Neuropsychologia 47 (2009) 1421–1433

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

When is grasping affected by the Müller-Lyer illusion? A quantitative review

Nicola Bruno [a,*], Volker H. Franz [b]

[a] Dipartimento di Psicologia, Università di Parma, Parma, Italy
[b] Abteilung Allgemeine Psychologie, Justus-Liebig-Universität Gießen, Gießen, Germany

ARTICLE INFO

Article history:
Received 31 March 2008
Received in revised form 28 August 2008
Accepted 22 October 2008
Available online 19 November 2008

Keywords:
Perception
Action
Grasping
Müller-Lyer illusion
Meta-analysis

ABSTRACT

Milner and Goodale (1995) [Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford, UK: Oxford University Press] proposed a functional division of labor between vision-for-perception and vision-for-action. Their proposal is supported by neuropsychological, brain-imaging, and psychophysical evidence. However, it has remained controversial in the prediction that actions are not affected by visual illusions. Following up on a related review on pointing (see Bruno et al., 2008 [Bruno, N., Bernardis, P., & Gentilucci, M. (2008). Visually guided pointing, the Müller-Lyer illusion, and the functional interpretation of the dorsal-ventral split: Conclusions from 33 independent studies. *Neuroscience and Biobehavioral Reviews, 32*(3), 423–437]), here we re-analyze 18 studies on grasping objects embedded in the Müller-Lyer (ML) illusion. We find that median percent effects across studies are indeed larger for perceptual than for grasping measures. However, almost all grasping effects are larger than zero and the two distributions show substantial overlap and variability. A fine-grained analysis reveals that critical roles in accounting for this variability are played by the informational basis for guiding the action, by the number of trials per condition of the experiment, and by the angle of the illusion fins. When all these factors are considered together, the data support a difference between grasping and perception only when online visual feedback is available during movement. Thus, unlike pointing, grasping studies of the Müller-Lyer (ML) illusion suggest that the perceptual and motor effects of the illusion differ only because of online, feedback-driven corrections, and do not appear to support independent spatial representations for vision-for-action and vision-for-perception.

1. Introduction

More than a decade ago, David Milner and Melvyn Goodale proposed a novel functional interpretation of the primate visual system. In their proposal, set forth in the influential book *The visual brain in action* (Milner & Goodale, 1995) and later popularized in their wonderfully accessible *Sight unseen* (Goodale & Milner, 2004), they suggested that the dorsal–ventral anatomical split after the primary visual cortex may be interpreted as the neural substrate of two independent visual modules: a vision-for-perception module (the V1–IT ventral pathway) and a vision-for-action module (the V1–PPT dorsal pathway). Although dichotomous models of the visual system were not new (Trevarthen, 1968; Ungerleider & Mishkin, 1982), the proposal substituted the earlier problematic distinction between "what" and "where" pathways with a more powerful distinction between two visual functions: recognizing and identifying objects (vision-for-perception) and guiding actions (vision-for-action). The idea has proved attractive, not only for its potential to resolve a long-standing controversy in perceptual theory (see for instance Norman, 2002) but also for its success in explaining a number of empirical facts in diverse research domains such as neuropsychology, functional imaging, and psychophysics.

Despite its success, however, the hypothesis of Milner and Goodale has remained controversial with regard to the degree of "encapsulation", or functional independence, between the two visual functions. Milner and Goodale made the strong prediction that, under certain conditions, vision-for-action should operate on the basis of spatial representations that have different properties than, and are fully independent from, the spatial representations at the basis for our conscious experience. In support of this idea they listed several lines of evidence. In the striking phenomenon of "blindsight" (Weiskranz, 1986), for instance, patients with cortical scotomas can point to visual targets presented in blind areas of their visual field, but report that they have no experience of having seen those targets. Patients with visual form agnosia, such as the much-

* Corresponding author at: Dipartimento di Psicologia, Borgo Carissimi 10, 34100 Parma, Italy.
E-mail address: nicola.bruno@unipr.it (N. Bruno).

0028-3932/$ – see front matter © 2009 Published by Elsevier Ltd.
doi:10.1016/j.neuropsychologia.2008.10.031

studied D.F. (Milner, 1997), cannot identify the objects they see, and yet they can reach for and grasp them in ways that are comparable to those of a healthy control. But perhaps the most important, and certainly more controversial, line of empirical findings bearing to this issue has been research on motor responses to visual illusions.

