The Effect of Pictorial Illusion on Prehension and Perception

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Abstract

■ The present study examined the effect of a size-contrast illusion (Ebbinghaus or Titchener Circles Illusion) on visual perception and the visual control of grasping movements. Seventeen right-handed participants picked up and, on other trials, estimated the size of "poker-chip" disks, which functioned as the target circles in a three-dimensional version of the illusion. In the estimation condition, subjects indicated how big they thought the target was by separating their thumb and forefinger to match the target's size. After initial viewing, no visual feedback from the hand or the target was available. Scaling of grip aperture was found to be strongly correlated with the physical size of the disks, while manual estimations of disk size were biased in the direction of the illusion. Evidently, grip aperture is calibrated to the true size of an object, even when perception of object size is distorted by a pictorial illusion, a result that is consistent with recent suggestions that visually guided prehension and visual perception are mediated by separate visual pathways. ■

INTRODUCTION

Vision provides us with a vast array of information about the world around us—information that can direct our thoughts and guide our actions. Yet our perception of the world can sometimes be misleading. Objects can appear to be larger or smaller, and sometimes closer or further away, than they really are. Nevertheless, we rarely notice these discrepancies between our perception and the real world until they are pointed out to us. Who has not been taken in by visual illusions at one time or another? And even when we know full well that objects and their spatial relations cannot be as they appear—when we watch events unfold on the television or movie screen, for example—the changes in the real size and distance of the distal stimulus have little effect on what we see (Gregory, 1995; Hochberg, 1987). In short, our perception of the world is remarkably insensitive to arbitrary changes in perspective and scale that commonly occur in movies and television. It is the *relative* size and distance of objects in the array, not their *absolute* size or location, that appear to be critical for perception.

Quite the opposite is true for the visual control of skilled actions. To pick up an object, such as coffee cup, it is not enough to know its relative size and location in the visual array; for the grasp to be successful, our visuomotor system must calculate the cup's absolute size and distance (for a discussion of these issues, see Bridgeman, Kirch, & Sperling, 1981; Goodale & Haffenden, in press; Milner & Goodale, 1995). In short, visuomotor computations must be metrically accurate. Moreover, those computations must be carried out in the appropriate egocentric frames of reference for the intended action. An accurate grasping movement, for example, requires computation of the parameters of the goal object in "arm-centered" coordinates (Graziano & Gross, 1994; Soechting & Flanders, 1992).

Dissociations Between Perception and Action in Neurological Patients

These differences in the requirements of visual perception and the visual control of action suggest that a single general-purpose representation of the world could not serve both functions. Instead, the different transformations required for perception and action would appear to require separate visual mechanisms, each adapted to the requirements of the output system it serves. This idea is supported by a number of studies in neurological patients who show dissociations between visual perception and the visual guidance of skilled actions following damage to different neural pathways. Patients with damage in the superior regions of the posterior parietal cortex, for example, are often unable to use information about an object's size, shape, orientation, or location, to control their visually guided reaching movements (Goodale et al., 1994; Jakobson, Archibald, Carey, & Goodale, 1991; Jeannerod, 1988; Perenin & Vighetto, 1988). Yet, their visual perception of objects remains relatively intact, and in many cases, they are able to identify or discriminate between the very objects they cannot grasp (for discussion of this issue, see Milner & Goodale, 1995).

Damage to occipito-temporal cortex may lead to the reverse disorder, in which the patient has impaired visual perception, with spared visually guided movements. This is the case with the patient D.F., whose grasping movements are well formed and accurate, even though she cannot visually discriminate between or identify the same objects to which she can direct well-formed grasps (Goodale et al., 1994; Goodale, Milner, Jakobson, & Carey, 1991; Milner & Goodale, 1995). On the basis of these neuropsychological studies and additional electrophysiological and behavioral studies in the monkey, Goodale and Milner (1992) have proposed that the distinction between vision for perception and vision for action can be mapped onto the two prominent pathways, or "streams," of visual projections that have been identified in the primate cerebral cortex: a ventral stream, which arises from the primary visual cortex and projects to the inferotemporal cortex, and a dorsal stream, which also arises from primary visual cortex but projects instead to the posterior parietal cortex (Ungerleider & Mishkin, 1982).

Ungerleider and Mishkin (1982) originally proposed that the ventral stream plays a special role in the identification of objects, whereas the dorsal stream is responsible for localizing objects in visual space. Goodale and Milner's reinterpretation of this story places less emphasis on the differences in the visual information that is received by the two streams (object features versus spatial location) than it does on the differences in the transformations that the streams perform upon that information (Goodale, 1993; Goodale & Milner, 1992; Milner & Goodale, 1993, 1995). According to their account, both streams process information about object features and about their spatial locations, but each stream uses this visual information in different ways. In the ventral stream, the transformations deliver the enduring characteristics of objects and their relations, permitting the formation of long-term perceptual representations. Such representations play an essential role in the identification of objects and enable us to classify objects and events, attach meaning and significance to them, and establish their causal relations. Such operations are essential for accumulating a knowledge-base about the world. In contrast, the transformations carried out by the dorsal stream provide the current location and disposition of a goal object in egocentric coordinates and thereby mediate the visual control of skilled actions, such as manual prehension, directed at that object. Of course, the two systems work together in controlling the rich stream of behavior that we produce as we live our complex lives. Their respective roles in this control differ, however. The perceptual representations constructed by the ventral stream are part of a high-level cognitive network that enables an organism to select a particular course of action with respect to objects in the world; the visuomotor networks in the dorsal stream (and associated cortical and subcortical pathways) are responsible for the programming and on-line control of the particular movements that the selected action entails.

Dissociations Between Perception and Action in Normal Observers

If visual perception and the visual control of action depend on different neural mechanisms in the human cerebral cortex, it should be possible to demonstrate a dissociation between these two kinds of visual processing in neurologically intact individuals. In other words, even in normal observers, the visual information underlying the calibration and control of a skilled motor act directed at an object might not always match the perceptual judgments made about that object. The trick is to find the right task to demonstrate this dissociation. The present study used one particular paradigm, a size-contrast illusion, to do this.

Most of the studies examining such dissociations in normal observers have focused on the spatial frames of reference used by visual perception and the visual control of action and have not looked at the effects of frames of reference on object size (for review, see Goodale & Haffenden, in press; Milner & Goodale, 1995). The bulk of this work on spatial location suggests that the mechanisms mediating the perception of object location operate largely in *allocentric* coordinates, whereas those mediating the control of object-directed actions (e.g., saccadic eye movements and aiming movements with the limb) operate in *egocentric* coordinates. In other words, perception uses a coordinate system that is world-based in which objects are seen as changing location relative to a stable or constant world; the systems controlling action systems, however, cannot afford these kinds of constancies and must compute the location of the object with respect to the effector that is directed at that target. In short, visuomotor control demands different kinds of visual computations than visual perception. As we suggested earlier, it is this difference in the computational requirements of the visual control of action and visual perception that explains the division of labor between the two streams of visual processing in the primate cerebral cortex.

Just as the perception of object location appears to operate within relative or allocentric frames of reference, so does the perception of object size. Although we often make subtle judgments about the relative sizes of objects, we rarely make judgments of their absolute size. Indeed, our judgments of size appear to be so inherently relative that we can sometimes be fooled by visual displays in which visual stimuli of the same size are positioned next to comparison stimuli that are either much smaller or much larger than the target stimuli. Such size-contrast illusions are a popular demonstration in many introductory textbooks in psychology and perception. One such illusion is the so-called Ebbinghaus Illusion (or Titchener Circles Illusion) in which two target circles of equal size, each surrounded by a circular array of either smaller or larger circles, are presented side by side (see Figure 1a). 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. Although the illusion is usually depicted in the way just described, it is also possible to make the two target circles appear identical in size by increasing the actual size of the target circle surrounded by the array of larger circles (see Figure 1b).

Although perception is 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. After all, when we reach out to pick up an object, particularly one we have not seen before, our visuomotor system must compute the object's size accurately if we are to pick it up efficiently. It is not enough to know that the target object is larger or smaller than surrounding objects; the visuomotor systems controlling hand aperture must compute its real size.

Moreover, the visual control of motor output cannot afford to be fooled by an accidental conjunction of contours in the visual array that might lead to illusions of size or location. There are situations in which the life or death of the organism will depend on the accuracy of a motor output; sensitivity to a visual illusion in the scene could be an enormous liability. For these reasons, therefore, one might expect grip scaling to be insensitive to the kind of size-contrast illusion seen in the Ebbinghaus Illusion.

