation of the experimental set-up. A monitor was connected to a SGI computer and was used to present two virtual objects on each trial. These virtual objects were reflected through a first-surface mirror, which was placed 35 cm below the monitor's display screen and could be viewed through 3-D stereo goggles (CrystalEyes). The distance between the near surfaces of the two virtual objects was 2 cm and the midpoint between them was positioned at the subject's midline. The far edges of both virtual objects were aligned at 20 cm from a start button (described below). A real object identical in size to one of the virtual objects was placed with a robot arm (251A, CRS Robotics, Burlington, Canada) at the corresponding location below the first-surface mirror. When subjects reached out to pick up the virtual object, they ended up grasping the real object under the mirror. For each subject, the distance between his/her two eyes was measured to calibrate the display of the virtual objects. In order to restrict the subject's head movements, the stereo goggles were fixed on a chin-rest, which is not shown in Figure 2 for simplicity. The start button was located 80 cm above the floor at the subject's midline.

Three infrared diodes (IREDs) were attached to the subject's index finger, thumb, and wrist, respectively. A conventional WATSMART system (Northern Digital, Waterloo, Canada) was used to record the spatial position of each IRED at sampling rate of 100 Hz. The accuracy of this system and data analysis techniques have been documented elsewhere (Hu et al., 1999).

As Figure 13 shows, target objects were three blocks measuring 4 × 4 × 3, 4 × 4 × 4, and 4 × 4 × 5 cm, respectively. Notice that only the dimension of object width was varied. In each trial, one virtual object was always larger than the other one. The difference in width between the two virtual objects was 0.5 cm. As shown in Figure 1, in one condition, a target object was paired with a smaller non-target object and the subject was instructed to pick up the larger one. In another condition, the same target object was paired with a larger non-target object, and the subject was instructed to pick up the smaller one. This meant that in both conditions the subject actually picked up the same target object.

Procedure

Subjects were divided into two groups: one group was tested in 'real-time'; the other group with a delay. For the subjects tested in real-time, subjects were instructed to reach out and pick up the target object as soon as the virtual objects were presented. When their fingers left the start button, the virtual object display disappeared. The subjects, therefore, executed the entire movement without seeing their hand or the target object. Data collection began when virtual objects were presented and stopped when the target object was picked up. For the subjects tested with a delay, there was a 5-sec delay following a 500-msec viewing period. During the delay period, in which subjects could see neither their hand nor the target objects, they were required to keep their hand on the start button. An auditory signal at the end of the delay period signaled to the subjects that they should initiate their grasping movement. Data collection began when the auditory signal was presented and stopped when the target object was picked up.

Both groups of subjects were tested in two different blocks of trials. In one block of trials, subjects were verbally instructed to pick up the larger of the two objects. In another block, they were requested to pick up the smaller of the two objects. The order of the blocks of trials was counterbalanced across subjects. Subjects were instructed to bring the tips of their index finger and thumb together and to depress the starting button before initiating a trial. Subjects were instructed to pick up the target object across its width (see Figure 13).

In each block of trials, the three target objects were each presented randomly four times on the left and four times on the right of midline for a total of 24 trials. Trials in which the subject dropped an object were repeated at the end of that block of trials.

