

## Visual illusions, delayed grasping, and memory: No shift from dorsal to ventral control

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### ABSTRACT

We tested whether a delay between stimulus presentation and grasping leads to a shift from dorsal to ventral control of the movement, as suggested by the perception–action theory of Milner and Goodale (Milner, A.D., & Goodale, M.A. (1995). *The visual brain in action*. Oxford: Oxford University Press.). In this theory the dorsal cortical stream has a short memory, such that after a few seconds the dorsal information is decayed and the action is guided by the ventral stream. Accordingly, grasping should become responsive to certain visual illusions after a delay (because only the ventral stream is assumed to be deceived by these illusions). We used the Müller-Lyer illusion, the typical illusion in this area of research, and replicated the increase of the motor illusion after a delay. However, we found that this increase is not due to memory demands but to the availability of visual feedback during movement execution which leads to online corrections of the movement. Because such online corrections are to be expected if the movement is guided by one single representation of object size, we conclude that there is no evidence for a shift from dorsal to ventral control in delayed grasping of the Müller-Lyer illusion. We also performed the first empirical test of a critique Goodale (Goodale, M.A. (2006, October 27). *Visual duplicity: Action without perception in the human visual system*. The XIV. Kanizsa lecture, Trieste, Italy.) raised against studies finding illusion effects in grasping: Goodale argued that these studies used methods that lead to unnatural grasping which is guided by the ventral stream. Therefore, these studies might never have measured the dorsal stream, but always the ventral stream. We found clear evidence against this conjecture.

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### 1. Introduction

It has been reported repeatedly that the effects of certain visual illusions on motor behavior increase if a delay is introduced between stimulus presentation and execution of the movement (e.g. Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Hu & Goodale, 2000; Westwood, Heath, & Roy, 2000; Westwood, McEachern, & Roy, 2001; Westwood & Goodale, 2003). In the perception–action framework (Milner & Goodale, 1995) this was interpreted as a shift between two completely different neuronal control systems: vision-for-action and vision-for-perception. The vision-for-action system is assumed to reside in the dorsal cortical stream and to be refractory to certain visual illusions (as, for example, the Ebbinghaus/Titchener illusion; Aglioti, DeSouza, & Goodale, 1995, or the Müller-Lyer illusion; Hu & Goodale, 2000, p. 858; Goodale

& Westwood, 2004, p. 208; Goodale, Westwood, & Milner, 2004, p. 137). In addition, the vision-for-action system is assumed to have an extremely short memory (“certainly less than 2 s”, Milner & Goodale, 1995, p. 173).

According to this hypothesis, it is easy to explain the increase of illusion effects if a delay is introduced between stimulus presentation and execution of the movement: the vision-for-action system has forgotten the exact parametric values of the target object and therefore has to rely on the stored visual information from the vision-for-perception system. This information, however, is affected by the illusion and therefore the illusion effect increases with the delay.

Recently, an even stronger version of this hypothesis has been proposed: the “real-time view of action” (Goodale et al., 2004; Westwood & Goodale, 2003). According to this view, the vision-for-action system only computes the exact parametric values of the movement at the very moment the movement is initiated. Consequently, introducing even a very brief delay between stimulus presentation and movement initiation should force the motor system to use ventral information and thereby lead to an illusion effect in motor behavior.

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### 1.1. Critique of the perception–action interpretation of grasping

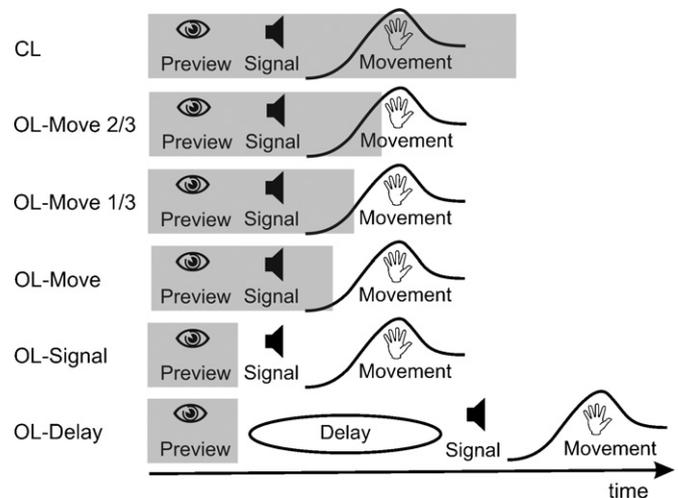
However, recent research has shown that some of the key-assumptions of the perception–action hypothesis might be based on problematic empirical evidence. For example, a number of researchers have argued that grasping is affected by the Ebbinghaus/Titchener illusion to a similar degree as perception (Franz, Gegenfurtner, Bühlhoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999; for reviews see: Franz, 2001 and Franz & Gegenfurtner, in press). They argued that the apparent dissociation between perception and grasping is mainly due to methodological problems, as for example a mismatch in task demands (Franz et al., 2000), or the fact that different responsiveness of the dependent measures were not taken into account (see below and Franz, 2003). This view is consistent with the results of van Donkelaar (1999) who found that pointing-movements also were affected by the Ebbinghaus/Titchener illusion to a similar degree as perception.