Aglioti, DeSouza, and Goodale (1995) tested this idea by using a three-dimensional version of the Ebbinghaus Illusion. Thin plastic disks, resembling poker chips, were used as the center circles; these disks were placed within a conventional Ebbinghaus array drawn on a horizontal display card. Two kinds of trials were used. On one, the two disks appeared to be different in size even though they were actually physically identical; in the other trial, the two disks appeared to be equal in size even though the disk in the annulus of large circles was actually slightly larger than the disk in the small circle annulus (see Figure 1). These two kinds of trials were randomly presented to the subjects and the left-right positions of the large and small annuli were also randomly interleaved. Subjects were asked to pick up the target disk on the left or right side of the display, based on whether they thought the two disks looked the same or different in size. The maximum aperture of the subjects' grasps were measured in flight using optoelectronic recording. Even though the subjects' choices clearly indicated that they were subject to the illusion throughout testing, they nevertheless scaled their grip appropriately to the physical size of the disks. In short, the calibration of grip size was largely impervious to the effects of the size-contrast illusion.

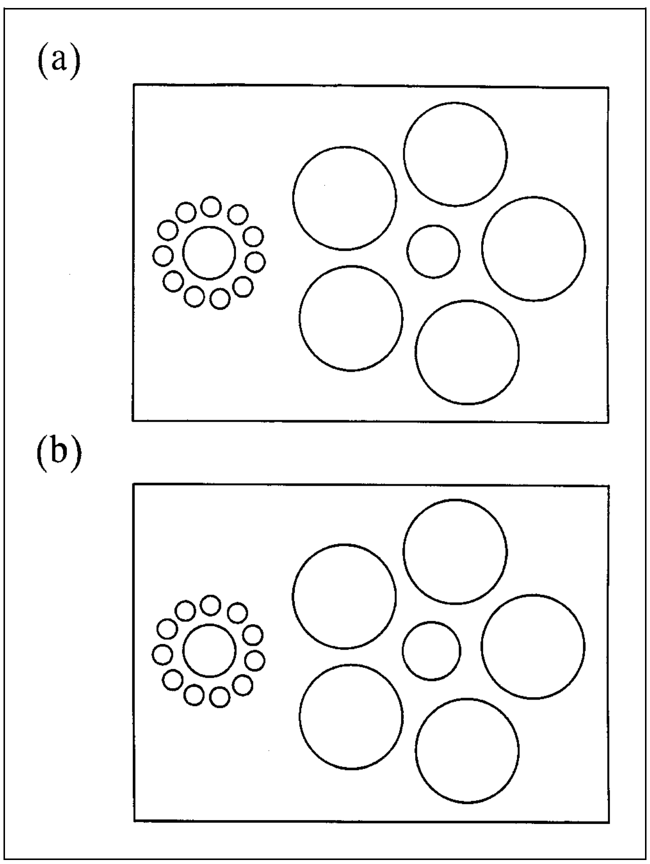


Figure 1. The Ebbinghaus Illusion. (a) The standard version of the illusion. The target circles in the center of the two annuli appear to be different in size even though they are physically identical. People typically report that the circle surrounded by the annulus of smaller circles appears to be larger than the circle surrounded by the annulus of larger circles. (b) A version of the illusion in which the target circle in an array of larger circles is physically larger than the other target circle. The two target circles should now appear to be identical in size.

The Present Study

Although the Aglioti et al. (1995) results appear to suggest that the perception of object size depends on different computations from those mediating the calibration of the grasp, there were some problems with the study that undercut this conclusion. First, there is the issue of visual feedback during the execution of the grasping movement. It is possible that subjects may have been adjusting their grip aperture in flight by comparing the size of the disk and the opening between their finger and thumb as they got closer and closer to the disk. Aglioti and his colleagues argued against this possibility and cited experiments showing that at least 500 msec were needed for processing visual information about changes in size and shape of the goal object before a new motor command could be produced. Maximum grip aperture, which was the kinematic marker used by Aglioti et al., is typically reached around 420 msec after a grasping movement has begun, or about 70% of the way through the reach (Jeannerod, 1984). This suggests that maximum grip aperture reflects early programming and not on-line adjustments to the grasp. More recent work challenges this conclusion, however. In an experiment examining rapid adjustments of the grasp to sudden and unexpected changes in object size, Castiello and Jeannerod (1991) found that a much shorter time was required for updating the motor output. In their experiment, subjects required an average of 320 msec to adjust the posture of their hand in order to accurately grasp a rod that changed in size when the reach was initiated. The fact that hand posture can be adjusted in such a short time, at least under certain conditions, makes it necessary to eliminate the possibility that subjects in an Ebbinghaus-type task were adjusting their grasp on the basis of the visual feedback. Clearly, it would be more convincing to run the Aglioti et al. study in visual open loop, in other words, under conditions in which the subjects have absolutely no opportunity to view their hand, or the target, during the execution of the grasping movement. Therefore, in the present experiment, we tested all our subjects under open-loop conditions to eliminate the possibility of on-line visual control of grip aperture.

There is no doubt that subjects will continue to scale for object size under open-loop conditions. Previous research by Jakobson and Goodale (1991), for example, has demonstrated that although there is an overall increase in maximum grip aperture during reaching movements when visual feedback is unavailable, maximum grip aperture is still scaled for object size in the absence of visual feedback, and the variance in grip aperture under these conditions does not differ from the variance when visual feedback is available. From this, we expected that when we presented subjects with the three-dimensional version of the Ebbinghaus Illusion, just as Aglioti et al. (1995) had done but under visual open loop, the maximum grip aperture achieved by subjects would still be scaled to the physical size of the disks.

A second issue that the present study addressed was the method of measuring the strength of the illusion. In the Aglioti et al. (1995) study, subjects' perceptions of disk size were measured by a same/different choice. This meant that a dichotomous measure of the perceptual effect of the illusion was being compared with a continuous measure of grip calibration. Clearly it would be better if a continuous measure were used for both outputs. An ideal measure of perceived size of course would be one that was directly comparable to the grip calibration measure. For this reason, we asked subjects to estimate the size of a disk by matching the distance between their thumb and index finger to the width of the disk. It is important to emphasize that, although hand and finger movements were required in this manual estimation task, the programming and execution of those movements does not involve the same control systems used in grasping. In the manual estimation task, subjects are simply asked to provide a kind of manual "read-out" of what they perceive. In the grasping task, they are engaging the visuomotor networks that mediate the skilled movements involved in human prehension. In short, the manual estimation task provided a measure of visual perception that could be more directly compared to the scaling of prehension. The manual estimation task was also carried out in visual open loop; after subjects viewed the object, estimations were made in the dark. Subjects were also allowed to reach out and pick up the target disk after the estimation, ensuring that they received the same amount of haptic feedback about the physical size of the disks as they did in the grasping task.

One final issue that was addressed in the present experiment was the question of the general effect on prehension of having an annulus surrounding a goal object. The influence of this factor on the grasp needs to be separated from any influence the illusion background might have on grip scaling. To investigate this question, two additional background conditions were used in the present experiment. The first consisted of two annuli made up of equal-sized circles, midway in size between the circles in the large annulus and the small annulus from the illusion background (Figure 2). The second control background involved no surrounding annuli; the target disks were presented on their own but in the same positions as when they were surrounded by annuli. By including these two conditions, it was possible to see if the scaling of the grasp was affected by reaching for a target surrounded by other forms (and whether or not this effect was independent of any effect the simple presence of annuli might have on perception). For example, reaching for an object surrounded by an annulus

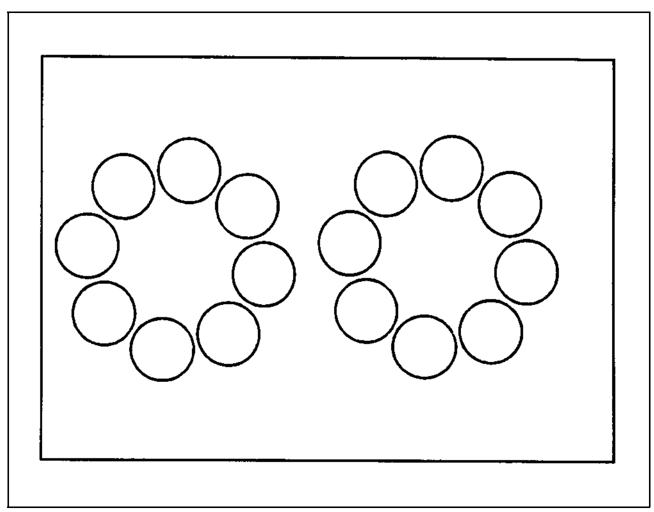


Figure 2. The equal annuli background. The circles composing the annuli are midway in size between the circles in the large annulus and the circles in the small annulus from the illusion background.

may be like reaching into a hole; the opening of the hand must be reduced to avoid hitting the sides of the hole but not so much as to miss the edges of the target.

