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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, Triest, 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.

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, Bülthoff, & 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 Roelof's 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, Bülthoff, & 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 feedback and the memory demands using a large number of visual conditions (cf. Fig. 1).

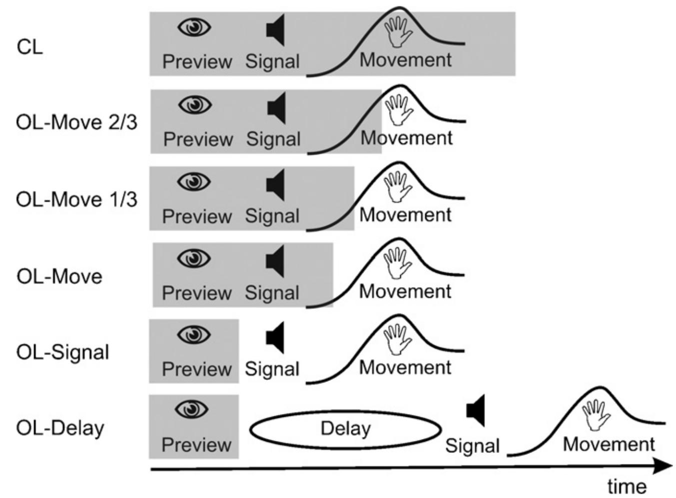

Fig. 1. Viewing conditions used in our experiments. In all conditions, participants viewed the stimulus for 1 s (preview-period) and an auditory go-signal indicated when the movement should be initiated. In the CL condition, participants had full vision of hand and stimulus during the movement (as indicated 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.

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 *illusionary* 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 *illusionary* 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).

Now, consider another measure. For example, manual size estimation (participants indicate the size of an object with index finger and thumb) which is very often interpreted as a perceptual measure (Haffenden & Goodale, 1998). This measure can have a larger slope. For example, Franz (2003) found a slope of 1.57 for this measure (other studies found even larger slopes; e.g. Haffenden, Schiff, & Goodale, 2001). Now, if we increased the physical size of the object by 1 mm, then manual size estimation will increase by approximately 1.57 mm. Similarly, if we induce an illusion of 1 mm, then manual size estimation will also increase by approximately 1.57 mm. This effect might look larger as the corresponding effect of 0.82 mm in grasping. However, both effects are created by the same illusion. Therefore, it is erroneous to compare the illusion effects of different measures if they have different slopes. Only the corrected illusion effects allow an adequate comparison. Unfortunately, the vast majority of studies comparing manual size estimation to grasping did not perform this correction—and thereby systematically overestimated the perceptual illusion in manual size estimation (for a review see Franz & Gegenfurtner, in press).

We avoided these problems by using classic perceptual measures, like an adjustment procedure and a comparison with a graded series (e.g. Coren & Girgus, 1972). These measures are known to produce slopes close to 1, such that the difference of the slopes between grasping and these perceptual measures is not as problematic as for manual size estimation. In addition, we measured the slopes for each condition and calculated the corrected illusion effects. This is especially important because we did not know whether the delay might change one of our measures. It could well be that after a delay the slopes in grasping or perception change. For example, because the information starts to decay, the slopes might get shallower. This could lead to the same problems as described above. Interestingly, we will see that this is not the case: the slopes in grasping (as well as in perception) do not change with increasing memory demands. This result and its implications will be discussed further in Section 5.

1.4. Overview of this study

Before describing our experiments in detail, we want to give an overview of the experiments and our main conclusions: in Experiment 1 we replicated the basic effect: in grasping, we found a clear increase of the illusion if a delay of 5 s is introduced between stimulus presentation and execution of the movement. This corresponds well to the literature (e.g. Gentilucci et al., 1996; Westwood et al., 2000, 2001). In addition, we show, that the perceptual effect of the illusion is not changed by the delay and that the illusion effects in perception and grasping are similar after the delay.

In the Experiments 2 and 3 we tried to disentangle the factors which might be responsible for the increase of the illusion effects in grasping. For this, we independently varied the memory demands imposed by the delay and the amount of visual feedback available during movement execution: in Experiment 2 we show that the memory demands do not change the illusion effect in grasping. This shows that the motor illusion is not changed by the delay and thereby contradicts the perception–action hypothesis and the real-time view of action. In Experiment 3 we systematically varied the amount of visual feedback available during grasping and found that the availability of visual feedback can explain the relatively small illusion effect under closed-loop conditions. We conclude that (at least for the Müller-Lyer illusion) there is no evidence for two separate representations of object size that guide actions. Instead, grasping behaves exactly as we would expect based on the classic notion of online correction of errors (Woodworth, 1899) and the idea that perception and grasping are guided by a single representation of object size that is deceived by visual illusions (common-representation model, Franz et al., 2000).

Finally, we took the opportunity to test in Experiment 3 an objection (Goodale, 2006, in press) that has been raised against all our studies on a potential dissociation between perception and action in visual illusions (e.g. Franz, 2003; Franz, Bülthoff, & Fahle, 2003; Franz et al., 2000, 2005). The main idea of this critique is that due to some specifics of our setup participants might have grasped in an unnatural and awkward way and that this grasping was guided by the ventral stream. Therefore, we might never have been measuring the vision-for-action system, but always the vision-for-perception system. In consequence it would be no surprise that we found effects of visual illusions in our grasping tasks. We performed the first empirical test of this conjecture by directly comparing our method with the method used by Goodale and co-workers (e.g. Aglioti et al., 1995; Haffenden & Goodale, 1998; Haffenden et al., 2001). We found no difference in the illusion effects on grasping, thereby clearly refuting this conjecture.

2. Experiment 1: replicating the increase of the motor illusion

In Experiment 1 we attempted to replicate the increased effect of the Müller-Lyer illusion on grasping if a delay is introduced between stimulus presentation and execution of the movement. For this, we tested two extreme cases: in the closed-loop (CL) condition, full vision of hand and stimuli is available and no memory component is involved. In the open-loop delay (OL-Delay) condition, no vision of hand and stimuli is available during performance of the task and the visual information has to be stored for 5 s. According to the literature, we expected a drastic increase of the illusion effect from CL to OL-Delay.

2.1. Methods

2.1.1. Participants

Twenty-eight volunteers (16 female, 12 male) participated in the experiment, ranging in age from 17 to 33 years (mean: 23.9 years). In return for their participation, they either received course-credit or were paid 8 EURO (app. 11.5 US$) per hour. Participants had normal or corrected-to-normal vision and were right-handed.

When setting up the experiment, we had a number of participants perform only the perceptual task in order to test the setup (we used these participants to test a graded series method versus an adjustment method). Therefore, twelve of the participants performed only the perceptual task and sixteen participants performed the perceptual task as well as the grasping task. Because the results were essentially identical, we pooled their data in the perceptual task (see below in Section 2.1.4).

2.1.2. Stimuli

We used three-dimensional versions of the Müller-Lyer illusion (Fig. 2a). The shaft of the Müller-Lyer figures were black plastic bars of different length (39 mm, 41 mm, 43 mm) and constant width (8 mm) and height (5 mm). For each bar we individually printed a fin-in (FinIn) and a fin-out (FinOut) version of the Müller-Lyer figure. In the FinIn figure the angle between shaft and fins was 35° and in the FinOut figure it was 145°. The fins were positioned such that the edges of the bar were clearly discriminable (Fig. 2a). The fins were 21 mm long.

