Research Report

A Double Dissociation Between Action and Perception in the Context of Visual Illusions

Opposite Effects of Real and Illusory Size

Tzvi Ganel,[1] Michal Tanzer,[1] and Melvyn A. Goodale[2]

[1]Ben-Gurion University of the Negev and [2]University of Western Ontario

ABSTRACT—*The idea that there are two distinct cortical visual pathways, a dorsal action stream and a ventral perception stream, is supported by neuroimaging and neuropsychological evidence. Yet there is an ongoing debate as to whether or not the action system is resistant to pictorial illusions in healthy participants. In the present study, we disentangled the effects of real and illusory object size on action and perception by pitting real size against illusory size. In our task, two objects that differed slightly in length were placed within a version of the Ponzo illusion. Even though participants erroneously perceived the physically longer object as the shorter one (or vice versa), their grasping was remarkably tuned to the real size difference between the objects. These results provide the first demonstration of a double dissociation between action and perception in the context of visual illusions and together with previous findings converge on the idea that visually guided action and visual perception make use of different metrics and frames of reference.*

A large body of evidence provides support for the idea that vision for action and vision for perception are mediated by distinct neuroanatomical (Goodale & Milner, 1992; Milner & Goodale, 2006) and functional (Ganel & Goodale, 2003; Kunde, Landgraf, Paelecke, & Kiesel, 2007) systems. Some of the most intriguing —but also the most contentious—evidence for dissociations between action and perception in healthy participants has come from studies of visual illusions (for reviews, see Bruno, 2001; Carey, 2001; Smeets & Brenner, 2006). Visual illusions, by definition, have robust effects on perceptual judgment. Nevertheless, accumulating evidence suggests that when people pick up objects in the context of visual illusions, the scaling of their grip aperture in flight is insensitive to the illusions, or in some cases less sensitive to the illusions than perceptual estimates of size (e.g., Aglioti, DeSouza, & Goodale, 1995; Ganel & Goodale, 2003; Haffenden & Goodale, 1998; Haffenden, Schiff, & Goodale, 2001; for a review, see Carey, 2001). This evidence suggests that the hand is not fooled by the information that deceives the observer—and supports the two-visual-systems proposal. However, this interpretation has been vigorously challenged over the past decade by investigators who advocate a more monolithic account of visual processing (for a review, see Smeets & Brenner, 2006). Indeed, some of these investigators did not find a dissociation between action and perception, but reported that grasping is as sensitive to an illusion as perceptual reports (e.g., Franz, Fahle, Bülthoff, & Gegenfurtner, 2001; Franz, Gegenfurtner, Bülthoff, & Fahle, 2000).

The empirical evidence in this debate has consisted of little more than repeated demonstrations of conflicting results by the two camps. Although there have been some attempts to reconcile these differences by appealing to the operation of different control mechanisms in different situations (Milner & Goodale, 2006), there has been no attempt to disentangle—within the same experiment—the effects of the real size and the apparent size of objects on action and perception in situations in which real size and apparent size would have opposite effects. To this end, we conducted the present study, using a version of the Ponzo size-contrast illusion (see also Gonzalez, Ganel, & Goodale, 2006). In this illusion, when two objects of equal size are presented at the sides of the display, the illusory display creates a distortion in the perceived length of the objects so that the

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Address correspondence to Tzvi Ganel, Department of Psychology, Ben-Gurion University of the Negev, Beer-Sheva 84105, Israel, e-mail: tganel@bgu.ac.il.