To recap, the purpose of this study was threefold: first, to replicate the findings of Aglioti et al. (1995), but with an open loop design to eliminate the use of visual feedback; second, to use a continuous measure of perceived disk size that can be more directly compared to grip calibration; and third, to examine the effect of the surrounding annulus on grasping and manual estimates of disk size, independent of the illusion. It was expected that grasp would not succumb to the illusion but that manual size estimations would correspond to the subjects' changing perceptions of the same disks. Such an outcome would be consistent with the idea that the visual mechanisms that mediate prehension are quite separate from those that mediate perception.

RESULTS

Psychophysical testing carried out during practice trials allowed us to determine the difference in size between the two target disks that produced judgments of perceptual equivalence for each subject (Figure 1b). This difference turned out to be 2.44 mm, averaged across the 18 subjects we tested; in other words, for a pair of disks to be judged as equivalent on the illusion background, the disk centered in the annulus of large circles had to be 2.44 mm larger than the disk centered in the annulus of small circles. For 11 subjects the required difference was 2 mm, for 6 subjects it was 3 mm, and for 1 subject it was 4 mm. The most common situation was a 28-mm disk placed in the small circle annulus and a 30-mm disk placed in the large circle annulus to achieve equivalence in perceived size. Because different combinations were required to create perceptual equivalence across the subjects, the disks are referred to in relative terms (i.e., as the large disk and the small disk). When subjects were presented with physically identical disk pairs, they were presented with two small disks on half of the trials, and two large disks on the other half of the trials.

Subjects were tested on both a grasping task (Figure 3a) and a manual estimation task (Figure 3b); the order of testing was counterbalanced across subjects. Post hoc comparisons were performed as paired t tests, using Bonferroni corrections to adjust the error rate for the number of tests performed. On one half of the 70 trials of each task, the two disks in the array were physically identical in size; on the other half of the trials, which were randomly interleaved, the two disks were physically different in size. The disks were surrounded either by the illusion display or the equal annuli display, or they were presented on a blank background (see "Methods" for details of counterbalancing). Subjects were instructed to look carefully at the disks when they were presented and to decide whether they were identical or different in size. If they appeared different, they were to pick up (or manually estimate) the disk on the left using the index finger and thumb of their right hand; if the two disks appeared identical, they were to pick up (or manually estimate) the disk on the right (instructions were reversed for half the subjects). As soon as their hand left the table, the overhead light went out, eliminating the subject's view of their hand and the target display. The amplitude of the opening between their index finger and thumb was tracked using optoelectronic recording of small infrared light-emitting diodes attached to the tips of both digits (see Figure 3).

All the subjects remained sensitive to the size-contrast illusion throughout testing. When an illusion background was present and the two disks were identical in size, the choice made by the subjects indicated that they thought the disks were different; on illusion trials in which the disks were physically different, they behaved as though the two disks were the same size. Quite the opposite pattern of results was observed when the surrounding annuli were the same size or the background was blank. On these trials, the subjects' choices reflected the real difference in size between the two disks.

A clear dissociation was observed on illusion trials between the calibration of the grip aperture during the grasping task and the separation between the index finger and thumb during the manual estimation task. As Figure 4a illustrates, on trials in which subjects reported that the disks were identical in size even though they were physically different, the calibration of grip aperture was scaled to the actual not the apparent size of the disks. In fact, the difference of 2.11 mm between the mean maximum grip apertures for the large and small disks was only slightly less than the average difference in disk size of 2.44 mm needed to produce perceptual equivalence on the illusion background. In contrast, as Figure 4b illustrates, when subjects manually estimated the size of the disks on trials in which they believed the disks were identical in size (even though they were different), their estimates corresponded to the apparent not the real size of the disks. In other words, their manual estimates of the size of the small and large disk were virtually identical.

When the illusion was presented in the traditional fashion with two physically identical disks that appear different in size (Figure 1a), the illusory perceptions again failed to fool the calibration of the grasp but were reflected in the manual estimations of disk size. Thus, as Figure 4c illustrates, grip scaling for the physically identical pairs of small or large disks was unaffected by the size of the circles in the surrounding annuli. In other words, subjects again scaled their grip to the actual size of the target disks rather than to their apparent size. The reverse effect was seen in the manual estimation task. Here the estimates of target disk size reflected the expected effect of the illusion; the disks surrounded by the small circle annulus were estimated as being larger than the disks surrounded by the large circle annulus (Figure

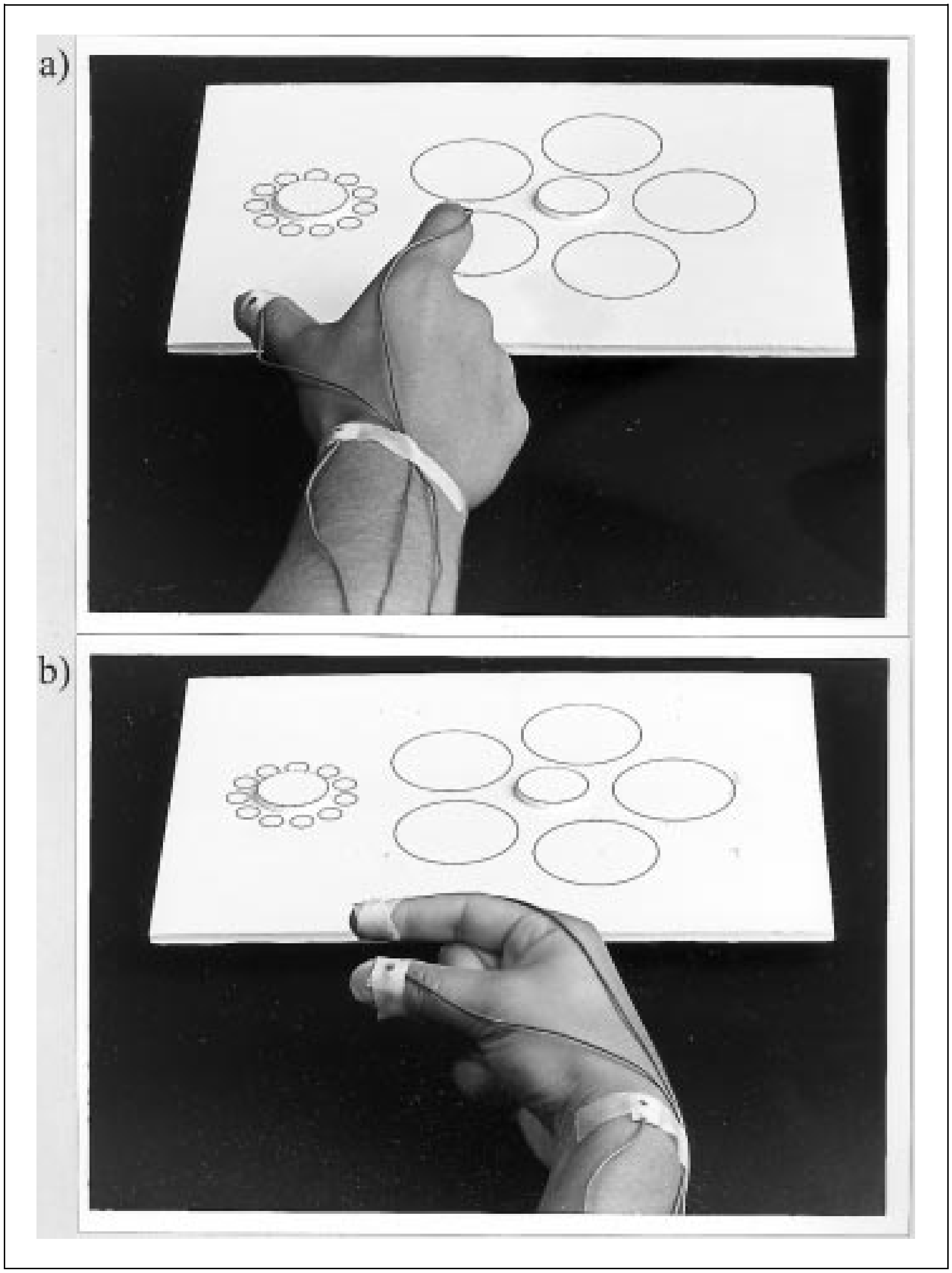


Figure 3. Photographs of the two tasks performed by each subject using a three-dimensional version of the Ebbinghaus Illusion. Note the infrared light-emitting diodes (IREDs) attached to the finger, thumb, and wrist that allowed for the optoelectronic tracking. (a) The grasping task. The subject's hand is pictured in-flight on the way to the target disk. (b) The manual estimation task. The heel of the subject's hand is resting on the table, and the thumb and index finger are opened a matching amount to the perceived size of target disk. In the actual tasks used in the present experiment, of course, the overhead light would have been turned off during the performance of the movements.