2.1.3. Apparatus

Participants sat on a chair and used a chin rest to keep the position of the head constant. They looked down at a 21-inch CRT monitor (Sony, Trinitron flat screen, resolution 1280 × 1024 pixels, refresh rate 85 Hz, effective screen diagonal: 48.5 cm) as if looking at the top of a table. The monitor was positioned at a distance of approximately 50 cm from the eyes. The screen of the monitor served as table for the presentation of the Müller-Lyer figure, which were positioned 390 mm away from the start position at which the participants rested their hand before each grasp. The screen was tilted to be oriented perpendicular to gaze direction (angle relative to horizontal: 45°). Participants wore liquid-crystal (LC) shutter glasses (Plato, Translucent Technologies Inc., Toronto, Ontario, Canada; cf. Milgram, 1987) which allow to efficiently suppress vision. The grasp trajectories were recorded using an Optotrak 3020 system (Northern Digital Inc., Waterloo, Ontario, Canada) at a sampling rate of 100 Hz. Six infrared light-emitting diodes (LEDs) were mounted on two small, lightweight flags (three LEDs per flag). The flags were attached to the finger nails of thumb and index finger (Fig. 2a) using adhesive pastels (UHU-patafix, UHU

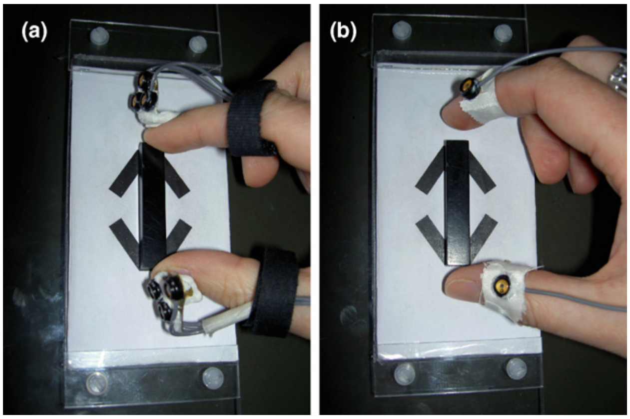

Fig. 2. (a) The 3-marker method traditionally used in our experiments on grasping visual illusions (e.g. Franz et al., 2000). This method allows to calculate the trajectories of the typical grasp-points on the finger tips (using mathematical rigid-body transformations) and ensures that the finger tips are completely free to receive tactile feedback. (b) The 1-marker method traditionally used in experiments of Goodale and co-workers (e.g. Aglioti et al., 1995). Goodale (2006, in press) argued that this method interferes less with the grasping movement, such that it might be better suited to tap the dorsal stream. We tested this notion in Experiment 3.

GmbH, Bühl, Germany). Before the experiment, the typical grasp points on the fingers were determined and measured relative to the markers on the flags. Employing mathematical rigid-body transformations on the three markers, this enabled us to determine the trajectories of the grasp points for each finger.

All experiments were programmed in Matlab (MathWorks Inc., Natick, MA, USA), using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and our custom build Optotrak Toolbox (URL: http://www.allpsych.uni-giessen.de/vf/OptotrakToolbox). Data–analysis was performed in Matlab and R (R Development Core Team, 2008).

2.1.4. Procedure

2.1.4.1. Grasping. Participants performed two motor conditions: Grasp-CL and Grasp-OL-Delay (cf. Fig. 1). The conditions were performed in two blocks, thereby employing the feedback schedule with maximum effect of delay (Heath et al., 2006). The order of the blocks was counterbalanced across participants. Each trial started with the experimenter preparing the Müller-Lyer figure. Then the LC-goggles opened for a preview period of 1 s. In the Grasp-CL condition a tone (sine-tone, 1000 Hz, 100 ms) followed, indicating that the participant should grasp with a precision grip the central bar of the Müller-Lyer figure with full vision of hand and stimuli. In the Grasp-OL-Delay condition, the goggles closed after the preview period for 5 s. Then the tone sounded, and the participant grasped the central bar without vision of hand or stimuli. Participants were instructed to grasp natural and fast. For the whole grasp (from the tone until removing the bar further than 50 mm away from the Müller-Lyer figure) they had a total time of 4 s. Each participant performed in each of the two conditions 48 trials (3 bar-lengths × 2 fin-orientations × 8 repetitions) in randomized order.

2.1.4.2. Perception. When setting up the experiment, we were worried whether a graded series would lead to different results than an adjustment method. To test this, we had twelve participants perform a grades series and sixteen participants perform an adjustment task (these sixteen participants also performed the grasping task). In the graded series, participants selected a matching stimulus from a graded series of bars (22 bars; lengths from 30 mm to 51 mm; stepsize: 1 mm; bar-widths: 8 mm) that was printed on paper and presented 145 mm below the Müller-Lyer figure. In the adjustment task, participants adjusted a comparison bar that was displayed on the monitor to match the length of the shaft of the Müller-Lyer figure. The comparison bar was presented 50 mm to the right of the target, randomly at one of two positions (vertical offset ±25 mm) and had a random initial size between 20 mm and 51 mm (step-size: 0.285 mm). We will see below that graded series and adjustment method gave similar results.

Using either the graded series or the adjustment method, participants performed two perceptual conditions: Perc-CL and Perc-OL-Delay. The conditions were performed in two blocks (with the order counterbalanced across participants). In the Perc-CL condition, each trial started with the experimenter preparing the Müller-Lyer figure and the comparison stimuli. Then the LC-goggles opened for a preview period of 1 s, followed by a tone indicating that the participant should either select a matching bar from the graded series or adjust the comparison bar (no time limit was imposed on these responses).

In the Perc-OL-Delay condition, the experimenter first prepared the Müller-Lyer figure (but not the comparison stimuli). After the 1 s preview period the goggles closed for 5 s. During this time, the experimenter removed the Müller-Lyer stimuli and prepared the comparison bars. Then the goggles opened and the tone sounded, and the participant either selected a matching bar from the graded series or adjusted the comparison bar (again without time limit).

Each participant performed in each of the two conditions 36 trials (3 bar-lengths × 2 fin-orientations × 6 repetitions) in randomized order. A repeated-measures ANOVA with the between-subjects factor response (graded-series vs. adjustment) and the within-subjects factors: condition (Perc-CL vs. Perc-OL-Delay), bar (bar-lengths of: 39, 41, 43 mm), and illusion (FinIn vs. FinOut) showed that the response had no differential effects (main effect response: $F(1, 26) = 0.46$, $p = .51$, all seven interactions of response: $p > .11$). We therefore pooled the two groups for all further analyses.

2.1.5. Data analysis

From each grasp trajectory, we determined the following parameters: reaction time (RT) was defined as the time between start of the auditory go-signal and movement onset (the first frame in which index finger or thumb exceeded a velocity threshold of 0.025 m/s). Movement time (MT) was defined as the time between movement onset and end of the movement (the first frame in which index finger or thumb came closer than 3 mm to the plane in which the grasp object was placed). MGA was the maximum distance between thumb and index finger during MT. Relative time to MGA was the relative time when MGA occurred within the MT.

If not specified otherwise, repeated measure ANOVAs were run on these parameters with the within-subject factors: condition (CL vs. OL-Delay), bar (lengths of 39, 41, 43 mm), and illusion (FinIn vs. FinOut).

To calculate corrected illusion effects we divided the mean illusion effects by the mean slopes of the linear functions that relate physical size to the dependent measure (MGA or perceived size). Standard errors for these corrected illusion effects were calculated using the Taylor-approximation:

$$\text{S.E.M.} = \frac{i}{s}\sqrt{\frac{\sigma_s^2}{s^2} + \frac{\sigma_i^2}{i^2} - 2\frac{\sigma_{is}}{is}}$$

with, i: mean illusion effect, s: mean slope, σ_i^2: S.E.M. of the illusion effect, σ_s^2: S.E.M. of the slope, σ_{is}: covariance of illusion effect and slope. This approximation is valid because the slopes were highly significant different from zero. The statistical rationale for this procedure is discussed in Franz et al. (2005) and Franz (submitted; preprint at arXiv:0710.2024); see also Buonaccorsi (2001).

A significance level of $\alpha = .05$ was used for all statistical analyses. p-Values above .001 are given as exact values. For parameters which are given as $A \pm$ S.E.M., S.E.M. is the standard-error of the mean.

2.2. Results

2.2.1. Grasping

MGA depended linearly on bar length with slopes of: 0.54 ± 0.098 (CL) and 0.48 ± 0.192 (OL-Delay); which is also reflected in a main effect of bar length in the ANOVA ($F(2, 30) = 20$, $p < .001$). Participants grasped overall larger in the OL-Delay condition than in the CL condition (main effect condition: $F(1, 15) = 35$, $p < .001$), as can be seen in the left panel of Fig. 3. Participants showed a reliable illusion effect (main effect illusion: $F(1, 15) = 17$, $p = .001$). The illusion effect depended strongly on the condition (interaction illusion × condition: $F(1, 15) = 38$, $p < .001$), All three other interactions were not significant (all $p > .17$). Separate analyses showed that the illusion effect was non-significant in the CL condition ($t(15) = 1.1$, $p = .27$) and significant in the OL-Delay condition ($t(15) = 5.2$, $p < .001$).

We also calculated temporal aspects of the grasping movement (RT, MT). These were in a normal range and are summarized for all experiments in Table 1.