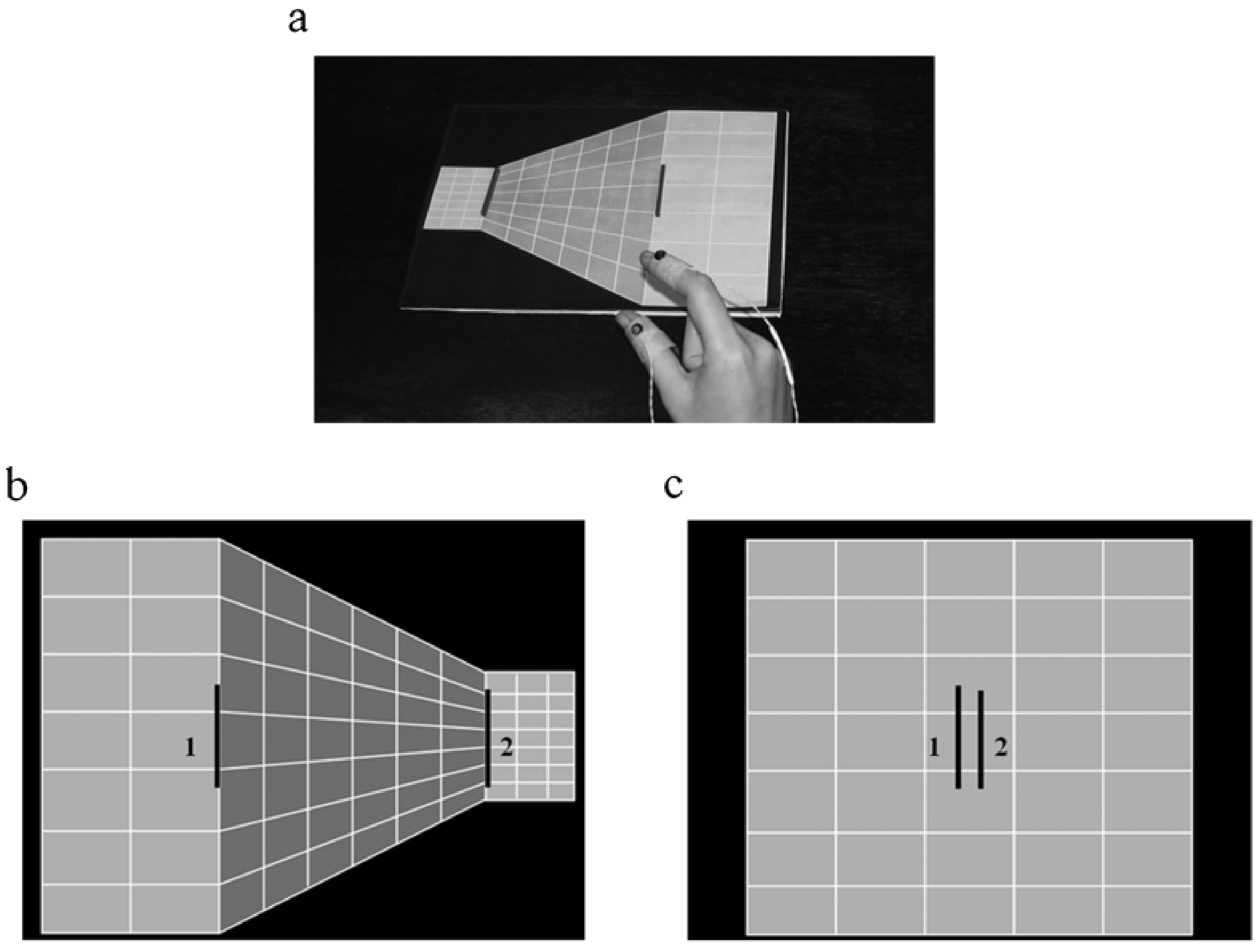

Fig. 1. Stimuli and experimental design. The illustration in (a) shows the overall setup. Distance between the fingers was measured with an Optotrak Certus device, which tracked the 3-D position of three infrared light-emitting diodes attached separately to each participant's index finger, thumb, and wrist with small pieces of surgical tape. The diagram in (b) illustrates the arrangement of the objects on critical incongruent trials, in which real size and the illusory size were pitted against one another. In this example, Object 1 is typically perceived as shorter than Object 2 (because of the illusory context), although it is actually longer. The real difference in size can be seen clearly in (c), which shows the two objects placed next to one another (for illustrative purposes) on the nonillusory control display.

object at the converging end of the display is erroneously perceived as longer than the other (see Fig. 1). In our experiments, however, the two target objects were always different in length. Critically, these different lengths were chosen on the basis of pilot testing to create a large number of trials in which the object that was perceived as the longer one was actually the physically shorter one (Figs. 1b and 1c). Our analyses focused on this subset of trials in which participants' perceptual judgments were erroneous. Participants were instructed to grasp either the shorter or the longer object by its ends, and we tested whether the opening between the fingers of the grasping hand reflected their erroneous judgment or the real size of the objects.