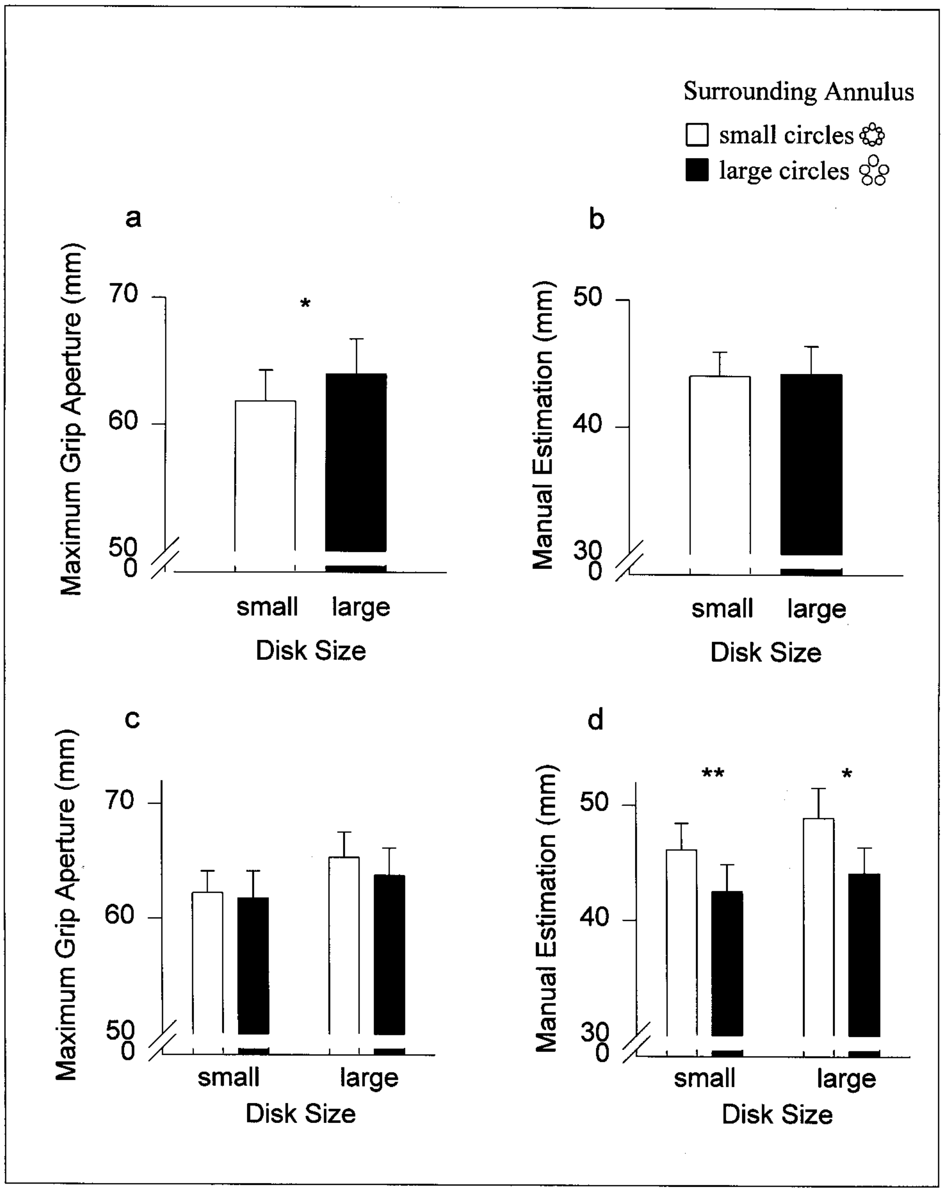
4d). This was true for both the small disk pair and the large disk pair.

In summary, when disks were presented on the illusion background, maximum grip aperture corresponded to the physical size of the disks, whether the disks appeared to be the same or different in size. Manual estimations of disk size showed exactly the opposite pattern; they were clearly influenced by the illusion. Importantly, this dissociation was seen despite the fact that the same effector, the hand, was used to produce the response for both tasks: in one case to reach out and grasp the disk and in the other case to "match" the size of the disk to the distance between the thumb and index finger.

Of course, when no illusion background was present, as in the case where the disks were presented either on a blank background or on an equal annuli background, we expected the grasping and manual estimation tasks to yield similar results. On these backgrounds, the perceived size of the disks and their actual size should coincide. The results for physically different pairs of disks are presented in Figure 5 and for physically identical pairs of disks, in Figure 6.

When a physically different disk pair (one large, one

Figure 4. Graphs illustrating grip aperture and manual estimations for trials where target disks were placed on the illusion background. (a) Mean maximum grip aperture on trials in which subjects reported that the disks were identical in size, even though they were physically different. The difference between the maximum grip aperture achieved for large disks was significantly greater than the maximum grip aperture achieved for the small disks, $t(17) = 3.92, p < 0.05$. (b) Mean manual estimations of disk size on perceptually identical, physically different trials. The manual estimations of large disk size were not significantly greater than those of small disk size, $t(16) = 0.14$, $p > 0.05$. (c) Mean maximum grip aperture on trials in which two physically identical disks appeared different in size. There was no significant difference between the maximum grip apertures achieved for small disks in the small annuli and the small disks in the large annuli, $t(17) = .62, p > 0.05$. Similarly, there was not a significant difference in maximum grip apertures for the large disk pair, $t(17) = 2.36$, $p > 0.05$. (d) Mean manual estimations on trials in which two physically identical disks appeared different in size. The disks surrounded by the small circle annulus were estimated as being significantly larger than the disks surrounded by the large circle annulus for both the small disk pair, $t(16) = 3.26, p < 0.05$, and the large disk pair, $t(16) = 4.37, p < 0.01$. Error bars depict standard errors of the means.