In summary, participants grasped after the delay with larger MGA, but with a similar slope. This result conforms well to the literature (cf. Hesse & Franz, submitted for publication). The illusion effect was much larger in the OL-Delay condition (4.1 ± 0.78 mm) than in the CL condition (0.4 ± 0.39 mm), as can be seen in the upper right panel of Fig. 3. The corresponding corrected illusion effects are shown in the lower right panel and show the same pattern of results.

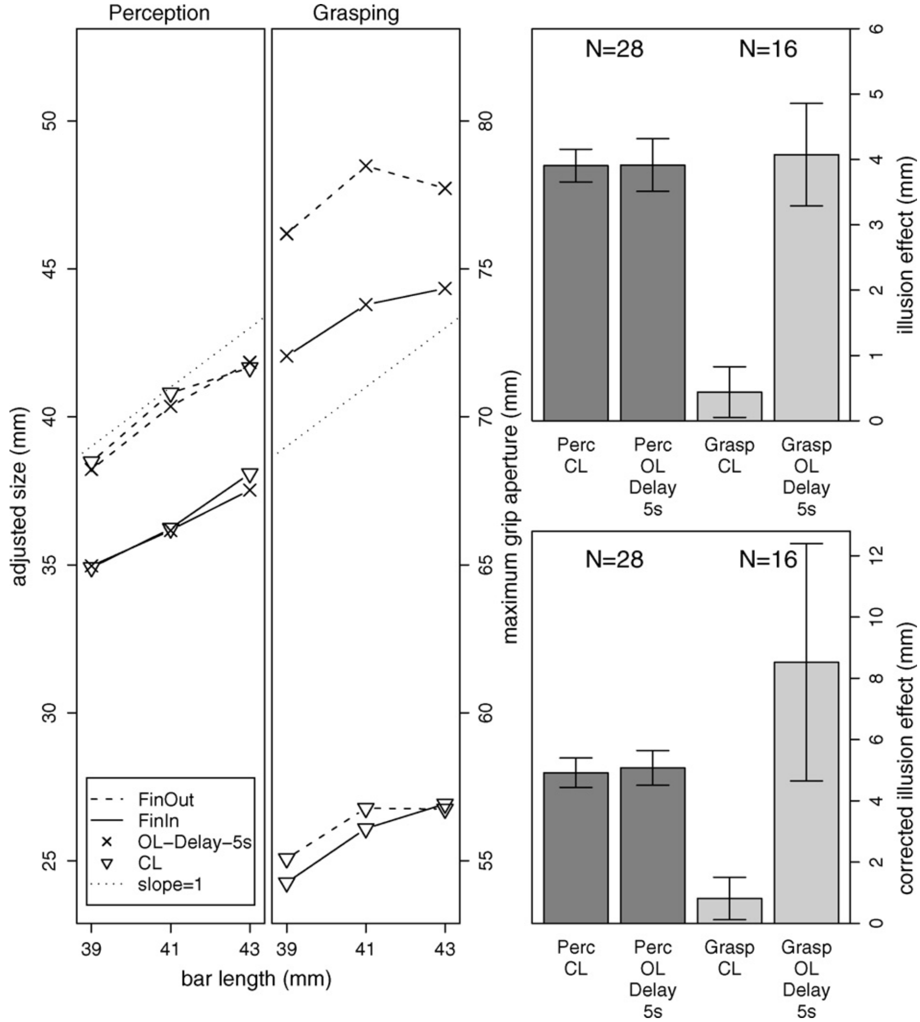

Fig. 3. Experiment 1: we replicated the increase of the Müller-Lyer illusion after a delay in grasping. The left panels depict the adjusted size in the perceptual task and the MGA in the grasping task as functions of object size. The upper right panel depicts the illusion effect (calculated as the mean difference between FinOut and FinIn conditions). The lower right panel depicts the corrected illusion effects (calculated by dividing the illusion effects by the slope). Errorbars depict ±1 S.E.M.

2.2.2. *Perception*

Perceived size depended linearly on bar length with slopes of: 0.79 ± 0.054 (CL) and 0.77 ± 0.064 (OL-Delay); see also the left panel of Fig. 3.

Participants showed a reliable illusion effect (main effect illusion: $F(1, 27) = 157$, $p < .001$). This effect was modulated by bar-length (interaction bar × illusion: $F(2, 54) = 10$, $p < .001$). Fig. 3 shows, however, that this interaction was small in comparison to the illusion effect and the effect of bar-length (main effect bar: $F(2, 54) = 181$, $p < .001$). The condition (CL vs. OL-Delay) had no effects (main effect condition: $F(1, 27) = 0.54$, $p = .47$; all three interactions with condition: $p > .08$). In summary, the illusion effect was quite similar in the CL and the OL-Delay conditions (3.9 ± 0.25 mm and 3.9 ± 0.40 mm, respectively), as is also shown in the upper right

Table 1
Temporal parameters of grasping

	Condition	RT		MT		t(MGA)	
		Mean	S.E.M.	Mean	S.E.M.	Mean	S.E.M.
Experiment 1 ($N = 16$)	CL	412	22	908	39	82	1.5
	OL-Delay	440	28	1207	49	74	1.7
Experiment 2 ($N = 8$)	OL-Move	549	37	1064	87	79	2.1
	OL-Delay	474	45	1182	96	80	3.2
Experiment 3 ($N = 40$)	CL	301	10	755	21	80	1.4
	OL-Move-2/3	304	11	748	22	81	1.3
	OL-Move-1/3	335	13	803	32	81	1.2
	OL-Move	354	16	813	31	80	1.2
	OL-Signal	304	12	829	28	78	1.0

Note: RT and MT are in ms, t(MGA) is the relative time to MGA in percent of MT.

panel of Fig. 3. The corresponding corrected illusion effects are shown in the lower right panel and show the same pattern of results.

2.3. Discussion

We found a strong increase of the effect of the Müller-Lyer illusion on grasping in the OL-Delay condition as compared to the CL condition. This replicates an effect that has traditionally been counted as evidence for a transition from dorsal to ventral control of the movement and for the notion that the undeceived dorsal stream has a too short memory to bridge the 5 s delay imposed in the OL-Delay condition (Goodale et al., 2004; Milner & Goodale, 1995; Westwood & Goodale, 2003).

However, in this traditional design there is a confound between memory demands and the availability of visual feedback during execution of the movement because the OL-Delay condition differs from the CL condition in two respects: participants have to store the visual information for 5 s and they don't see their hand during execution of the movement. It is to be expected from the motor literature that visual feedback during execution of the movement leads to online corrections which will reduce the measured illusion effect, but are not indicative of a switch from dorsal to ventral control (Post & Welch, 1996). To disentangle these possibilities we varied the availability of visual feedback independent of the memory demands in the Experiments 2 and 3.

A second finding is that our classic perceptual measure of the Müller-Lyer illusion gives similar illusion effects in the CL and the OL-Delay conditions. This indicates that the perceptual illusion is fairly constant, a fact which greatly simplifies the interpretation of the data. In the Experiments 2 and 3 we can therefore concentrate on grasping.

3. Experiment 2: the increase of the motor illusion is not due to delay

In Experiment 2 we tested the influence of memory on the illusion effects while matching the amount of visual feedback available during execution of the grasping movement. For this, we used the same OL-Delay condition as in Experiment 1 but replaced the CL condition with a condition, in which participants had full vision of hand and stimuli during programming but not during execution of the movement. That is, vision of hand and stimuli was prevented as soon as the participants started to move their hand (OL-Move condition, cf. Fig. 1). This condition ensures that participants cannot perform online corrections during execution of the movement and can therefore be seen as the "standard" condition for studies on the effects of visual illusions on grasping (as argued by numerous researchers, e.g. Haffenden & Goodale, 1998; Post & Welch, 1996).

The availability of full visual information during programming of the movement should, according to the perception–action hypothesis and to the real-time view of action, lead to an accurate, undeceived programming of the movement in the dorsal stream. Therefore, both theories predict that the illusion effect should increase from the OL-Move condition to the OL-Delay condition. If, on the other hand, the increase of the motor illusion found in Experiment 1 is due to online corrections performed in the CL condition then the illusion effects should be similar in the OL-Move and OL-Delay conditions.

3.1. Methods

Eight volunteers (3 female, 5 male) participated in the experiment, ranging in age from 21 to 29 years (mean: 27.6 years). The methods were identical to the grasping task of Experiment 1, except that we now replaced the CL condition with an OL-Move condition (cf. Fig. 1): the LC-goggles closed as soon as the participant had moved the hand away by 20 mm from the start position, thereby preventing vision as soon as the movement had started.