Typical visual illusions are contextual effects. For instance, in the Ebbinghaus-Titchener illusion, the same disk appears larger when surrounded by smaller disks, and smaller when surrounded by larger disks (a size-contrast effect). In an influential paper, Aglioti, DeSouza, and Goodale (1995) hypothesized that the representation of the disk's size used in the vision-for-action module should be immune from such contextual effects. The rationale for the prediction was straightforward and descended directly from the two-visual-system hypothesis. Although both pathways receive the same information from primary visual cortex, this information may be processed in different ways for the purposes of action and perception. To guide actions towards the disk, visual information must be represented within a body-relative reference frame. Within this frame, the relationship of the disk to its surroundings is not important. For instance, to guide the hand towards the disk, what is important is the position of the hand relative to the disk itself. To grasp the disk, what is important is the size of the disk in relation to the current opening of the fingers. Thus, one may find that the kinematic parameters associated with a reach-to-grasp movement are not influenced by the contextual disks, even though the context of course influences the conscious perception of the target disks. This prediction was confirmed by data on the maximum in-flight grip aperture (MGA) of the thumb and index fingers while performing a precision grip of the disks embedded in the illusion. Aglioti and collaborators reported that the MGA remained constant, and correlated to the disk true width, even though participants judged the disks to be of different sizes. This finding quickly became popular under the heading that "size-contrast illusions deceive the eye but not the hand" (the paper's own title). But it also quickly stirred a heated controversy.

For the sake of concision, we will not attempt to summarize all the positions and issues that characterized the controversy (but see Bruno, 2001; Carey, 2001; Franz, 2001; Glover, 2002; Milner & Dyde, 2003). We will limit our discussion to two main points. The first concerns the methodology of perception–action comparisons. Soon after the publication of the early Aglioti paper, methodological criticism were raised casting doubts on the validity of the reported dissociation (Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farne, 1999). The brunt of these criticism consisted in pointing out that differences between the motor and perceptual stimulus conditions in the Aglioti experiment could account for the seeming dissociation without invoking separate representations of size in vision-for-action and vision-for-perception. In response to this and similar criticisms, as well as to novel findings reporting illusion effects in some conditions but not others, the focus of the controversy has steered towards a more articulated issue concerning the conditions under which actions responses may be insensitive, or at least less responsive, to illusions than perceptual responses. This debate has helped to clarify the different ways in which one may propose a distinction between spatial representations in vision-for-action and vision-for-perception, in turn allowing for better focusing of the related experimental predictions. Both are discussed in the section below.

1.1. Perception and action: where do we draw the line?

We suggest that there are five different ways in which one may cast a functional division of labor between perception and action, in particular with regard to the issue of independent representations. In addition, we propose that the vast literature on motor responses on illusions in fact contains quite a wealth of information to decide which may be true. Four of the five hypotheses assume that there are two independent representations, one for perception and one for action. For this reason, we will group them into the common category of two-visual-system hypotheses (TVSH) but parse them into the "naïve TVSH", "strong TVSH", "weak TVSH", and "planning-control TVSH". In addition, we also illustrate a fifth possibility, the "motor control hypothesis", which preserves the idea of a functional division of labor but rejects the notion of independent representations.

1.1.1. Naïve TVSH

Adopting a simple-minded conception of perception and motor control, one may propose that *any* motor response is based on a separate representation than that underlying conscious perception. This proposal is naïve, for it neglects that behavioral responses, be they in the form of object-directed actions or of verbal reports of one's conscious experience, always ultimately entail some kind of movement. For instance, speaking is needed for a verbal report but it is obviously also a motor response. Conversely, there are silent motor behaviors that one can perform to describe one's experience, such as gesturing or pantomime. And finally, a number of experimental results have shown that certain classes of motor responses are clearly affected by illusions just as much as phenomenal reports. Thus, naïve TVSH can be dispensed with. However, we deem it important to list it here, not only because this simple-minded account is sometimes found in literatures outside the cognitive neurosciences, but also because it helps us to focus on what is the theoretically relevant question at issue. This question is often stated in this way: "Do actions resist visual illusions?" If one refers this statement to actions in general, the answer is obviously no. A more relevant question is instead: "*When* do actions resist visual illusions?" As discussed in what follows, different answers to this question in fact correspond to different ways of conceiving the hypothesized independence between the two-visual systems, and to different theoretical implications of the answer.

1.1.2. Strong TVSH

In its strongest but non-naïve form, the notion of independent functions for action and perception proposes that a certain class of visually driven motor responses is based on representations that are fully independent of those employed to achieve conscious percepts. The exact definition of which responses have these properties is not completely clear, but there seems to be some consensus that "low level elementary" visuomotor processing (Jacob & Jeannerod, 2003) controls movements that are rapid, automatic, programmed on the basis of visual information rather than memory, and performed in tasks that do not force object-relative codlings of spatial variables. For instance, rapid pointing or reaching towards an object may be thought to be distinguishable from deictic pointing, which calls into play a more cognitive, symbolic function. Similarly, rapid object-directed grasping may be distinguished from "pantomimed" grasping or from grasping involving a representation derived from one's memory. Thus, the strong version of the TVSH proposes that these types of actions are based on spatial representations that are context-insensitive and independent of one's phenomenology. Within the illusion literature, strong TVSH amounts to predicting what may be called *immunity* of these types of motor processes from visual illusions. Immunity implies evidence that at least some motor responses are not affected by visual illusions, that is, that quantitative assessments of these effects are consistent with random samples from a population of effect measures whose mean equals zero. Conversely, perceptual responses to comparable visual displays should show clear illusion effects.