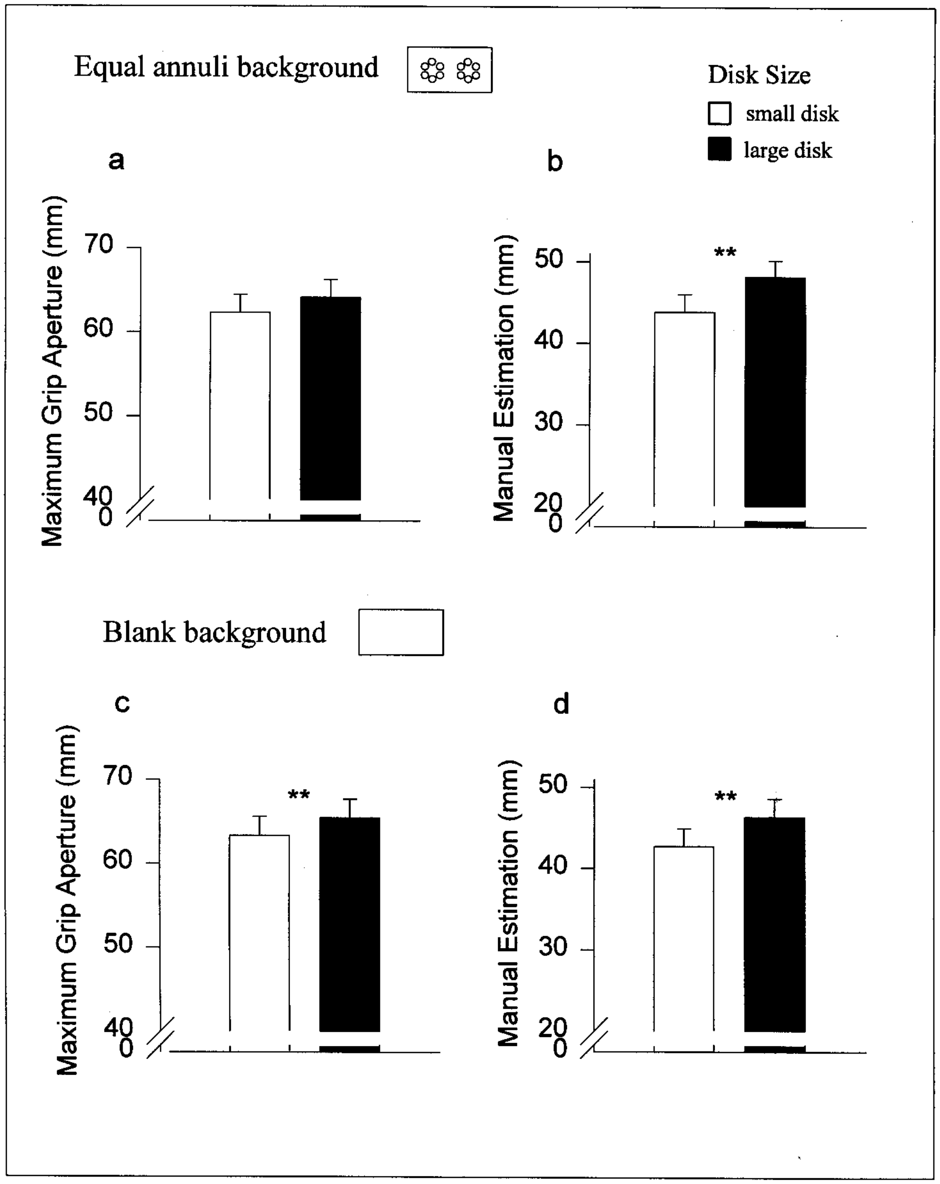


small) was placed on a background consisting of two annuli of equal mid-sized circles or no surrounding annuli, both grip scaling (Figure 5a) and manual estimations (Figure 5b) reliably reflected the difference in size between the disks. A similar pattern of results was observed when the disks were placed on a plain white background. Physically different disks generally produced significantly greater grip apertures (Figure 5c) and significantly greater manual estimates (Figure 5d) for the large disk than for the small disk.

When identical disks were used (both large or both small), no significant differences were seen between identical disks in either the grasping task or the manual estimation task for either the equal annuli background or the blank background (Figure 6). Comparisons of average response to both large disks and both small disks revealed appropriate scaling in both the grasping and the manual estimation task. Moreover, grip scaling and manual estimations showed comparable levels of accuracy.

In short, when no illusion was present, manual estimations and grip scaling both followed the true size of the disks. Nevertheless, the presence of the equal annuli did have an effect on the magnitude of the responses, and this effect differed between the visuomotor and the perceptual tasks. These differences are illustrated in Figure 7. In the grasping task, disks on the background consisting of equal-sized annuli produced smaller maximum grip apertures than the same disks presented on their own with no surrounding annuli. Conversely, in the

Figure 5. Results for the conditions in which a physically different disk pair (one large, one small) was placed on a either a background consisting of two annuli of equal mid-sized circles (a and b) or a blank background with no surrounding annuli (c and d). (a) Mean maximum grip apertures achieved for large disks on the equal annuli background were larger than those achieved for small disks. This difference was not significant, $t(17) = 3.06, p > 0.05$. (b) Manual estimations of large disks on the equal annuli background were significantly larger than those for small disks, $t(16)$ $4.42, p < 0.01$. (c) Maximum grip apertures achieved for large disks were significantly greater than those for small disks, $t(17)$ $4.25, p < 0.01$. (d) Manual estimations were significantly larger for the large disk than for the small disk, $t(16)$ 5.57, $p < 0.01$. Error bars depict standard errors of the means.



manual estimation task, the disks surrounded by the medium circle annuli were estimated as being larger than the disks that were presented without surrounding annuli.

DISCUSSION

The results of the present experiment provide strong support for the idea that the visual mechanisms underlying perception are distinct from those underlying the control of skilled actions. Despite the presence of the size-contrast illusion created by the Ebbinghaus display, the scaling of the grasp corresponded to the actual, not the apparent, size of the target disks. Although these results parallel those of Aglioti et al. (1995), the present study was run in visual open loop. In the present experiment, there was no opportunity for subjects to use visual feedback from their hand or the target to adjust their grip aperture in flight. The fact that maximum grip aperture under these conditions continued to correspond to the physical rather than the perceived size of an object suggests that this real-world metrical calibration could not have been based on adjustments made during the execution of the grasp. Instead, subjects must have programmed the aperture of their grasp on the basis of their initial glimpse of the target disk, presumably in relation to its real size. Moreover, the accurate scaling of the grasp occurred while subjects were in the act of indicating their illusory perceptions by reaching out and picking up the appropriate target disk. This striking dissociation in normal human observers is consistent with the proposal put forward by Goodale and Milner