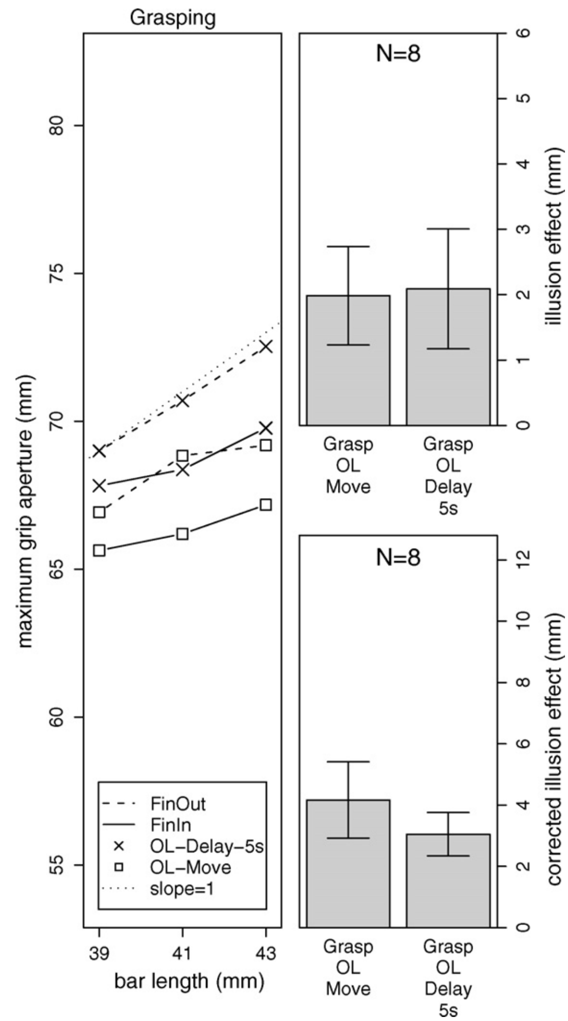

Fig. 4. Experiment 2: increasing the memory demands did not change the effect of the Müller-Lyer illusion on grasping. The perception–action theory and the real-time view of action both predict a large increase of the motor illusion between the OL-Move and OL-Delay conditions. This was, however, not the case. The left panel depicts the MGA in the grasping task as function of object size. The upper right panel depicts the illusion effect (calculated as the mean difference between FinOut and FinIn conditions). The lower right panel depicts the corrected illusion effects (calculated by dividing the illusion effects by the slope). Errorbars depict ±1 S.E.M.

3.2. Results

Results are shown in Fig. 4. MGA depended linearly on bar length with slopes of: 0.48 ± 0.104 (OL-Move) and 0.69 ± 0.168 (OL-Delay). This is also reflected in a main effect of bar length in the ANOVA ($F(2, 14) = 19$, $p < .001$). Participants also showed a reliable illusion effect (main effect illusion: $F(1, 7) = 7.7$, $p = .027$), which did not differ between the OL-Delay and OL-Move conditions (interaction illusion × condition: $F(1, 7) = 0.017$, $p = .9$), All other main effects and interactions were not significant (all $p > .45$).

Because the OL-Delay condition is identical to Experiment 1, we compared the results of this condition across experiments. For this, we calculated an ANOVA with the between-subjects factor experiment and the within-subjects factors bar length and illusion. As in the separate analyses for each experiment, we found main effects of bar length ($F(2, 44) = 9.3$, $p < .001$) and of the illusion ($F(1, 22) = 32$,

$p < .001$), while none of the other main effects or interactions were significant. Most importantly, all effects involving the factor experiment were not significant (all $p > .14$), suggesting that we succeeded in replicating the condition. As in the other experiments, we also calculated the temporal aspects of the grasping movement (RT, MT). These are shown in Table 1.

In summary, participants showed similar illusion effects in the OL-Move and the OL-Delay conditions (2.0 ± 0.75 mm and 2.1 ± 0.92 mm, respectively), as can be seen in the upper right panel of Fig. 4. The corrected illusion effects showed a similar pattern of results (lower right panel of Fig. 4).

3.3. Discussion

We found no difference between the illusion effects in the OL-Move and OL-Delay conditions. That is, the memory demands imposed by the 5 s delay in the OL-Delay condition did not lead to a strong increase of the illusion. In Section 5 we will present a summary of all our experiments and of other studies and show that the result of Experiment 2 is consistent with these other data and therefore likely not due to a lack of statistical power.

Taken together, this result suggests that the availability of visual feedback during execution of the movement led to the difference between CL and OL-Delay conditions in Experiment 1 (and not the memory demands). In the next experiment we explored the effects of visual feedback further.

4. Experiment 3: the increase of the motor illusion is due to visual feedback

In Experiment 3 we attempted to further test our interpretation that the availability of visual feedback during execution of the grasping movement is the critical factor for the relatively small illusion effects in the CL condition of Experiment 1. For this, we systematically decreased the amount of visual feedback in five conditions (see also Fig. 1): (i) CL: full vision during execution of the movement (this is identical to the CL condition in Experiment 1); (ii) OL-Move-2/3: full vision until the hand had been transported 2/3 of the distance to the grasp object; (iii) OL-Move-1/3: full vision until the hand had been transported 1/3 of the distance; (iv) OL-Move: full vision until the hand had started to move (this is identical to the OL-Move condition in Experiment 2) and (v) OL-Signal: full vision until the auditory start signal. If our interpretation is correct, then we expect the illusion effects to vary systematically with the amount of visual feedback, such that the illusion effects should increase from CL, OL-Move-2/3, OL-Move-1/3, OL-Move, OL-Signal. In addition, the OL-Signal condition allowed us to test the central assumption of the real-time view of action (Goodale et al., 2004; Westwood & Goodale, 2003). According to this variant of the perception–action hypothesis, there should be a large difference between the illusion effects in the OL-Move and OL-Signal conditions. The real-time view of action assumes that the dorsal vision-for-action system only computes the exact parametric values of the movement if the target object is visible at the moment of movement programming. This is the case in the OL-Move condition (because vision is available until the hand starts to move, i.e. during programming of the movement), but not in the OL-Signal condition (because vision is suppressed as soon as the go-signal comes up, i.e. before programming of the movement). Consequently, there should be no illusion effect in the OL-Move condition (controlled by the dorsal stream) and the full illusion effect in the OL-Signal condition (controlled by the ventral stream).

4.1. Did we make a fundamental mistake in all our studies?

Before presenting the results, we need to explain one more experimental manipulation used in Experiment 3. As discussed in the Introduction, we had repeatedly found effects of certain visual illusions on grasping in recent studies. Typically, these motor illusions were of similar size as the perceptual illusions if the task demands of motor task and perceptual task were carefully matched (for reviews see: Franz, 2001; Franz & Gegenfurtner, in press). This contradicts Milner and Goodale's (1995) interpretation of grasping, because they argued that grasping is immune to these illusions.

To explain our results, Goodale (2006, in press) suggested that we might have used a problematic method to assess the motor illusion—and that this method might not tap the vision-for-action system, but only the vision-for-perception system. Consequently, it would be no surprise that we found similar effects of visual illusions on grasping and on perception.

This argument is based on the fact that we used a different method to attach the infrared markers to the fingers than was used in the studies of Goodale and co-workers (e.g. Aglioti et al., 1995; Haffenden & Goodale, 1998; Haffenden et al., 2001). The idea is that our method led to unnatural grasping which might make the right hand behave like an unskilled left hand. Because Gonzalez, Ganel, & Goodale, 2006 suggested that the left hand is always controlled by the vision-for-perception system, this would mean that we actually never measured vision-for-action with our grasping task, but always vision-for-perception.

An example of our method can be seen in Fig. 2a: we attached to the finger-nails of index finger and thumb small, lightweight flags, each holding three infrared markers. Goodale and co-workers on the other side attached only one marker to each finger (Fig. 2b). Our 3-marker method has two advantages: (a) employing mathematical rigid-body transformations on the three markers, we determined the trajectories of the grasp points for each finger. This is not possible with the methods of Goodale and co-workers. Therefore they always had an additional measurement error; depending on the thickness and orientation of the fingers (b) with our method the finger tip is completely free, allowing for full tactile feedback. This is not guaranteed with the method of Goodale and co-workers because the tape they used to attach the single marker could cover parts of the finger tip (as can, for example, be seen in Fig. 2 of Aglioti et al., 1995 and Fig. 3 of Haffenden & Goodale, 1998).