METHOD

In Experiments 1a and 1b, 27 right-handed healthy volunteers (14 participants in Experiment 1a, 13 different participants in Experiment 1b) were seated in front of a tabletop on which the illusory context and the two objects were presented. Participants were asked to grasp one of the objects by its ends (Experiment 1a) or to make psychophysical estimates of its length by opening their index finger and thumb a matching amount (Experiment 1b; see also Ganel & Goodale, 2003). Such manual estimations are affected by perceptual processing and are probably controlled by the ventral stream (see Ganel & Goodale, 2003; Haffenden & Goodale, 1998). Prior to each trial, participants were asked to place the thumb and index fingers of their right hand on a starting position while depressing a button located on the tabletop. Chair height was adjusted so that each participant would be able to grasp the objects comfortably. The distance between the two objects was 12 cm, and the imaginary midline between the objects was located 15 cm from the starting position. Viewpoint was not fixed during the experiments. Vision was controlled using computer-controlled PLATO goggles (Translucent Technologies, Toronto, Ontario, Canada) with liquid-crystal shutter lenses. Grip amplitude (and manual length estimations in Experiment 1b) were recorded by an Optotrak Certus device (Northern Digital, Waterloo, Ontario, Canada), which tracked the 3-D position of three infrared light-emitting diodes attached separately to the participant's index finger, thumb, and wrist.

Following a short practice and equipment-calibration block, 40 experimental trials were presented. On each trial, a verbal command ("long" or "short") was followed by the opening of the goggles, so that vision was allowed. After a 1.5-s delay, an auditory "go" command (a short beep) sounded. Participants were to grasp or estimate either the longer or the shorter object, depending on the earlier verbal command. In Experiment 1b, participants moved their thumb and index finger to a position about 5 cm to the right or left of the starting position in order to indicate whether the object on the left or the right was the target object, and indicated their size estimation at that position. They were asked to hold their fingers still for at least 1 s so that their responses could be properly recorded. To ensure that participants in the two experiments had equivalent haptic feedback, we asked participants in Experiment 1b to pick up the object after estimating its length. In both experiments, vision was occluded 3.5 s following the onset of each grasp.

Twenty-four of the experimental trials were critical incongruent trials, in which the long object was 42 mm long and the short object was 40 mm long, and illusory and real size were pitted against one another (i.e., the difference in the objects' physical size was in the direction opposite that of the size difference induced by the illusion). In most of these cases, participants erroneously decided that the longer object was actually the shorter one, or vice versa (88.49% of the trials in the grasping experiment; 88.16% of the trials in the estimation experiment). To prevent participants from adopting automated decision strategies, we included eight catch incongruent trials; as in the critical incongruent trials, illusory and real size were pitted against one another, but in this case the difference in physical length of the objects was more noticeable (49 mm and 42 mm). For the same reason, we included eight congruent trials, in which the real and illusory size differences went in the same direction. The presentation order of these different trials was pseudorandomized.

The main dependent variable of interest in the grasping experiment was the anticipatory opening between the thumb and index finger during grasping movements. To measure this, we used the maximum grip aperture (MGA), which is known to be well correlated with the size of the goal object (Jakobson & Goodale, 1991). The main dependent variable of interest in the estimation experiment was the opening between the fingers during psychophysical length estimation.

To establish baseline performance, we conducted two control experiments (8 participants in the grasping control experiment, 9 participants in the estimation control experiment) using the same experimental design but with a control display (see Fig. 1c) instead of an illusory display. An additional open-loop experiment in which vision was blocked during the execution of the grasp (Jakobson & Goodale, 1991) was conducted to refute the possibility that participants used vision on-line to compare the relative position of the fingers and the edges of the object. The design was similar to that used in Experiment 1a; each trial began with a verbal command ("long" or "short"), followed by a 1.5-s delay during which the goggles were open and then the auditory "go" signal. The difference was that vision was occluded immediately when participants (21 volunteers) initiated their grasping movements. To minimize the possibility of fumbling, the experimenter reinstated vision manually at the moment the participants' fingers made contact with the object or were near the end of the reaching movement. (In a follow-up movement analysis, we compared when the goggles opened and when MGA was reached on each trial. Trials in which the goggles opened before the participant reached MGA were discarded from the analysis.)

RESULTS AND DISCUSSION

As Figure 2 (top panel) shows, despite the fact that participants in Experiment 1a erroneously perceived the physically longer object to be the shorter one, the opening of the fingers in flight as participants reached out to grasp the objects reflected the real difference in size between them, $t(13) = 2.63$, $p_{\text{rep}} = .92$. In other words, grip aperture reflected the real—not the illusory—size of the object. This pattern of results was robust, with the MGAs of 12 of the 14 participants being correctly tuned to the real size differences between the objects, despite the fact that these participants had made erroneous decisions about the relative sizes of the objects.

