Hemispheric Specialization for the Visual Control of Action Is Independent of Handedness

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Gonzalez, Claudia L. R., Tzvi Ganel, and Melvyn A. Goodale. Hemispheric specialization for the visual control of action is independent of handedness. J Neurophysiol 95: 3496–3501, 2006. First published February 22, 2006; doi:10.1152/jn.01187.2005. The idea that visually guided action is independent of visual perception has been supported by neurological, neuropsychological, and behavioral studies. In healthy subjects, evidence for this distinction has come from psychophysical studies of the effects of visual illusions on perceptual judgments and object-directed grasping. This evidence is limited, however, by the fact that virtually all studies have involved right-handed subjects using their dominant hand, which is presumably controlled by the left hemisphere. There is tentative evidence from earlier neurological studies that the left hemisphere may in fact play a special role in the integration of visual and motor information during grasping. We designed two experiments to test this idea. The first experiment involved pictorial illusions, which are known to have robust effects on perceptual judgments but little influence on grasping. Right- and left-handed subjects reached out and grasped objects embedded in two different visual illusions with either their dominant or their nondominant hand. For both right- and left-handed subjects, precision grasping with the left hand, but not with the right, was affected by the illusions. In a follow-up experiment, we examined precision grasping in a more natural setting and showed that left-handed subjects use their nondominant (right) hand significantly more as compared with right-handed subjects. We conclude that visuomotor mechanisms encapsulated in the left hemisphere play a crucial role in the visual control of action and that this hemispheric specialization evolved independently of handedness.

INTRODUCTION

According to Goodale and Milner’s two-visual-systems proposal (Goodale and Milner 1992; Milner and Goodale 1993), the ventral stream of visual projections provides the rich and detailed perceptual representation of the world, whereas the dorsal stream provides the flexible control required to act on that world. Studies of neurological patients have provided considerable support for this proposal (Goodale et al. 1991; James et al. 2003; Jeannerod et al. 1994). In healthy subjects, some of the most compelling (but controversial) evidence for a dissociation between vision-for-perception and vision-for-action has come from psychophysical studies of the effects of visual illusions on perceptual judgments and object-directed grasping. Numerous studies have shown that pictorial illusions, which—by definition—have a robust effect on perceptual judgments, have little or no effect on the scaling of grip aperture during grasping (Aglioti et al. 1995; Dewar and Carey 2006; Haffenden et al. 2001). Other studies have reported contradictory findings, however, showing that both perceptual judgments and grasp can be affected by the same visual illusion (Franz 2001; Franz et al. 2000, 2003; Pavani et al. 1999).

Remarkably, almost all of these studies are based entirely on evidence from right-handed subjects using their dominant hand. In none of these studies has performance with the right hand been compared with performance with the left. Yet there is reason to believe that the resistance to visual illusions during grasping might be limited to situations in which people use their right hand. There is some neurological evidence, for example, that target-directed movements with the right hand are more severely impaired after damage to the left hemisphere than are similar movements with the left hand after damage to the right hemisphere. This evidence comes from the study of patients with optic ataxia, who show a “hand” effect after damage to the left but not the right posterior parietal cortex (Perrinet and Vighetto 1988). In other words, these patients have great difficulty reaching toward objects and shaping their grasp appropriately with their right hand anywhere in space. With their left hand, however, the deficit is apparent only in the contralesional hemisphere. Patients with right-hemisphere damage show a contralesional field effect but not the hand effect. This neurological evidence suggests that the encapsulated visuomotor networks that mediate rapid target-directed movements may have evolved preferentially in the left hemisphere alongside the well-established specialization of the left hemisphere for the selection of hand postures and other complex movements (praxis) (Fisk and Goodale 1988; Gazzaniga 2000; Koski et al. 2002).

To test this idea, we compared grasping in the right and left hands of neurological intact participants. In our main experiment, we asked right- and left-handed participants to reach out and grasp simple objects embedded in two different size-contrast illusions (the Ponzo and Ebbinghaus illusions). We included left-handed participants to eliminate the possibility that any right hand advantage in right-handers was simply a reflection of using that hand more often in interacting with the world. After all, it is widely believed that hemispheric “specialization” is organized in most left-handers much the same way as it is in right-handers. This is certainly true for the control of speech (Bryden 1982; Kimura 1993) and there is some suggestion that this is also the case for praxis (Frey et al. 2005; Meador et al. 1999). Whether this left-hemisphere spe-
cialization extends to visuomotor control is unknown, and thus by testing left-handers we had an opportunity to examine this possibility. In other words, if there is indeed a left-hemisphere specialization for visuomotor control, then the right hand in both left- and right-handers should be resistant to pictorial illusions, whereas the left hand in both groups might be vulnerable to these same illusions.