But, maybe we traded these advantages for the disadvantage of missing the dorsal vision-for-action system altogether—as suggested by Goodale (2006, in press)? We decided to perform the first direct, empirical test of this notion. For this, we split the participants in two groups. Both groups performed exactly the same task, except that for one group we used our 3-marker method and for the other group the 1-marker method. If the conjecture of Goodale (2006, in press) is correct, then there should be large differences between these groups.

4.2. Methods

Forty volunteers (33 female, 7 male) participated in the experiment, ranging in age from 19 to 34 years (mean: 23.2 years). The methods were almost identical to the grasping task of the other experiments, except for the following modifications:

As visual conditions we used, CL: full vision of hand and stimuli during grasping (identical to the CL condition of Experiment 1). OL-Move-2/3 (OL-Move-1/3): full vision until the hand had traveled 2/3 (1/3) of the way to the target; that is until it had approached the target object by 120 mm (240 mm). OL-Move: the LC-goggles closed as soon as the movement had started (identical to the OL-Move condition of Experiment 2). OL-Signal: the LC-goggles closed when the start tone sounded, thereby preventing vision during the RT-phase of the movement.

As in the other experiments, participants were instructed to grasp natural and fast. For the whole grasp (from the tone until removing the bar further than 50 mm

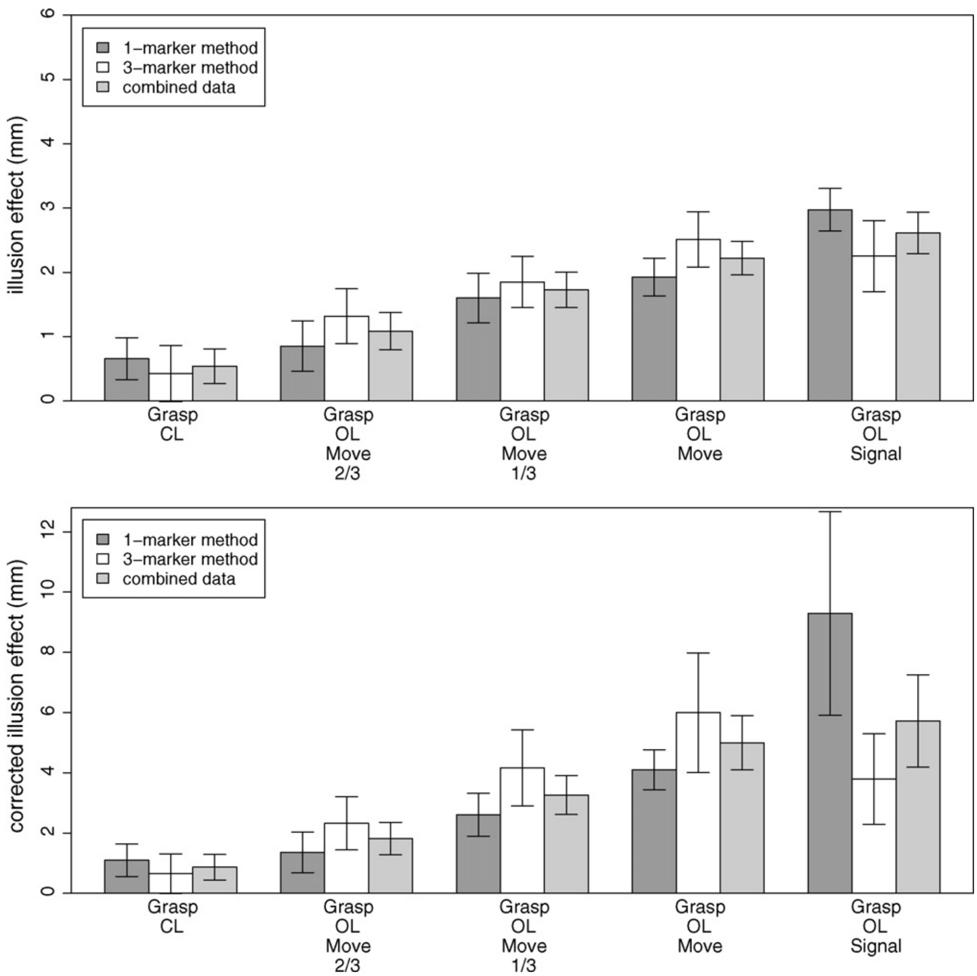

Fig. 5. Experiment 3: we split our sample in two groups and tested whether 3-marker method and 1-marker method (cf. Fig. 2) lead to different illusion effects, as hypothesized by Goodale (2006, in press). This was not the case. The upper panel depicts the illusion effect (calculated as the mean difference between FinOut and FinIn conditions). The lower panel depicts the corrected illusion effects (calculated by dividing the illusion effects by the slope). Errorbars depict ±1 S.E.M.

away from the Müller-Lyer figure) we reduced the total allowed time from 4 s (as was used in the other experiments) to 3 s. This was done because we now had a much larger number of conditions and the previous experiments had shown that participants were much faster than 4 s to complete the movement. Each participant performed 36 trials in each visual conditions, resulting in a total of 180 trials (3 bar-lengths × 2 fin-orientations × 6 repetitions × 5 visual conditions).

We split the forty participants in two groups. One group performed the experiment with our traditional 3-marker method (Fig. 2a) and the other group with the 1-marker method of Goodale and co-workers (Fig. 2b).

4.3. Results

First, we compared the illusion effects as determined by the two methods to measure grasping (1-marker vs. 3-marker methods). These results are shown in Fig. 5. We found a highly significant overall effect of the illusion on grasping (main effect illusion: $F(1, 38) = 76$, $p < .001$). This effect did neither depend on the method used to measure grasping (main effect 1- vs. 3-marker methods: $F(1, 38) = 0.042$, $p = .84$) nor was there an interaction of the method with the visual condition (interaction method × condition: $F(4, 152) = 1.3$, $p = .28$). The visual condition (CL, OL-Move, OL-Move-2/3, OL-Move-1/3, OL-Move, OL-Signal) had a highly significant effect on the illusion effect (main effect condition: $F(4, 152) = 12$, $p < .001$).

Due to the lack of difference in illusion effects between the 1-marker and 3-marker methods, we pooled the data for further analyses. A summary of these pooled data is shown in Fig. 6. In all conditions, MGA depended linearly on bar length with slopes of CL: 0.62 ± 0.087 mm, OL-Move-2/3: 0.60 ± 0.067 mm, OL-Move-1/3: 0.53 ± 0.072 mm, OL-Move: 0.44 ± 0.073 mm, OL-Signal: 0.46 ± 0.097 mm, as shown in the left panel of Fig. 6. As shown by the ANOVA above, the illusion effects depended strongly on the visual feedback condition. The mean illusion effects were CL: 0.54 ± 0.27 mm, OL-Move-2/3: 1.08 ± 0.29 mm, OL-Move-1/3: 1.73 ± 0.28 mm, OL-Move: 2.22 ± 0.26 mm, OL-Signal: 2.61 ± 0.32 mm, as shown in the upper right panel of Fig. 6. The corresponding corrected illusion effects show the same pattern of results and are shown in the lower right panel of Fig. 6. For the temporal aspects of the grasping movement (see Table 1).

4.4. Discussion

We found two things: first, the illusion effects depended strongly on the availability of visual feedback. Second, the illusion effects as measured by the 1-marker and the 3-marker methods did not differ. We will discuss these findings successively.

The main objective of Experiment 3 was to determine whether the availability of visual feedback can explain the relatively small illusion effect in the CL condition. And indeed, this is the case: the more visual information about hand and stimuli was available during execution of the movement the smaller were the illusion effects.