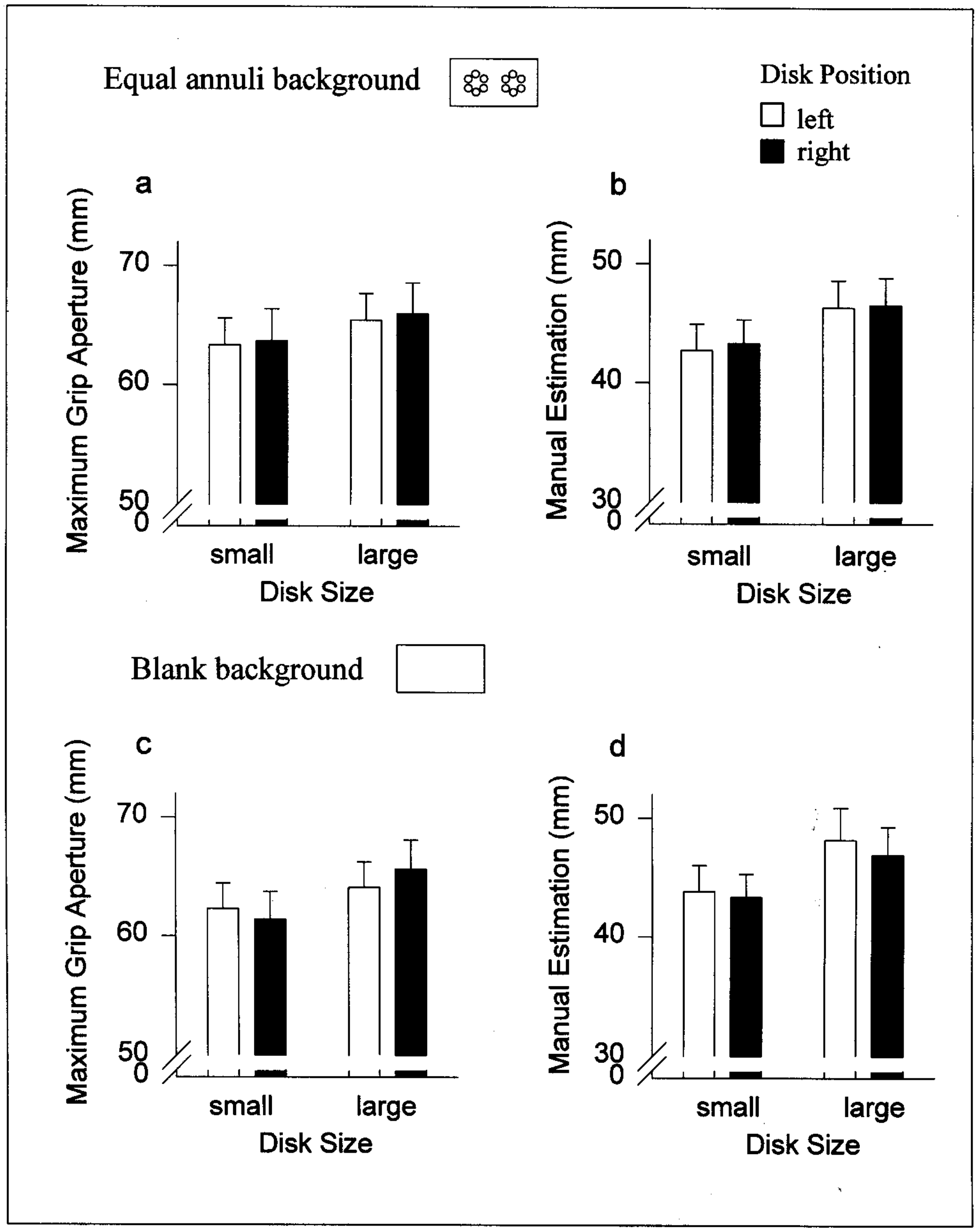


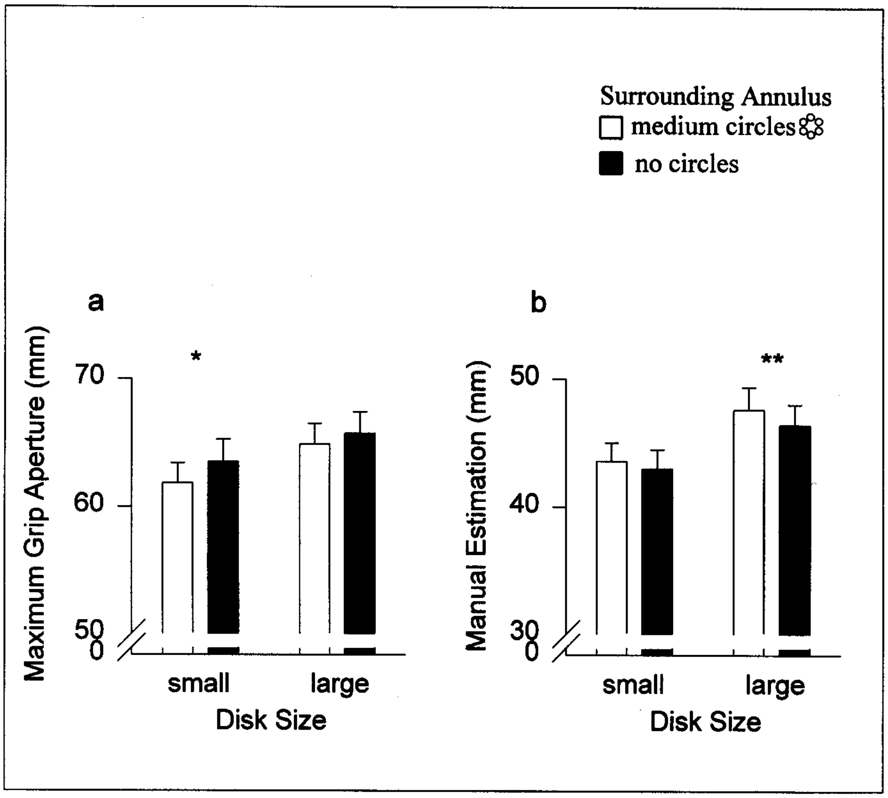
Figure 6. Results for physically identical disk pairs (both large or both small) placed on either the equal annuli background (a and b) or the blank background (c and d). All comparisons between means achieved for physically identical disks were not significant in either the grasping task or the manual estimation task, $p > 0.05$. (a) Small: $t(17) = 0.82$; large: $t(17) = 1.98$. (b) Small: $t(16) = 0.84$; large: $t(16) = 1.82$. (c) Small: $t(17) = 0.58$; large: $t(17) = 0.77$. (d) Small: $t(16) = 1.03$; large: $t(16) = 0.42$. Error bars depict standard errors of the means.

(1992), on the basis of neuropsychological evidence, that there are separate neural substrates for visual perception and the visual control of action.

The relative insensitivity of reaching and grasping to pictorial illusions has been demonstrated in two other recent experiments employing classical pictorial illusions. Vishton and Cutting (1995) have shown that grasping movements are relatively insensitive to the horizontal-vertical illusion, and Ian Whishaw (personal communication, 1996) has obtained similar findings using the Ponzo illusion. In neither of these studies, however, was an explicit comparison made between the calibration of grasp and perceptual judgments using the same readout—the separation between the finger and thumb. In our experiment, however, we compared grip scaling with manual estimations of the size of the same target stimuli. When subjects estimated the size of a disk by opening their finger and thumb a matching amount, their estimations corresponded to the apparent rather than the real size of the disk. In other words, their manual estimation of disk size, unlike their visuomotor scaling, was completely driven by the illusory condition in which the disk was placed—even though subjects had the same amount of haptic feedback in both conditions. (They always picked up the disk after estimating its size.) These results are particularly compelling because, as we have already emphasized, in both the manual estimation task and the visuomotor task, movements of the hand and fingers were required. Yet, in one case, the perceived size of the object dominated the response, whereas in the other, the real size of the object dominated.

Some of the other findings in the present study also

Figure 7. Results showing the effect of a surrounding annulus on grasp and on manual estimations. (a) In the grasping task, small disks on the background consisting of equal-sized annuli produced significantly smaller maximum grip apertures than small disks presented on the blank background, $t(35) = 2.53, p < 0.05$. (b) In the manual estimation task, large disks surrounded by the equal annuli produced significantly larger estimations than the large disks that were presented on the blank background $t(34) = 3.05, p < 0.01$. Error bars depict standard errors of the means.



point to separate mechanisms for perception and visuomotor control. For one thing, not only did the illusion have different effects on manual estimation and maximum grip aperture, but the amplitude of the opening between the finger and thumb was quite different in these two response conditions (even though the same effector was being used). (It is worth noting again that the opening between the thumb and forefinger was measured using the same method for both manual estimates and grip scaling.) Manual estimations produced finger-thumb apertures of about 40 mm, a distance that was only slightly larger than the physical size of the disks. In short, subjects were showing us what they saw. Grasping, however, produced maximum apertures that were around 60 mm wide, a value that was often twice as large as the actual size of the disks. Such large grip apertures are quite typical. Many investigators have demonstrated that even though grip aperture is highly correlated with object size, subjects always achieve maximum apertures that are quite a bit larger than the goal object (e.g., Jakobson & Goodale, 1991; Jeannerod, 1984). In other words, subjects are not trying to match their grip in flight to the object's actual size. Instead, they open their hand in a remarkably stereotyped fashion, reaching maximum aperture approximately 70% of the way through the reach and then clamping down on the object as the hand gets closer (Jeannerod, 1984). In our experiment, subjects behaved in exactly the same way. It is difficult to argue therefore that subjects were somehow consciously and deliberately scaling their grip aperture to match the size of the target disk. If this were the case, why would they use an estimate that was often twice as large as the object they were trying to pick up? Instead, the large mismatch between the amplitude of the grip aperture and the size of the target disk probably reflects the normal processes underlying visuomotor control of object-directed actions—just as the relatively closer match between manual estimates and the size of the disk reflects the operation of the normal processes underlying the visual perception of those same objects.

Another aspect of the results that lends support to the idea of a dissociation between perception and visuomotor control is the observation that subjects remained sensitive to the illusion over the 2-hr testing period—despite the fact that they were receiving haptic feedback about the real size of the disks throughout testing. Many subjects commented that they were surprised by the size of the disk when they picked it up; it was smaller or larger than they had expected. Yet, this feedback from prehension of the disks did not diminish the effect of the illusion. In addition, the continued exposure to the same pairs of disks on the illusion background did not cause the illusory effect to diminish.

Although it is clear that the calibration of grasping must use the real size of the target object, it is not immediately apparent why perceptual judgments of object size are taken in by the illusion. Again the explanation turns on the fact that perception typically involves relative not absolute judgments of object size. Indeed, the Ebbinghaus Illusion, like a number of size-contrast illusions, appears to depend on rather high-level perceptual processes in which relative size judgments of similar objects are being made (Coren & Enns, 1993; Coren & Miller, 1974; Weintraub & Schneck, 1986). For example, the strength of the illusion depends more on whether or not the surrounding context stimuli are the same class of object as the test stimulus rather than on whether or not they have the same visual geometry (Coren & Enns, 1993). This implies that some sort of comparison is being made between the surrounding annuli and the test stimuli. Indeed, it has been suggested that the illusion depends on a size-constancy computation in which the array of smaller circles is assumed to be more distant than the array of larger circles; as a consequence, the target circle within the array of smaller circles is perceived as more distant (and therefore larger) than the target circle of equivalent retinal image size within the array of larger circles (Coren, 1971; Gregory, 1963).