In addition to our illusion experiments, we also examined precision grasping in a more natural setting. For this experiment, participants had to put a puzzle together or to create different figures with small LEGO® pieces without specific instruction about which hand to use. This allowed us to measure spontaneous hand preference in a task requiring natural grasping.

**METHODS**

**Experiment 1: grasping illusions**

**SUBJECTS.** Eleven right-handed (10 females, one male) and nine left-handed (five females; four males) participants were tested in the Ponzo illusion (see Fig. 1), and 13 right-handed (seven females; six males) and 13 left-handed (six females; seven males) participants were tested in the Ebbinghaus illusion (see Fig. 1). Handedness was assessed by a modified version of the Edinburgh Handedness Inventory (Oldfield 1971), where the criterion for inclusion was scores >70 or ≤70 for right- or left-handers, respectively. The studies were approved by the local ethics committee and all participants gave written informed consent before participating in this study.

**APPARATUS AND STIMULI.** Grip scaling and reaction times were recorded by an Optotrak (Northern Digital, Waterloo, ON, Canada), which tracked the three-dimensional (3D) position of three infrared light-emitting diodes attached separately to each participant’s index finger, thumb, and wrist with small pieces of surgical tape, allowing complete freedom of movement of the hand and fingers.

Illusions and control displays were mounted on black foam board (25 × 19 cm × 5 mm thick) and rested on a black wooden table.

**The Ponzo illusion.** Targets were 3-mm-thick black plastic rectangles 10 mm wide with heights of 40 (small) or 50 (big) mm. The target objects were placed against one of two 2D background contexts, one showing the Ponzo figure and the other one a gray board marked with grid lines that served as a control background (Fig. 1). Across the two contexts, the absolute location of the objects remained the same. During the illusion trials, two identical stimuli were placed against the background (either two small rectangles or two big ones); for the control trials, one of each (a small rectangle and a big one) was placed on the right and on the left of the display in counterbalanced order.

**The Ebbinghaus illusion.** Target disks were constructed of 3-mm-thick white plastic material with diameters of 25 (small) or 31 (big) mm. The disks were placed against the illusion or the control backgrounds (Fig. 1). The illusion and control backgrounds were similar to those used in previous grasping experiments with the Ebbinghaus illusion (Haffenden and Goodale 1998). The experimental display consisted of an annulus of small circles (each of the 11 circles was 10 mm in diameter) and an annulus of large circles (each of the five circles was 50 mm in diameter). The inner diameter of the small annulus was 39 mm and the inner diameter of the large annulus was 55 mm. The centers of the two annuli were 120 mm apart. The control display consisted of two identical annuli of medium-sized circles (each of the eight circles was 22 mm in diameter). The inner diameters of the annuli were 41 mm and the centers of the two annuli were 120 mm apart. During the illusion trials, the two identical disks were placed against the 2D illusory background (either the two small disks or the two big ones) and for the control trials one of each (a small disk and a big one) was placed on the right and left of the 2D control display in a counterbalanced order.

**PROCEDURES.** Participants were seated in front of a black tabletop on which the objects were placed at a viewing distance of about 60 cm.

**FIG. 1.** Examples of stimuli used in the main experiment. Ponzo (A) and Ebbinghaus (C) displays and stimuli. Two objects that are seen against the two-dimensional (2D) illusory background are usually perceived as different in size, although they are identical. In the control conditions (B and D), 2 different stimuli were placed against a matched, but nonillusory background. Note scales on the diagrams of the illusion and control displays.
(35 cm from a start button). Participants wore PLATO liquid-crystal goggles (Translucent Technologies) that changed from clear to opaque to control stimulus-exposure time. In both the Ponzo and Ebbinghaus experiments, participants were asked to grasp simple objects embedded in the illusory or control displays using a precision grip (index finger and thumb). The control trials were included to test for possible differences in grip scaling between the two hands. Participants started with their thumb and index finger pinched together, pushing down on the start button. All trials began with the verbal command “big” or “small” accompanied by a full view of the display. Once the participants had released the start button they had a full view of the display for 1,000 ms at the end of which the goggles became opaque. Participants were instructed to pick up the appropriate target stimulus based on the verbal command and their initial impression of size. Starting hand was counterbalanced between participants. Each hand was given a practice block of 24 trials followed by an experimental block of 24 trials. Each block consisted of 16 illusion trials and eight control trials presented in random order. For the illusion trials, the display’s orientation (left–right orientation) was randomized.