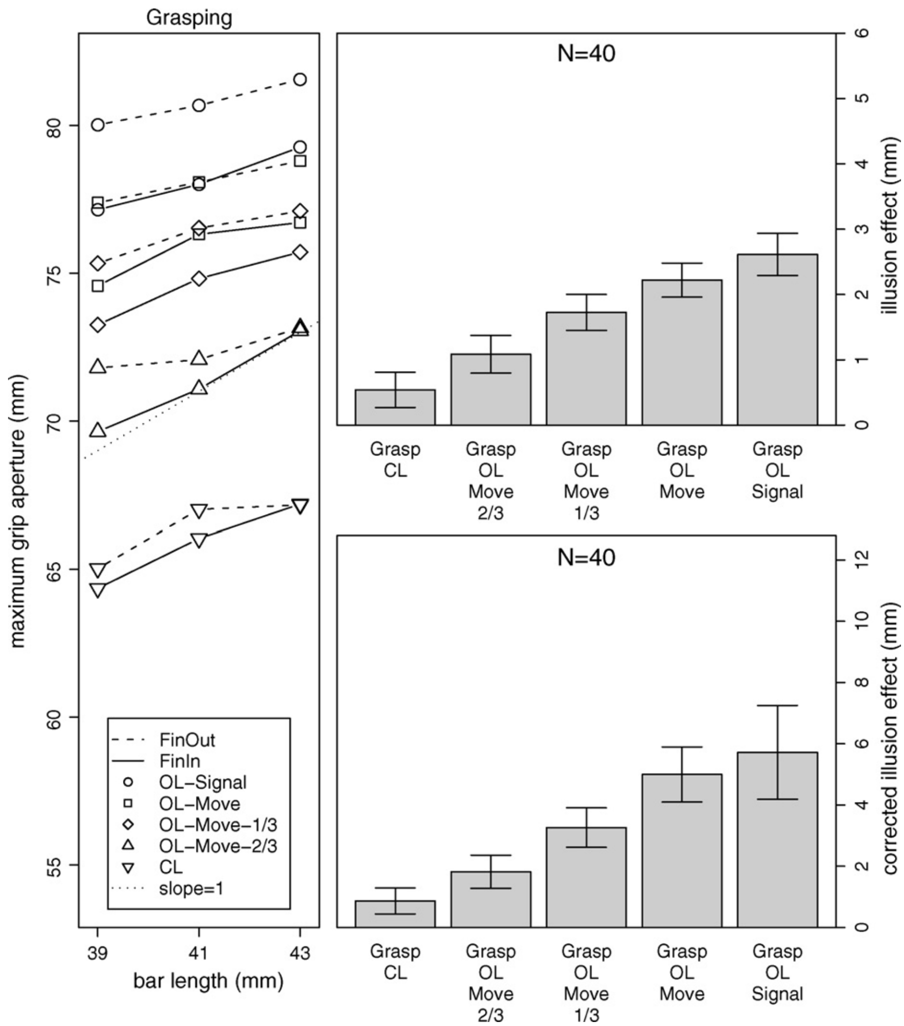

Fig. 6. Experiment 3: changing the amount of visual feedback during movement execution changed the effect of the Müller-Lyer illusion on grasping. This indicates that visual feedback is the critical factor for the increase of the illusion. The left panels depict the MGA in the grasping task as function of object size. The upper right panel depicts the illusion effect (calculated as the mean difference between FinOut and FinIn conditions). The lower right panel depicts the corrected illusion effects (calculated by dividing the illusion effects by the slope). Errorbars depict ±1 S.E.M.

This suggests that the availability of visual feedback is the critical factor (and not memory demands) that leads to a modulation of the illusion effects in grasping.

We also tested the real-time view of action by using the OL-Move and OL-Signal conditions. The real-time view of action would predict that between these two conditions the shift from dorsal to ventral control happens. Therefore the main variation of the illusion effects should also happen between these two conditions. This, however, was not the case. The illusion effects in OL-Move and OL-Signal conditions were very similar, thereby providing evidence against the real-time view of action.

Finally, we compared the illusion effects as measured by the 1-marker method and the 3-marker method. Goodale (2006, in press) had suggested that in all our studies on grasping visual illusions (e.g. Franz, 2003; Franz et al., 2000, 2001, 2003, 2005) we erroneously had measured vision-for-perception instead of vision-for-action and therefore it would be no surprise that we consistently found illusion effects on grasping. We performed the first empirical test of this notion and found that our 3-marker method leads to similar illusion effects as the 1-marker method used by Goodale and coworkers, thereby refuting this conjecture.

Note, that there is a second reason why we think the conjecture of Goodale (2006, in press) is not valid: if it were correct, then our results should be "atypical". That is, we should have obtained larger illusion effects for grasping than other studies. But this is not the case. In fact, the grasping data are surprisingly consistent across all laboratories, as has been demonstrated recently in a detailed review by Franz and Gegenfurtner (in press). We will show in Section 5 that this is also true for the present data on the Müller-Lyer illusion.

5. General discussion

We tested whether a delay between stimulus presentation and response leads to an increase of the effects of the Müller-Lyer illusion on grasping. In Experiment 1 we found that this is indeed the case. Similar findings of an increased illusion effect on grasping have been counted as evidence for a shift from a dorsal representation of object size (non-deceived, short memory) to a ventral representation of object size (deceived, long memory).

However, in Experiment 2 we found that this increase of the motor-illusion is not due to memory because removing visual information about hand and stimulus during movement execution restored the motor-illusion to about the same level as the motor illusion after 5 s delay. In Experiment 3 we tested this notion further by removing visual information about hand and stimulus at different times during movement execution.

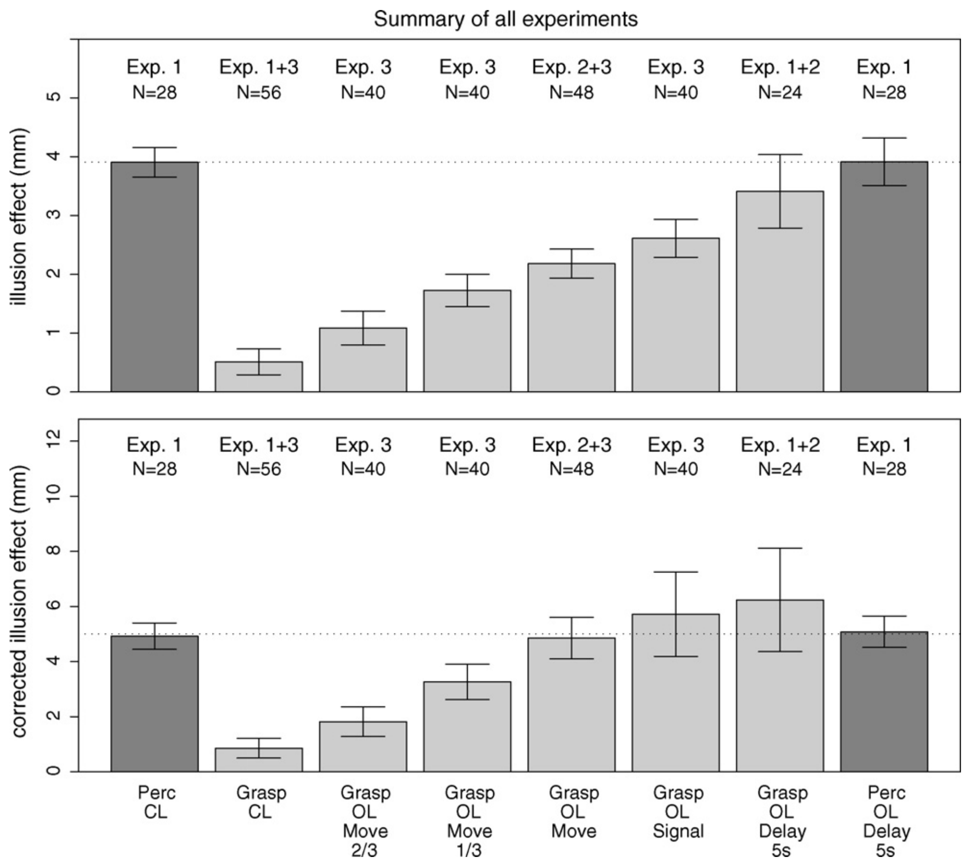

Fig. 7. Summary of all experiments. The data show that the perceptual illusion is not affected by delay and that the motor illusion depends on the time the hand is visible during grasping. If vision of the hand is suppressed during grasping (in OL-Move, OL-Signal, and OL-Delay), then the corrected motor illusion is as strong as the corrected perceptual illusion. Therefore the decrease of the illusion effect in grasping is due to the availability of visual feedback during the movement and not to memory demands. For statistics on the difference between OL-Move (the standard grasping condition) and all other conditions see Table 2. Of course, the error correction by visual feedback is not perfect such that we find even in the CL-condition some residual illusion effect ($t(55) = 2.3$, $p = .024$). Errorbars depict ±1 S.E.M.