Mechanisms such as these, in which the relations between objects in the visual array play a crucial role in scene interpretation, are clearly central to perception. Moreover, such comparisons are quite obligatory. We cannot but fail to see some things as smaller or larger (or closer or further away) than others. But if such an obligatory analysis is being carried out on the visual array, inappropriate comparisons might sometimes be expected to take place. In other words, illusions could arise because of accidental conjunctions and alignments of contours, objects, or surfaces in the visual array. Psychologists have capitalized on this fact by creating pictorial illusions. By studying the errors in judgment that subjects make when they look at such illusions, psychologists have learned a good deal about normal perception. Such illusions are probably quite rare in our daily lives. But even when they do arise, they will have little consequence for our behavior since we are rarely asked to make explicit judgments about object size and distance.

Although small errors in size and distance estimation might have little consequence for our perception of the world, such miscalculations in the visuomotor domain could be devastating. To be successful, a goal-directed act like prehension must use computations that deal with the metrical properties of the object independent of the context of the visual array in which that object is embedded. The real distance of the object must be computed, presumably on the basis of reliable cues such as stereopsis and retinal motion, rather than on the basis of pictorial cues, which as we have seen can be quite unreliable. Once distance has been computed, this estimate combined with the retinal image size of the object will deliver the true size of the object for calibrating the grasp. By relying on these sorts of cues, the computations mediating grasping movements are quite insensitive to the cues that drive the size-contrast illusions in which more relative scene-based calculations are at work.

Even though relative judgments of size and distance appear to be central to our perception of the world, why is it that we do not routinely incorporate the accurate metrical information that is clearly available to the visuomotor system? There could be a number of reasons for this. First, many perceptual judgments involve distal stimuli in the visual array that are beyond the range of mechanisms like stereopsis that are designed to deliver accurate metrical computations. Second, as we have already suggested, there is little consequence anyway for any errors in perceptual judgments that we might make. Finally, because perceptual representations, unlike a goal-directed movement, involve an analysis of the entire visual array, a metrically accurate representation would be computationally expensive.

The proposed dissociation between the mechanisms underlying visually guided movements and those underlying perception does not preclude the possibility of perception influencing visually guided movements. Indeed, under normal circumstances perception acts in concert with prehension, and our hand posture varies depending on the perceived identity of the target object. For example, our hand posture when we reach for a fork that we are going to put away is very different from the posture we adopt when we are going to use the same fork to eat with (for a discussion of this issue, see Milner & Goodale, 1995). In the present study, scaling of the grasp was largely dependent on the physical size of the disks; yet, a small influence of perception on grasp could be seen in reaches to the physically identical disk pairs on the illusion background. In other words, subjects sometimes opened their hand slightly wider when reaching for a disk surrounded by the small circle annulus than when reaching for a physically identical disk surrounded by the large circle annulus. Although this effect was not significant, a similar perceptual effect on grip calibration was seen in the Aglioti et al. (1995) study and in their case was significant. This suggests that the perception of size can exert some influence on the programming of hand posture for prehension. Indeed, although the visual mechanisms underlying perception are largely separate from the visual mechanisms underlying prehension, this separation does not mandate that there be no communication between the mechanisms. In fact, as was just discussed, such communication would appear to be necessary for generating hand postures that are appropriate to the function of the goal object.

An influence of perception on action has also been demonstrated in certain neurological cases. Jeannerod, Decety, and Michel (1994), for example, have described a patient with damage to the posterior parietal cortex who was unable to scale her grasp for "neutral" objects even though she could scale her grasp to familiar objects of the same size. In another patient, an interesting disconnection between visual recognition and functional control of the grasp has been demonstrated (Sirigu et al., 1995). This patient, who shows good metrical scaling of her grasps to objects, cannot incorporate functional elements into the grasp even though the patient recognizes the identity of the object. Taken together, these results suggest that perception makes an important, but perhaps somewhat independent, contribution to the organization of manual prehension movements. The neural pathways supporting this perceptual or cognitive mediation of grasping remain unknown.

Nevertheless, it is important to emphasize that the principal determinant of grip calibration is the real size of the object and that in the present experiment the illusion reduced the correlation between object size and maximum grip aperture only very slightly. Grip aperture was still scaled to the real size of the objects. Moreover, this scaling was sensitive to rather small differences in the size of the goal objects; the actual difference in size between the large and the small disks was only 2.44 mm on average. Evidently the visual processes underlying prehension are finely tuned to the real size of an object, and these processes are quite resilient to the influence of perceptions that are at odds with the actual object size.

There was another feature of the illusion design that may have played a role in the calibration of the grasp, the fact that the target disk was surrounded by other visual forms. The equal and no annuli backgrounds in the present study were employed to examine the effect that the presence of surrounding annuli may have had on the calibration of the grasp. It is possible that, independent of any possible illusory effects, having an annulus surrounding the target disk may have created a situation similar to reaching into a hole, with the end result that grip aperture was programmed to be tapered so that it would fit into that hole. In fact, the difference seen between reaches to disks on the equal annuli background and disks on the no annuli background may have reflected such an effect; grasps made to the target disk when it was surrounded by the equal-sized annuli had smaller apertures than grasps to the same disk when it was presented on a blank background. This was particularly true for the small disk. This difference may have resulted from an attempt to taper the grasp appropriately. This effect was not observed in the manual estimation condition. In fact, the effects were quite the opposite. In the manual estimation condition, the presence of a surrounding annulus increased rather than decreased the magnitude of the opening between the finger and thumb. The fact that the disks were apparently perceived as larger when surrounded by annuli suggests that some sort of illusory effect was at work. Although the equal-sized annuli were designed to measure the direct effect of having a surrounding annulus on both response modes, the annuli were still composed of circles, inevitably evoking a size-contrast effect based on a relative size comparison. Because the two annuli were identical, however, any perceptual influence of the annuli would be the same for both disks. Nevertheless, the perceptual effect could be seen when the manual estimates with this background were compared to those seen when no annuli were present in the background.

In conclusion, a clear dissociation was shown between the visual mechanisms underlying prehension and the visual mechanisms underlying perception in neurologically intact individuals. Scaling of the grasp corresponded to the actual not the perceived size of the target disks; manual estimations of the size of the disks corresponded to the perceived not the actual size. These findings are consistent with recent neuropsychological evidence, suggesting that there are separate visual systems for perception and action in the cerebral cortex (Goodale & Milner, 1992; Milner & Goodale, 1995). Each system has evolved to transform visual inputs for quite different functional outputs and as a consequence is characterized by quite different transformational properties. The parallel operation of these two systems lies at the heart of the paradox that what we think we "see" is not always what guides our actions. In everyday life, of course, the two systems work as an integrated whole—just as all systems in the brain do. Nevertheless, the two systems are complementary to each other, and their separate evolution reflects the different information requirements of perception and action.

METHOD

Subjects

The 18 subjects (9 males and 9 females) in this study ranged in age from 19 to 28 years (mean 22.67 years) and were all strongly right-handed as assessed by a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971). Their vision was normal or corrected-to-normal and their stereoacuity was within the normal range, as assessed by the Randot Stereotest (Stereo Optical, Chicago). All subjects were paid for their participation.

Apparatus and Procedure

Hand position was recorded using the Optotrak (manufactured by Northern Digital Inc., Waterloo, Ontario), which creates a 3-D representation of the trajectory of the hand and fingers by recording infrared light signals. Three high-resolution infrared-sensitive cameras monitored the position of infrared light-emitting diodes (IREDs), the positions of which were digitized at 100 Hz. Off-line, the data were run through a low-pass second-order Butterworth filter with a 7-Hz cutoff.

Subjects had IREDs placed on their index finger, thumb, and wrist. The IREDs were held in place with small pieces of cloth adhesive tape, which allowed freedom of movement of the hand and fingers. The IREDs on the thumb and index finger were placed at the corners of the opposing nails. (If one imagines the right hand placed flat on a table, the IRED on the index finger would be on the left side of the base of the nail, and the IRED on the thumb would be on the right side of the base of the nail.) The distance between these IREDs was the measure for maximum grip aperture and the manual size estimations. The wrist IRED was placed opposite the styloid process on the ulna and provided measurements of the transport component of the reach to the display platform (e.g., time to initiate the reach, and velocity).