DATA ANALYSIS. The main dependent measure was the maximum grip aperture (MGA; the maximum distance between the index finger and thumb achieved in flight during the grasp). The effects of the size contrast illusions were expressed in millimeters by subtracting the MGA of the small object from the MGA of the big object for the different hands and handedness groups.

1) Ponzo illusion: left-handers, lh = 9.2 mm, rh = 9.3 mm; right-handers, lh = 10 mm, rh = 8.3 mm. 2) Ebbinghaus illusion: left-handers, lh = 5.8 mm, rh = 6.3 mm; right-handers, lh = 6.0 mm, rh = 6.4 mm. A TWO-way ANOVA between group (right and left-handed participants) and hand (left and right) for the control trials in the Ponzo experiment showed no main effect of group, $F(1,18) < 1$; no main effect of hand, $F(1,18) < 1$; no significant interaction between group and hand, $F(1,18) = 3.4, P = 0.08$. Similarly, no main effect of group, $F(1,24) < 1$; no main effect of hand, $F(1,24) < 1$ and no significant interaction between group and hand, $F(1,24) < 1$ were found for the control trials in the Ebbinghaus experiment.

In sharp contrast to the control data and regardless of handedness, grip aperture in the left hand was more affected by the illusory displays than grip apertures in the right hand (Fig. 2). Thus when grasping with their left hand, both right- and left-handed participants opened their left hand wider for the target that was perceived as the bigger one than they did for the target that was perceived as the smaller one, even though both targets were identical in size. For the Ponzo illusion in the left-handed group, seven of nine participants showed a greater effect of the illusion in the left hand when compared with the right. In the right-handed group nine of 11 showed this pattern. For the Ebbinghaus illusion, 10 of 13 left-handed participants and 11 of 13 right-handed participants were more affected by the illusion with the left hand.

For the Ponzo illusion, a two-way ANOVA between group (right- and left-handers) and hand (right and left hand) revealed a main effect of hand, $F(1,18) = 17.25, P < 0.001$, no effect

**Experiment 2: natural grasping**

The same participants that participated in the Ebbinghaus illusion (13 right handed and 13 left handed) were recruited for this experiment. The 24 pieces (about $8 \times 6$ cm) of a Disney© puzzle or the 95 LEGO© pieces ($1 \times 0.5$ cm, the smallest; $1.5 \times 6$ cm, the biggest) were randomly distributed across a tabletop (Fig. 3). Participants were instructed to reproduce models as fast and as accurately as possible; 3 min were given for the puzzle and 5 min for the LEGO©. Participants were videotaped and hand preference for grasping in ipsilateral and contralateral space was measured by judges who were blind to the purpose of the experiment.

**RESULTS**

**Experiment 1: grasping illusions**

Fewer than 10% of the trials were categorized as error trials and were omitted from the analyses. There were no differences between the hands with respect to these eliminated trials. Nevertheless, it is important to note that when these error trials were included in the analysis, the results were virtually identical to those described below. All participants in all groups started their movements within the 1,000-ms period of full vision. Moreover, there were no differences in movement time between the two hands.

For the control trials in the Ponzo and Ebbinghaus experiments, no differences were found in grip aperture between the left and right hands of right- or left-handers, which in both groups were equally affected by real differences in the size of the target object. We compared the slopes of the MGA by subtracting the MGA of the small object from the MGA of the
of group \(F(1,18) = 3.2, P > 0.05\), and no significant interaction between group and hand \(F(1,18) = 3.9, P > 0.05\). Similarly, for the Ebbinghaus illusion, a main effect of hand \(F(1,24) = 16.29, P < 0.001\), no effect of group \(F(1,24) = 0.01, P > 0.05\), and no significant interaction between group and hand \(F(1,18) = 1.1, P > 0.05\) were found.