Note that these results by themselves provide the first clue that action and perception can be fully dissociated when real and illusory object size are pitted against one another. After all, on the same trials on which participants had erroneously decided that the shorter object was the longer one (or vice versa), the anticipatory opening between their fingers reflected the real direction and magnitude of the size differences between the two objects. Still, it could be argued that these findings reflect the fact that within a given trial, the overt decision about object size always preceded the grasp. In particular, it could be argued that grasping performance showed accurate tuning to real size differences as a consequence of the additional time during which participants were exposed to the stimuli during grasping. To refute this alternative account, we ran Experiment 1b, in which participants first made overt size decisions but then, instead of actually grasping the object, estimated its size by opening their finger and thumb a matching amount. The pattern of results was completely reversed, and estimates reflected the illusory, not the real, size of the objects (Fig. 2, top panel), $t(12) = 3.96$, $p_{\text{rep}} = .98$. Not surprisingly, therefore, we found a significant interaction between object size and experiment, $F(1, 25) = 21.63$, $\eta_p^2 = .46$, $p_{\text{rep}} > .99$. In other words, the real and apparent differences in the size of the objects had opposite effects

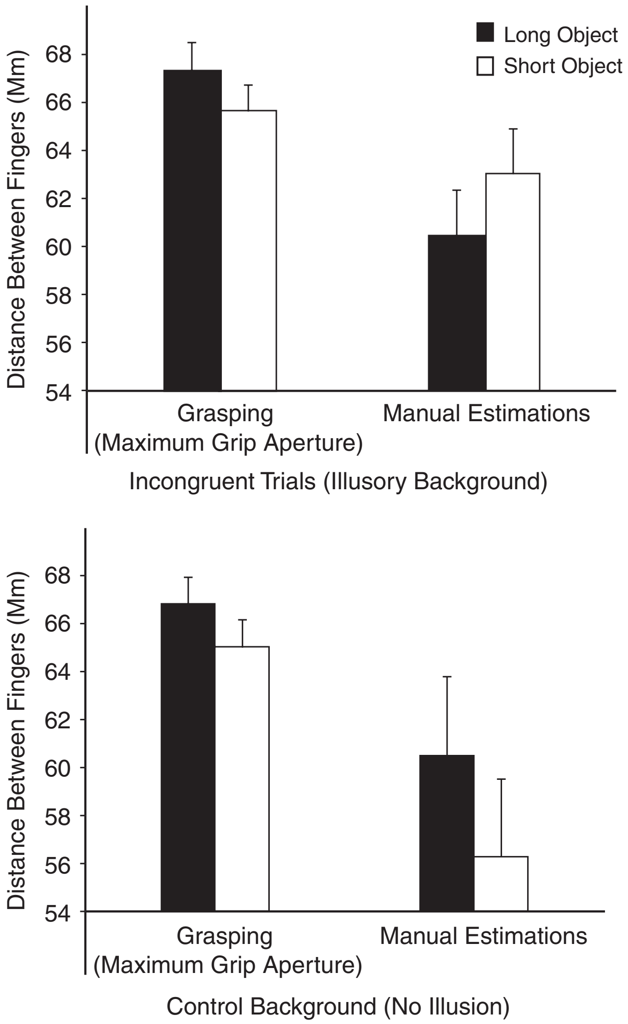

Fig. 2. Results of Experiments 1a and 1b (top panel) and the control experiments (bottom panel). For incongruent trials, only those on which participants made erroneous decisions about real size are included. Error bars represent standard errors.

on action (grasping) and perception (manual estimation) in the two experiments.

Comparison of Experiment 1a with its control experiment (Fig. 2, bottom panel) revealed no differences in grasping performance between the illusory and control conditions, $F(1, 20) < 1$. In contrast, the comparison between Experiment 1b and its control experiment (Fig. 2, bottom panel) revealed that the manual estimations of object size in the context of the illusory display went in the direction opposite that of the manual estimations made in the context of the control display, $F(1, 20) = 67.23$, $\eta_p^2 = .77$, $p_{\text{rep}} > .99$.

As Figure 2 shows, the illusory display had a more pronounced effect on manual estimation of the short object, $t(12) = 1.93$, $p_{\text{rep}} = .85$, than of the long object, $t(12) < 1$. This asymmetric effect on estimations could have resulted from the fact that on incongruent trials, the short object was placed on the side of the display that is typically perceived as the more "distant" side (the right-hand side in Fig. 1b). Compared with the control display (Fig. 1c), this side is perceived as more distant in the vertical plane; in contrast, the "closer" side (on which the long object was placed) is typically perceived to be on the same plane as the control background. Thus, the more pronounced effect of the illusion on the short object probably arose from the asymmetric depth effect produced by the two sides of the Ponzo-illusion display.