Other researchers showed similar problems for the classic studies (Bridgeman, Kirch, & Sperling, 1981; Bridgeman, Peery, & Anand, 1997) on the induced Roelofs effect and showed that these findings can better be explained by a common representation of space, thereby corroborating our results regarding the Ebbinghaus illusion (Dassonville, Bridgeman, Bala, Thiem, & Sampanes, 2004; Dassonville & Bala, 2004a, 2004b). Similarly, Schenk (2006) questioned whether the dissociation in the famous patient D.F. is really between perception and action as suggested by Milner and Goodale (1995). Specifically, the notion that object size is calculated twice, once in the ventral stream for perception (deceived by certain visual illusions, but with long memory) and once in the dorsal stream for action (not deceived by certain visual illusions, but with short memory) seems problematic.

For these reasons, we decided to test the empirical evidence for the differential effects of delay on illusions in perception and action. We used the Müller-Lyer illusion, as the illusion which was used first in this area of research (Gentilucci et al., 1996) and very often subsequently (e.g. Daprati & Gentilucci, 1997; Franz, Fahle, Bühlhoff, & Gegenfurtner, 2001; Heath, Rival, & Binsted, 2004; Heath, Rival, & Neely, 2006; Westwood et al., 2000, 2001). We employed grasping as motor response because grasping is the typical response used in studies investigating the dissociation between perception and action (e.g. Aglioti et al., 1995) and because grasping likely minimizes the problem that position and extent might be dissociated in the Müller-Lyer figure (Gillam & Chambers, 1985; Mack, Heuer, Villardi, & Chambers, 1985).

### 1.2. The critical role of visual feedback

Besides replicating the earlier studies, we were interested in two potential methodological problems: the first issue is related to the use of visual feedback. The condition with minimal memory load would be a full-vision condition. That is, the participants grasp the shaft of the Müller-Lyer figure with full vision of hand and stimulus (following the tradition in the motor literature, we will call this “closed-loop” condition). In this closed-loop condition, visual information is available all the time such that there is no need to employ memory mechanisms. While that seems to make the closed-loop condition an ideal baseline for the memory conditions, there is one serious limitation of this condition: during execution of the movement, feedback mechanisms (e.g. Woodworth, 1899) could detect the “error” introduced by the illusion and lead to online corrections. These online corrections, however, could hide an illusion present in the motor system (Post & Welch, 1996). Therefore, we took great care to disentangle the effects of visual feedback and of memory demands. For this, we systematically varied the amount of visual



**Fig. 1.** Viewing conditions used in our experiments. In all conditions, participants viewed the stimulus for 1 s (preview-period) and an auditory go-signal indicated when the movement should be initiated. In the CL condition, participants had full vision of hand and stimulus during the movement (as indicated by the gray bar). In the OL-Move-2/3 (1/3) condition, participants only had vision until the hand had traveled 2/3 (1/3) of the way to the target object. In the OL-Move condition, vision was suppressed as soon as the hand started to move. In the OL-Signal condition vision was suppressed after the preview-period and when the go-signal started. In the OL-Delay condition, an additional delay of 5 s was introduced between end of the preview and the go-signal.

feedback and the memory demands using a large number of visual conditions (cf. Fig. 1).

### 1.3. Correcting illusion effects for comparisons across action and perception

The second issue is related to the potentially different responsiveness of each of the dependent measures to a physical variation of object size. Because this issue sometimes leads to confusion, we will discuss it in some detail here. The perceptual and motor measures must respond to a physical variation of object size. Otherwise we would not be able to evaluate their response to an *illusory* variation of size. But, this is not enough. We need to know, how exactly each measure responds to a physical change of, say, 1 mm. Only if we know this, we can say that an illusion had a corresponding effect of, say, 1 mm. Luckily, most dependent measures used in this area of research are linearly related to physical size. This simplifies things. For example, in grasping the standard measure is the maximum grip aperture (MGA; i.e. the maximum aperture between index finger and thumb during the reach phase of the grasp movement). The MGA is a linear function of physical size (Jeannerod, 1981, 1984): it has a certain intercept, such that the MGA is always larger than the object allowing for a certain safety margin. And it has a certain slope. This slope tells us, how much the MGA will change if we change physical size by 1 mm. In a meta-analysis, Smeets and Brenner (1999) determined an average slope of 0.82 for MGA. That is, if we increase the physical size by 1 mm, then MGA will increase by approximately 0.82 mm. This implies that, if we measured an increase of MGA of 0.82 mm in response to an *illusory* change of size, we can conclude that the illusion had an effect that corresponds to a 1 mm increase of the *physical* size. More generally, if we measured an illusion effect of X mm in MGA then we can conclude that this corresponded to an  $X/0.82$  mm change in physical size. In the following we will call this ratio (illusion-effect divided by slope) the “corrected” illusion effect (Franz, 2003; Franz et al., 2001; Franz, Scharnowski, & Gegenfurtner, 2005). Some authors also call it the “scaled” illusion effect (Glover & Dixon, 2002).

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