To further explore the effect that the illusions had on each hand, one-sample t-tests (with test value = 0) were carried out in each group to determine whether the mean for each hand differed from zero. We found that, in right-handers, both illusions had a strong effect on grip aperture in the left hand \([Ponzo: t(10) = 4.0, P < 0.01; Ebbinghaus: t(12) = 4.0, P < 0.01]\). Conversely, grasping with the right hand remained unaffected by the visual illusions \([Ponzo: t(10) = 1.5, P = 0.15; Ebbinghaus: t(12) = 1.4, P = 0.18]\). In the left-handers, both illusions again affected grasping with the left hand \([Ponzo: t(8) = 3.6, P < 0.01; Ebbinghaus: t(12) = 4.2, P < 0.001]\). The effect of the Ebbinghaus illusion on grasping with the right hand was not significantly different from zero \([t(12) = 1.5, P = 0.14]\). There was, however, a significant effect of the Ponzo illusion on the right hand in the left-handed participants \([t(8) = 3.36, P < 0.01]\).

Because it has been suggested that females are more susceptible to the perception of visual illusions (Grabowska et al. 1999), we tested for possible gender differences in our illusion experiments. A two-way ANOVA with gender (female and male) and hand (left and right) was performed on the right- and left-handed participants. No main effect of gender or interaction was found to be significant in either handedness group \((P > 0.1)\).

**Experiment 2: natural grasping**

Although right-handers, as expected, showed a marked preference for their dominant hand when picking up objects (78%), left-handers did not show this preference and in fact used their right hand 52% of the time. Furthermore, compared with right-handers, left-handers used their nondominant hand significantly more often to pick up objects in both ipsilateral and contralateral space \((P < 0.01; \text{Fig. 3})\). Thus although left-handers do not use their right hand as often as right-handers, they nevertheless show evidence that their handedness does not extend to precision grasp. Instead the right hand/left hemisphere advantage for grasping attenuates their “left-handedness” and emerges when they have to pick up small objects quickly and accurately.

**DISCUSSION**

Little is known about the specific mechanisms that contribute to the resistance of grasping to visual illusions. There is some suggestion that the visuomotor networks controlling grasping make use of information derived from vergence and retinal image size, rather than pictorial cues, to fine-tune grip aperture (Krolickz et al. 2005; Marotta et al. 1997, 1998). Whatever the specific cues might be, in this study, we have shown that left-hemisphere mechanisms play a crucial role. Overall, target-directed movements with the right hand showed greater resistance to visual illusions than movements with the left hand, even in left-handers. Our results are consistent with the fact that patients with optic ataxia after a left-hemisphere lesion show a “hand effect” as well as a contralateral field effect, whereas patients with a right-hemisphere lesion show only a field effect (Perenin and Vighetto 1988).

The results of our study also converge nicely with a recent study by Radoeva and colleagues (2005) of patients with left- and right-hemisphere brain damage. Patients with right-hemisphere damage showed normal sensitivity to the Müller–Lyer illusion when estimating the length of a target object, but showed no effect when grasping the same object with their right hand. In contrast, patients with left-hemisphere damage were susceptible to the illusion when estimating the length of the object and also when grasping it with their left hand. Although the patients in the Radoeva et al. study were not tested with the contralesional hand (because the patients were hemiparetic), their results are consistent with a model that posits a special role for the left hemisphere in visuomotor control. One puzzling difference between their study and ours is that they found that both hands (in right-handers) were affected by the illusion and to the same degree. Even though we cannot offer a definitive account for the disparity between the two studies, we suspect that it is related to differences in

![Hand preference](image)

![Grasps with Non-Dominant Hand](image)

**Fig. 3.** A and B: examples of the puzzle and LEGO® displays used in experiment 2. C: illustration of hand preference for grasping in ipsilateral and contralateral space \((±SE)\). Note that left-handers used their nondominant hand more frequently than right-handers.
procedure. One possible explanation could be that the method Radoeva et al. used to record grip aperture, which was some-
what intrusive, constrained the hand and thus led to a more awkward grasp. We recently found (Gonzalez et al. 2006) that the more unpracticed and awkward the grasp (even with the right hand), the more likely it is that the grip aperture will be susceptible to visual illusions. We have speculated that these more deliberate actions might not engage the “automatic” visuomotor control mechanisms but would instead invoke cognitive control that is dependent on perceptual processing.