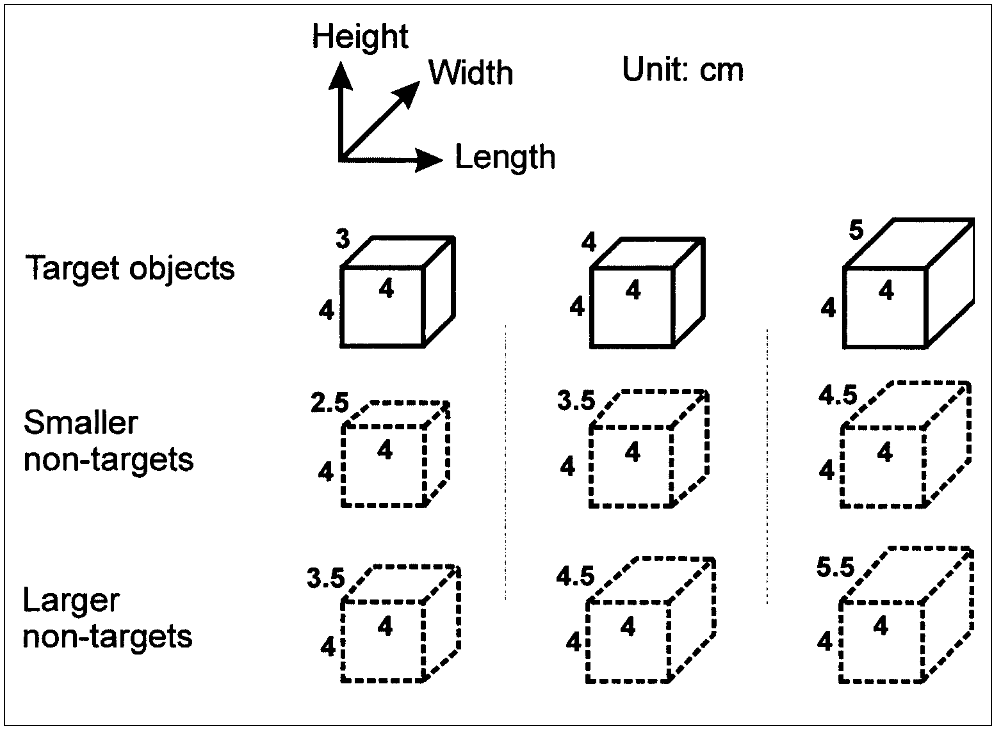

Figure 13. Illustration of target objects.

Dependent Measures

The following kinematic parameters were computed from the stored 3-D position for each IRED: movement duration and maximum grip aperture. Movement duration was calculated by subtracting the onset time from the time at which the target object was picked up. (Onset time was measured from the moment the resultant velocity of the wrist IRED exceeded a value of 5.0 cm/s over 10 consecutive sampling frames.) Maximum grip aperture was the maximum resultant distance that was achieved between the index finger and thumb as the subject reached out to grasp the object.

In each condition, means of each kinematic parameter were calculated from the eight replications of grasping movements made to each of the target objects. Only trials that had complete data available for all kinematic parameters were included in the analysis. Less than 3% of the trials were eliminated using this criterion and each mean was based on a minimum of three trials.

Experiment 2

Subjects

The 28 subjects (mean age = 21.5 years) tested in this experiment were strongly right-handed, as determined by a modified version of the Edinburgh handedness inventory (Oldfield, 1971). All subjects had been tested for vision and stereoacuity in the same procedure as described in Experiment 1. As well, all subjects were students at the University of Western Ontario and were paid for their participation.

Apparatus

As Figure 13 shows, target objects were three blocks in size of 4 × 4 × 3, 4 × 4 × 4, and 4 × 4 × 5 cm, respectively. The apparatus was identical to those in Experiment 1 except that each target object for grasping had been marked in the middle of its top surface with a red dot in a diameter of 6 mm (see Figure 6).

Procedure

Subjects were also divided into two groups as in Experiment 1. One group was tested in the real-time grasping; and the other group was tested in the delayed grasping. The timing of the display and the signals to initiate the grasping movements were identical to those used in Experiment 1.

In contrast to Experiment 1, subjects were tested in only one block of 72 trials in which they were simply instructed to pick up the marked object on each trial. The marked object was paired with either a larger, smaller or identical non-target object, and was presented on the left or right in random order. The criteria for processing data were same as in Experiment 1.

Dependent Measures

The dependent measures were identical to those in Experiment 1.

Experiment 3

Subjects

The 10 subjects (mean age = 22.0 years) tested in this experiment were strongly right-handed, as determined by a modified version of the Edinburgh handedness inventory (Oldfield, 1971). All subjects had been tested for vision and stereoacuity in the same procedure as described in Subjects of the Experiment 1. As well, all subjects were students at the University of Western Ontario and were paid for their participation.

Apparatus

Same as in Experiment 2.

Procedure

In contrast to Experiment 1 and 2, subjects in this experiment were asked to estimate the width of the target object by opening their index finger and thumb a matching amount. The target object was marked with a red dot just as it had been in Experiment 2 and was paired with either a larger, smaller or identical viewing object (see Figure 6). In one block of trials, subjects estimated the width of the target object as soon as the display was turned on. In another block of trials, they estimated its width after a 5-sec delay. The viewing time for the delay trials was identical to that used in Experiment 2; and the viewing time for the no-delay trials was comparable to that used in Experiment 2. The recording of the opening between the finger and thumb began when the subject's fingers left the start button and lasted for 2.5 sec. Finally, an auditory signal indicated that the subject should reach out and pick up the marked object using their index finger and thumb.

Dependent Measures

The dependent measure was the aperture (resultant distance) between the IREDs on the index finger and thumb when subjects estimated the width of the marked object. The aperture was measured when no changes had occurred for at least 10 consecutive frames.

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Notes

1. The term 'conscious' is used here to refer to perceptual phenomenology—the notion that we experience a visual world beyond our bodies. For a more complete discussion of this issue, see Milner and Goodale (1995).

2. The term 'absolute' is used here to refer to the actual size of an object. An object's absolute size, unlike its relative size, does not vary with respect to other objects in the scene.

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