This can also be seen in Fig. 7 which gives a summary of the results of all three experiments: in the OL-Move condition the corrected motor illusion is already at the level of the corrected perceptual illusion. In this condition, participants perform their motor programming under full vision such that according to the perception–action hypothesis and to the real-time view of action the dorsal stream should control the movement and there should be hardly any illusion effect. However, we find a clear illusion effect in this condition. If we now introduce delays relative to the OL-Move condition (in the OL-Signal and OL-Delay conditions), these theories predict a switch to ventral control, such that only now the motor illusion should emerge. But, again, this is not the case: the corrected motor illusion is already at the level of the corrected perceptual illusion and stays about constant at this level (for statistics of these differences, see Table 2).

On the other hand, if we allow more visual feedback during movement execution (OL-Move-2/3, OL-Move-1/3, and CL conditions), we find a reduction of the motor illusion. This reduction is to be expected according to classic notions of online correction of errors (Woodworth, 1899; Post & Welch, 1996).

Based on these results, we conclude that it is the availability of visual feedback and not a switch from dorsal to ventral control that leads to the change of the illusion effects. But what about all the other studies reporting evidence for an increase of the effects of visual illusions on grasping after a delay? We will discuss these studies in the following sections and argue that, surprisingly, our data are not inconsistent with these studies and that the evidence for a switch from dorsal to ventral control in most of these studies is weak.

5.1. Other studies on delayed grasping of the Müller-Lyer illusion

Westwood et al. (2001) and Westwood et al. (2000) also investigated delayed grasping of the Müller-Lyer illusion. The conditions used by them are a subset of the conditions used by us. Fig. 8 summarizes their results (using for consistency our terminology to label the conditions). Comparing their results to our results shows that the data for grasping are very consistent: both studies found essentially the same pattern of results for the motor illusion. We even

Table 2
Differences in corrected illusion effects between OL-Move and all other conditions

Condition	Lower	Mean	Upper	Sign
Perc-CL	−2.0	0.1	2.1	ns
Grasp-CL	−5.4	−4.0	−2.6	*
Grasp-OL-Move 2/3	−4.7	−3.0	−1.3	*
Grasp-OL-Move-1/3	−3.5	−1.6	0.3	ns
Grasp-OL-Signal	−2.2	0.9	3.9	ns
Grasp-OL-Delay	−2.7	1.4	5.5	ns
Perc-OL-Delay	−2.0	0.2	2.4	ns

Note: Differences are in mm and are relative to the OL-Move condition of grasping (positive value: larger than in OL-Move). For an overview of the conditions, see also Fig. 7. The column "Mean" is the mean difference; "Lower" and "Upper" are 95% confidence limits as calculated by a Taylor-approximation; "Sign" denotes the significant differences: $^{*}p < .05$.

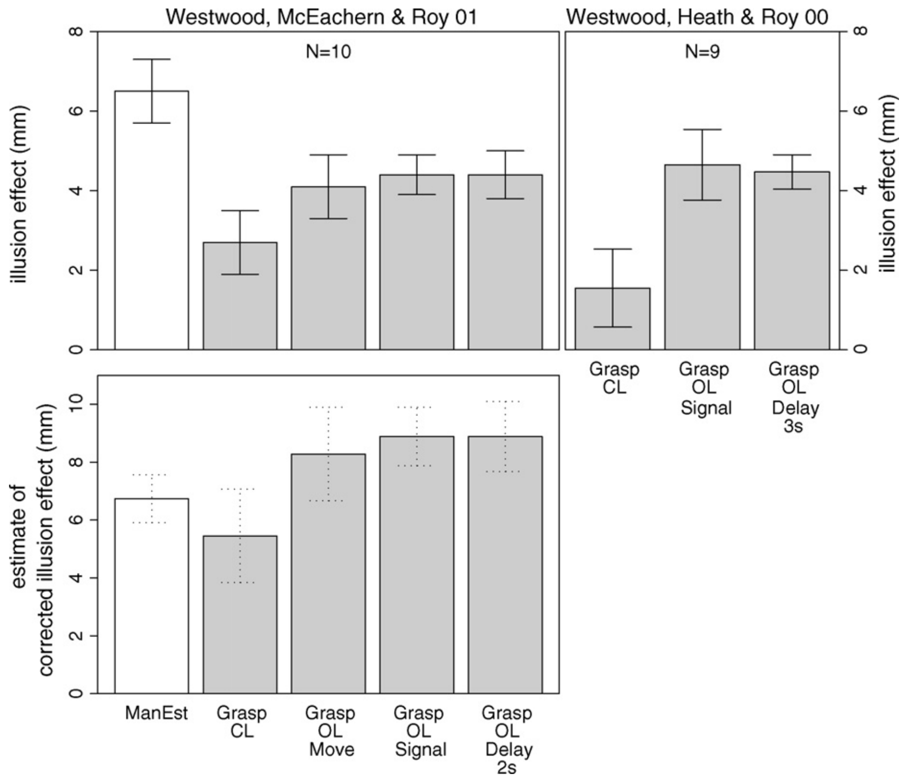

Fig. 8. Results of Westwood et al. (2001) and Westwood et al. (2000). These results are very similar to our results: The motor illusion increases from CL to OL-Move and OL-Signal and the additional memory demands in OL-Delay do not further change the motor illusion. Note that the full motor illusion in OL-Move clearly contradicts both, the perception–action theory and the real-time view of action. In the lower panel, we performed a rough estimate of the corrected illusion effects for Westwood et al. (2001). This was done because the perceptual task (manual size estimation) had a larger slope than grasping and therefore the perceptual illusion cannot be compared to the motor illusion without correction (Franz, 2003). After correction, the illusion in manual size estimation is similar to the motor illusion in grasping. Data are from: Westwood et al. (2001); Table 1, Figs. 3 and 4. Slopes for the conditions OL-Move, OL-Signal, and OL-Delay were estimated as being equal to the slope in CL (these slopes were not reported, but no big difference in the slopes is to be expected between these conditions, cf. Hesse and Franz (submitted). Westwood et al. (2000); data are from a personal communication with D. Westwood (June, 18th 2001). Errorbars depict ±1 S.E.M. For the corrected illusion effects these errorbars underestimate the size of the S.E.M. because we needed to assume a S.E.M. of zero for the slopes (because these S.E.M. were not reported).

found a larger suppression of the motor illusion in the CL condition than these studies.

At first sight, there seems to be only one slight inconsistency: Westwood et al. (2001) found a somewhat larger perceptual illusion than motor illusion (the perceptual illusion is even larger than the motor illusion in the OL-Delay condition). This can, however, easily be explained by the fact that they used manual size estimation as perceptual measure, but did not correct for the larger slope that is present in this measure (see Section 1 why this is important). Because we know from other studies that manual size estimation has often a larger slope than grasping (Franz, 2003), it can lead to unusual large illusion effects as long as no correction is performed. In the lower panel of Fig. 8 we performed a rough estimate of the corrected illusion effects. This shows that after correction the illusion effect in manual size estimation likely is similar to the illusion effect in grasping.

Therefore, even the data of Westwood et al. (2001) and Westwood et al. (2000) do not provide strong evidence for the perception–action theory and the real-time view of action. Also, the fact that Westwood et al. (2001) found a strong illusion effect in the OL-Move condition is clearly at odds with these theories, because both theories predict that there should be no illusion effect in this condition (the illusion should only emerge in the OL-Signal condition).

Now, one might also argue that the Müller-Lyer illusion is a bad test-case for the perception–action hypothesis, because this illusion might be created very early, before the split of dorsal and ventral streams. Therefore, it would be no surprise to not find a perception–action dissociation for this illusion (Milner & Dyde, 2003). This would, however, not be a counter-argument against our position, because all we are saying is that the Müller-Lyer illusion does not provide positive evidence for the perception–action hypothesis. Why this is the case (because of an early split, or because the perception–action hypothesis is wrong) we cannot decide yet. But, our study provides important information, given that the same authors did count studies on the Müller-Lyer illusion as positive evidence for the perception–action hypothesis. For example, Goodale et al. (2004) write with respect to the study of Hu and Goodale (2000; we will discuss this study in detail in the next section): “the participants are presumably scaling their grasp on the basis of their perceptual memory of the target’s size, which was originally encoded in scene-based relative metrics. Similar increases have been demonstrated in a variety of pictorial illusions in which relative metrics and scene-based frames of reference drive the illusion” (p. 137)—and then cite the studies of Gentilucci et al. (1996) on pointing in the Müller-Lyer illusion and the study of Westwood et al. (2000) which we just discussed. Similar citations can be found, for example, in Goodale & Westwood (2004, p. 206).