As we suggested earlier, it is possible that the left-hemisphere advantage for visuomotor control is related to the specialization of this hemisphere for praxis. In this regard, it is interesting to note that a similar right-hand/left-hemisphere advantage has been observed in both left- and right-handed callosotomy patients asked to pantomime actions associated with tools (Frey et al. 2005). Again it appears that the left hemisphere can demonstrate its special relationship with the right hand even in left-handers (see also Meador et al. 1999). The idea that praxis and visuomotor control are intimately related is just a conjecture of course, but it seems likely that the precision required for rapid and accurate movements of the hands and fingers during grasping could capitalize on the availability of praxis networks in the left hemisphere. In any case, our results point to a special role for this hemisphere in visuomotor control that is reflected in a right-hand advantage for precision grasping. The fact that in left-handers, grasping with the right hand showed sensitivity to one of the illusions (although this effect was never as large as that seen in the left hand) may suggest that the distribution of networks controlling visuomotor behavior are somewhat different from those of right-handers. In fact, there may be individual differences in the organization of these networks, even in right-handers. After all, a small number of individuals in both handedness groups showed sensitivity to the illusion when grasping with the right hand. Whether this reflects an underlying difference in the neural substrates of visuomotor control remains to be explored—particularly in neurological populations. There are, for example, some reports of apraxia after right-hemisphere damage (e.g., Marchetti and Della Sala 1997; Raymer et al. 1999), even though the evidence for left-hemisphere specialization for praxis is well established (for review, see Bryden 1982; Kimura 1993).

Although our findings suggest a right-hand/left-hemisphere advantage for visuomotor control, it is not yet clear whether this advantage extends beyond grasping to other visually guided actions such as reaching or pointing. Certainly there is evidence that the areas in the dorsal stream that mediate the visual control of grasping components of prehension movements are distinct from those mediating the visual control of the reaching (or transport) components (Tunik et al. 2005). Because the emphasis of the current work was on the scaling of grasping rather than the control of reaching, additional research is needed to determine whether hemispheric lateralization is also a factor in the visual control of target-directed reaching movements.

The results of our study also provide additional support for the two-visual-systems proposal put forward by Goodale and Milner (1992). If there were only one visual system serving both perception and action, then there should be no difference between the sensitivity of the right and left hands to pictorial illusions. Our demonstration that the right hand shows greater resistance to size-contrast illusions than the left provides compelling evidence that the visuomotor networks controlling grasping (in the right hand) make use of visual information that is different from that used by the networks driving our perception.

It is important to note that our experiment was designed to maximize the effect of the size-contrast illusion. In other words, not only did we present two target objects at the same time (thus invoking a direct comparison between them), but we also instructed participants to choose the target that appeared to be bigger (or smaller), which again highlighted the apparent difference in size. It has been suggested that presenting two targets rather than one on such illusory displays can lead to an underestimation of the effect of the illusion on grip scaling (Franz et al. 2000). According to this argument, a perceptual judgment, which would quite naturally take into account the apparent difference in size between the two targets, cannot be directly compared with the effect of the illusion on the scaling of a grasping movement, which would be directed at only one of the targets. This may or may not have been a legitimate concern in a number of earlier studies, but it has no bearing on our experiment in which we did not directly compare perceptual judgments with grip scaling. We were instead interested in finding out whether a powerful size-contrast illusion would have different effects on grasping with the left or right hand. Finally, it should be noted that emphasizing the apparent difference in size by using the words big and small could potentially have affected grip scaling through some sort of language-based influence on motor programming (Gentilucci and Gangitano 1998; Glover et al. 2004). If this were the case, however, then one would expect the right hand to be affected by the illusions, particularly in the right-handers; yet we saw no evidence for this.

One other possible explanation for our illusion findings invokes right- rather than left-hemisphere specialization. The sensitivity of the left hand to the size-contrast illusions may reflect the well-known specialization of the right hemisphere for visuospatial processing. In other words, the use of the left hand might have preferentially engaged the right hemisphere and thus precision grasping with the left hand would reflect any perceptual bias that was present, although this possibility is unlikely. First of all, it begs the question as to why the right hand escaped the perceptual bias. Second, it has been shown that pictorial illusions presented separately to each visual hemifield have equivalent effects on observers’ judgments (Bertelson and Morais 1983). Finally, patients with right- or left-hemisphere damage are both affected by pictorial illusions (Grabowska et al. 1992; Radoeva et al. 2005).

In summary, the results of the present experiment suggest that, regardless of handedness, the left hemisphere plays a special role in the visual control of skilled grasping movements. This hemispheric specialization could be another piece of the puzzle surrounding the evolutionary origins of handedness.

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