To explore the possibility that the illusion could have affected grip aperture before the MGA was reached, we conducted an analysis of changes in grip aperture throughout the movement in Experiment 1a. Movement times from initiation of the movement to the point at which MGA was achieved were computed and normalized (in terms of percentage of movement time; for a similar analysis, see Glover & Dixon, 2001) for each trial. Specifically, six movement time points were analyzed: 15%, 30%, 45%, 60%, 75%, and 90% of the total movement time to reach MGA. A similar analysis was conducted for the grasping control experiment. Data from 1 subject in the control experiment were omitted because of a large proportion of missing data points during the initial portion of many of the grasps.

Overall, comparable patterns of results were found for the experimental and control trials: Both showed that the difference in grip aperture between long and short objects increased as movement progressed. At 90% of movement time prior to reaching MGA, grip apertures were significantly tuned to the real difference in size between the two objects in both Experiment 1a, $t(13) = 3.26$, $p_{\text{rep}} = .96$, and the control experiment, $t(6) = 3.64$, $p_{\text{rep}} = .95$. Moreover, as in the control experiment, grip apertures in Experiment 1a did not show an influence in the direction of the illusion at any of the time points analyzed. There was, however, some indirect evidence that the effects of the real difference in the size of the objects might have emerged earlier in the control trials than in the experimental trials. In the control experiment, the difference in grip apertures for long and short objects was significant at the 75% point in the movement prior to reaching MGA, $t(7) = 2.42$, $p_{\text{rep}} = .87$, but this difference was not evident at the same time point in Experiment 1a, $t(13) < 1$. Although these results are not inconsistent with the idea that perceptual effects can intrude upon grasping during early stages of action (Glover & Dixon, 2001), there was no direct evidence for an effect of the illusion in Experiment 1a.

The results of the open-loop experiment, in which vision was occluded during grasping, replicated those of Experiment 1a. Specifically, the direction of MGAs reflected the real size differences between the two objects (73.29 mm for the long object and 72.47 mm for the short object), $t(20) = 2.2$, $p_{\text{rep}} = .89$. A between-subjects analysis of variance comparing the results of this experiment and of Experiment 1a revealed no interaction between experimental condition (no vision, full vision) and object size, $F(1, 33) = 1.68$, $\eta_p^2 = .05$, $p_{\text{rep}} > .72$. The main effects of object size, $F(1, 33) = 13.12$, $\eta_p^2 = .28$, $p_{\text{rep}} = .99$, and experimental condition, $F(1, 33) = 7.98$, $\eta_p^2 = .19$, $p_{\text{rep}} = .96$, were both significant. In particular, MGAs in the open-loop experiment were 6.42 mm larger overall compared with MGAs in Experiment 1a (see Fig. 2). Such an increase in MGAs is typical of open-loop conditions and of other conditions that induce uncertainty during grasping movements (Jeannerod & Biguer, 1982; Westwood & Goodale, 2003).

Note that although the effect was not statistically significant, there was a trend for a smaller size effect in the open-loop experiment (0.82 mm) than in the grasping experiment (1.74 mm). In other words, although in both experiments the opening between the fingers reflected the direction of the real, rather than the illusory, size difference between the two objects, a smaller effect size was obtained in the open-loop experiment. One possible explanation for this pattern of results is that grasping in the open-loop experiment could have been based, at least in part, on memory representations of the visual array. Such memory representations have already been shown to be based on perceptual information and affected by visual illusions (Westwood & Goodale, 2003), which could explain why the effect size was smaller in the open-loop experiment than in Experiment 1a. This pattern of results is also in agreement with the analysis of changes in grip aperture throughout the movement in Experiment 1a, which indicated that the illusion may have had a small effect on grasping during early stages of movement.

Yet findings that interactions between action and perception sometimes occur are not surprising; after all, there are many instances in which the two visual systems could interact (see Culham & Valyear, 2006). The power of our design is that it goes beyond the question of whether or not the two systems interact and instead tests whether or not they are functionally distinct. The fact that we found a double dissociation between action and perception in the context of a visual illusion strongly supports the idea that vision for action and vision for perception can function independently in healthy individuals. These findings also converge with similar dissociations found in both neuropsychological (Goodale, Milner, Jakobson, & Carey, 1991; Perenin & Vighetto, 1988) and neuroimaging (Shmuelof & Zohary, 2005) studies. More important, our findings provide compelling evidence that vision for action works with real-world metrics, reflecting the actual dimensions of objects, and that these metrics are computed independently of the scene-based metrics delivered by vision for perception, which are typically influenced by contextual cues.

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