The display platform sat in a cardboard frame that was attached to the table to maintain a constant position. The table was covered with a black cloth, which provided a uniform viewing background for the display. A circular overhead fluorescent light, positioned approximately 75 cm above the display, provided illumination during the viewing period. Onset and offset of the light were controlled by a computer; with this system, the light could be turned on by the experimenter for a specific length of time or, in other conditions, could be turned on and then turned off when the subject released the start button. The latter arrangement was used to create the open-loop conditions in the visuomotor task, thus preventing the possible influence of visual feedback on the scaling of the opening between the finger and thumb.

The target disks were constructed of 3-mm-thick white plastic with a thin black line drawn around the circumference on the top surface and ranged in diameter from 27 to 32 mm (in 1-mm steps). During presentation, two disks were placed on the display platform, with the center of the disks spaced 120 mm apart. The display sat parallel to the surface of the table on a platform incorporating a rotating ball-bearing mechanism, which operated in much the same fashion as a turntable. This allowed the experimenter to easily alternate the left/right position of the display when necessary.

The Ebbinghaus Illusion background was mounted on Bristol board and attached to the rotating ball-bearing mechanism. This formed the display platform. The illusion background consisted of a small circle annulus (each of the 11 circles was 10 mm in diameter) and a large circle annulus (each of the 5 circles was 54 mm in diameter). The inner diameter of the small annulus was 38 mm; the inner diameter of the large annulus was 55 mm. The centers of the two annuli were 120 mm apart. In order to examine the effect produced by having the target disk surrounded by an annulus, independent of illusion, two additional backgrounds were employed. An equal annuli background was used, consisting of six circles, (each circle 22 mm in diameter); the inner diameter of each annulus was 42 mm. The centers of the annuli were also 120 mm apart. A final condition was used in which no annuli were present. The target disks in this condition were always positioned 120 mm apart center to center (the positions were indicated by small marks on the background that were covered by the disks during presentation). The equal annuli background and no annuli background were presented in the same manner as the regular Ebbinghaus display. The absolute position of the target disks was identical for each background condition.

In order that prehension and perception could be directly compared, a visuomotor task and a perceptual task were employed, the order of which were counterbalanced across subjects. The elements common to both tasks will be described first. Following this, the specifics of each task will be outlined separately.

During testing, subjects stood in front of the table, looking down at the display surface. This gave them a bird's eye view of the display, thus allowing them to see the display straight on. In both the visuomotor task and the perceptual task, subjects were asked to choose the target disk on the left or right side of the display based on whether they thought the two disks looked the same or different in size. Half the subjects were instructed to choose the disk on the left if they thought the two disks looked the same; the other half were asked to choose the disk on the right. The same instructions were maintained for individual subjects across the two tasks. Subjects were first given some practice trials. In addition to receiving practice on the task, they were systematically tested with different sizes of disks to establish which pair would be reliably judged as equivalent in size on the illusion background. In other words, the size of the disk in the large annulus of the illusory display was made larger than that in the small annulus until the subjects reported that the two disks appeared equivalent in size. Subjects were not told that this psychophysical procedure was being carried out during the practice trials.

The within-subjects variable for both the visuomotor and the perceptual task was the display condition in which the two disks were presented. There were 14 levels of this variable, each of which consisted of a combination of three different components: the background display on which the disks were placed, the left/right orientation of this display, and the disk pairs that were presented (i.e., physically identical or physically different).

The background displays (Ebbinghaus Illusion, the equal annuli, and the no annuli displays) were presented in randomly alternating trials. As previously mentioned, the display was mounted on a rotating ball-bearing mechanism, which allowed for easy alternation of the left/right position of the display. Thus, for the illusory display, sometimes the small annulus was on the left and sometimes the large annulus was on the left.

For each of the three background displays, two different disk pairs were presented. In the first type of trial, the disks were physically different. The size of the large and small disks used in these pairs had been determined for each subject during the practice trials. On the illusion background, the large disk was always placed in the large circle annulus, and the small disk was placed in the small circle annulus, creating the illusion that the disks were the same size. With the equal annuli and no annuli backgrounds, the large disk and the small disk were presented an equal number of times on the left and right sides of the display. This ensured that the subjects would have the opportunity to pick up a large disk and a small disk from the pair an equal number of times. In the second type of trial, the two disks were physically identical; on half the trials the two disks were both small and on the other half they were both large. The small disk pair was composed of two versions of the same small disk from the physically different disk pair used to achieve perceptual equivalence with the illusory background; the large disk pair was composed of two versions of the large disk from the perceptually equivalent pair. On the illusion background the physically identical pairs appeared to be different, with the disk in the large circle annulus appearing smaller than the disk in the small circle annulus. To create a situation in which both the large and small target disks would be surrounded by each annulus on the illusion background an equal number of times in each annulus position, both pairs were presented with the illusion background in both left/right orientations. In this way, half the time the target disk would (ideally) appear to be perceptually smaller and half the time it would appear to be perceptually larger. For the equal annuli and no annuli background conditions, this counterbalancing was not required because the displays were symmetrical with respect to the display background. As a check for scaling constancy with the equal annuli and no annuli backgrounds, comparisons were made between responses to each target disk from the physically different pair, and those made to the target disk of matching size from each of the physically identical pairs. (This meant, of course, that comparisons were being made between responses directed to target disks on the left of the display and those directed to the physically identical disk on the right.)

The 14 different disk presentation conditions were randomly displayed five times each, for a total of 70 trials in each task. Subjects were given a break every 35 trials. Two different versions of randomized trials were used. The order in which these two randomized trial versions were presented and the task (visuomotor or perceptual) assigned to each version were counterbalanced across subjects. In other words, every subject performed both the visuomotor task and the perceptual task and received both variations of the randomized trials. Subjects were asked to keep their eyes closed between trials while the experimenter set up the display.

The Visuomotor Task

At the beginning of each trial, an overhead light came on, allowing subjects to view the display and make their decision about whether the two disks looked the same or different in size. Then, when subjects took their thumb and index finger off of the start button to reach for their chosen disk, the overhead light turned off, thus eliminating their view of both the target disk and their hand during the reach. Subjects were instructed to close their eyes between trials while the display and disks were being set up. The next trial began when the instructions were given regarding the same/different decision and subjects had verbally indicated they were in the ready position with their thumb and index finger together on the start button. Half the subjects were given the instructions "pick up the disk on the right if the two disks look the same, and pick up the disk on the left if the two disks look different." The other half of the subjects were given the opposite instructions concerning the target disk for the same/different choice.

In the visuomotor task, subjects were instructed to pick up the disks with the index finger and thumb of their right hand, at approximately the 1 and 7 o'clock positions. This position, which is spontaneously adopted by many people, was used to maintain consistency throughout the subjects. Subjects were asked to place the disk that they had picked up on the table, to the right of the display platform. This allowed the experimenter to determine the subjects' same/different judgment of disk size (based on whether they had picked up the disk on the left or right side of the display) without requiring them to make a verbal report of their perception, which might have influenced the way they tried to form their grip as they picked up the disk.

The Perceptual Task

For the estimation task, subjects were allowed to view the display for a fixed period of 1 sec—a period of time that approximated the average length of time the display was in view during the visuomotor task in which the light went off as soon as the subjects initiated their reach. Although this period of time was sufficient to view the display, the manual estimate was always made while the light was off. Thus, in both the perceptual estimation task and the visuomotor task, the subjects were responding in visual open-loop conditions.

In the manual estimation task the subjects used the same decision criteria as in the reaching task, only this time they estimated the size of the disk before reaching for it. Half the subjects were given the instructions "estimate the size of the disk on the right if the two disks look the same, and estimate the size of the disk on the left if the two disks look different." The other half of the subjects were given the opposite instructions. A trial was initiated after the subjects were given these instructions and had indicated that they were in the ready position with the heel of their hand resting on the start button and their index finger and thumb held together above the surface of the table. At this point, the light came on for 1 sec, allowing subjects to view the display. Subjects then estimated the size of the chosen disk with their thumb and index finger by matching the distance between them to the diameter of the disk, thus producing a perceptual measure of disk size. The subjects indicated when they had their size estimation ready and, at this point, their hand posture was recorded for 500 msec without the subjects being aware of when the recording was taking place. Subjects were then cued with a tone, which indicated that they could reach out and pick up the disk they had just estimated. In doing so, subjects received the same amount of haptic feedback about the physical size of the disks size as they had during the visuomotor task. As in the visuomotor task, the same/different perceptual decisions were noted based on whether the right or left disk was placed beside the display.

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