In short, the data on delayed grasping the Müller-Lyer illusion are surprisingly consistent across laboratories and do not provide positive evidence for the perception–action hypothesis or the real time view of action.

5.2. Other studies on delayed grasping of visual illusions

What about studies on delayed grasping of other visual illusions? It turns out that there are currently only two such studies. The first and most prominent study on delayed grasping of visual illusions was performed by Hu and Goodale (2000). Participants grasped virtual cubes that were accompanied either by a larger or a smaller second cube. This constitutes a simple size-contrast illusion. In two experiments, Hu and Goodale (2000) found that in their OL-Move condition (we again use our terminology for consistency) grasping was not significantly affected by the illusion, while it was significantly affected in their OL-Delay condition. They concluded from this pattern of results (no significant effect in one condition vs. significant effect in the other condition) that there is a difference between the conditions and interpreted this as evidence for a shift from dorsal to ventral control. However, this conclusion is statistically not valid. To come to the conclusion that the two conditions are affected differently one would have to test the *difference* of the effects in these conditions. This statistical problem is discussed in detail in Franz and Gegenfurtner (in press) and the same issue has already been raised earlier by Cantor (1956).

This is not a negligible problem. For the study of Hu and Goodale (2000) it is possible to perform a recalculation of the correct analysis from the published data, testing the difference of the illusion effects between OL-Move and OL-Delay conditions (cf. the appendix of Franz & Gegenfurtner, in press). This analysis shows that neither in Experiment 1 the difference of the illusion effects between OL-Move and OL-Delay is significant ($t(24) = 0.81$, $p = .42$) nor in Experiment 2 ($t(26) = 1.68$, $p = .10$). Even if we pooled the two experiments to increase power, the combined difference is not significant ($t(52) = 1.12$, $p = .27$). Therefore, we should not count Hu and Goodale (2000) as strong evidence for an increase of the motor illusion after a delay.

The second study on grasping other illusions than the Müller-Lyer illusion with a delay was performed by Westwood and Goodale (2003). This study used a size-contrast illusion similar to Hu and Goodale (2000). And indeed, this study did find a significant increase of the motor illusion when going from an OL-Move to an OL-Signal condition. After this, there was no increase when going to the OL-Delay condition.

In short, we are left with one study showing the increase of the illusion effect (as suggested by the perception–action hypothesis and the real-time view of action) and a number of studies on the Müller-Lyer illusion not showing the increase. Therefore, the data on delayed grasping of visual illusions are not as strong as they are often presented in the literature and it seems necessary to replicate the results of Westwood and Goodale (2003) if a strong argument in favor of the perception–action hypothesis or the real-time view of action shall be made.

Here is one reason why we tend to be skeptical that such an endeavor will be successful: Westwood and Goodale (2003) used a simple size contrast illusion (one object was accompanied by a larger or smaller object). This is very similar to the Ebbinghaus illusion (one object is surrounded by a number of larger or smaller objects). For the Ebbinghaus illusion, however, we and other researchers argued that the motor illusion in OL-Move conditions is already at the level of the perceptual illusion (Franz, 2001; Franz et al., 2000, 2003; Franz & Gegenfurtner, in press; Pavani et al., 1999). If this is true (not every researcher is convinced by this view, cf. Haffenden et al., 2001; Goodale, in press), it already contradicts both, the perception–action hypothesis and the real-time view of action because both theories assume that in the OL-Move condition there should be hardly any motor illusion. In addition, if the motor illusion is already at the level of the perceptual illusion, then introducing a delay cannot increase the illusion further, even if we assume that during the delay a shift from dorsal to ventral control would happen.

5.3. Relation to the planning-control model of Glover and Dixon (2001)

We argued that the availability of visual feedback leads to the changes of the illusion effects reported in most of the literature on delayed grasping of the Müller-Lyer illusion—and not a switch from dorsal to ventral control due to memory demands. But, if visual feedback is important, how does this relate to the planning-control model of Glover & Dixon (2001; Glover, 2004) which stresses the online-control during a movement? Although the planning-control model was not in the focus of this study (we tested and criticized this model in detail in Franz et al., 2005), we want to shortly discuss the implications of the current results for this model. We will argue that the data do not support the planning-control model, but are better explained by a common representation of object size for perception and action which is deceived by the illusion and corrected if visual feedback is available during movement execution (i.e. the common representation model, Franz et al., 2000).

Glover and Dixon proposed that motor acts are guided by two different processes, first by a planning process and later by a control process (Glover & Dixon, 2001, 2002; Glover, 2002, 2004). They assume that the planning process is ventral and deceived by visual illusions, while the control process is dorsal and not deceived by visual illusions. Therefore, they argue that a late movement parameter as the MGA will be little affected by visual illusions, because at the time of the MGA the control system has already corrected the "error" introduced by the illusion (e.g. Glover, 2004, p. 5, 11). Note, that Glover and Dixon specify two sources for the correction: the non-deceived representation in the dorsal control system and visual feedback.

However, the use of visual feedback is not specific to their model but is also assumed by classic motor control theories (Woodworth, 1899) and by the common-representation model (Franz et al., 2000). Therefore, the predictions of the planning-control model do not differ from the common-representation model as long as visual feedback is available. Both models assume that the error introduced by the illusion can be corrected by the use of visual feedback and that therefore the illusion effect in MGA can be reduced if visual feedback is available.

The predictions differ only in an open-loop condition without visual feedback: the common-representation model assumes that the illusion cannot be corrected because there is no visual feedback available. Therefore the MGA should be affected by the illusion to a similar degree as perception. The planning-control model, on the other hand, assumes that the illusion might still be corrected due to the switch to the non-deceived dorsal representation during late phases of the movement (Glover & Dixon, 2002).

However, the corrected illusion effect in MGA in the OL-Move condition was similar to the corrected illusion effect in perception (Fig. 7). This is exactly what we expect from the common-representation model. Therefore, we don't need to assume a switch from ventral to dorsal control and a non-deceived representation in the dorsal system, as suggested by Glover and Dixon in their planning-control model.

In short, our data do not support the planning-control model and are better described by the common-representation model. This is consistent with other studies which also came to a negative appraisal of the planning-control model (e.g. Franz et al., 2005; Handlovsky, Hansen, Lee, & Elliott, 2004; Meegan et al., 2004). We now return to our discussion of the perception–action hypothesis.

6. Conclusions

We found that delayed grasping of the Müller-Lyer figure does not provide evidence for a switch from one internal representation (dorsal, not-deceived) to the other (ventral, deceived). The changes found in the motor effects of the illusion can easily be explained by the availability of visual feedback during movement execution. This removes one piece of evidence that has traditionally been counted as positive evidence for the perception–action hypothesis.

This result is consistent with Hesse and Franz (submitted for publication), where we tested other evidence that has been put forward for a shift from dorsal to ventral control of grasping after a delay (Hu, Eagleson, & Goodale, 1999). We found the well-known exponential decay of visual information for grasping—and also no indication for a shift between two qualitatively different neuronal control systems that control actions.

This fits well to other, similar critique of the evidence for the perception–action hypothesis. For example, the finding that the Ebbinghaus illusion should not affect grasping (Aglioti et al., 1995) has been criticized seriously (for summaries of the critique, see Franz & Gegenfurtner, in press; Smeets & Brenner, 2006). Similarly the classic distinction between cognitive vs. sensorimotor maps (Bridgeman et al., 1981, 1997) which is a predecessor of the perception–action hypothesis has also been challenged (Dassonville & Bala, 2004a, 2004b). These studies are intriguing because Bridgeman had a similar notion that illusion effects on pointing movements should increase after a delay—which should also be indicative of a shift from one representation (motor map, not deceived) to the other representation (cognitive map, deceived). However, in a collaborative study Dassonville and Bridgeman found that these findings can be better explained by a unitary representation of space (Dassonville et al., 2004). Also, Schenk (2006) questioned whether the dissociation in the famous patient D.F. is really between perception and action as suggested by Goodale and Milner or maybe between different task demands. Other researchers raised further concerns against Goodale and Milner's interpretation of the patient data (e.g. Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006).

In summary, this criticism might indicate that the division of labor in the brain is not as suggested by the perception–action hypothesis. Specifically, the notion that object size is calculated twice, once in the ventral stream for perception (deceived by visual illusions and with long memory) and once in the dorsal stream for action (non-deceived and with short memory) seems problematic, given our results on the effects of delay on visual illusions and grasping.

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