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RESEARCH ARTICLE

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Grasp effects of the Ebbinghaus illusion: obstacle avoidance is not the explanation

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Abstract The perception-versus-action hypothesis states that visual information is processed in two different streams, one for visual awareness (or perception) and one for motor performance. Previous reports that the Ebbinghaus illusion deceives perception but not grasping seemed to indicate that this dichotomy between perception and action was fundamental enough to be reflected in the overt behavior of non-neurological, healthy humans. Contrary to this view we show that the Ebbinghaus illusion affects grasping to the same extent as perception. We also show that the grasp effects cannot be accounted for by non-perceptual obstacle avoidance mechanisms as has recently been suggested. Instead, even subtle variations of the Ebbinghaus illusion affect grasping in the same way as they affect perception. Our results suggest that the same signals are responsible for the perceptual effects and for the motor effects of the Ebbinghaus illusion. This casts doubt on one line of evidence, which used to strongly favor the perception-versus-action hypothesis.

Keywords Motor control · Visual pathways · Illusions · Prehension · Human

Introduction

Goodale and Milner proposed that visual information is processed in two functionally distinct systems, which they identified anatomically with the dorsal and ventral cortical streams (Goodale and Milner 1992; Milner and Goodale 1995). According to this perception-versus-action hypothesis, the dorsal stream transforms visual information to guide motor acts, while the ventral stream creates a visual percept of the world. The perception-versus-action hypothesis can explain seemingly paradoxical symptoms of neurological patients. For example, patient D.F. is able to grasp an object accurately, but is unable to use the same visual information in perceptual judgments (Goodale et al. 1991). Similarly, blindsight patients are unable to perceive objects in a blind region of their visual field; nevertheless they are able to indicate the position of the objects (Pöppel et al. 1973; Weiskrantz et al. 1987). Both symptoms could be explained by selective impairment of the vision-for-perception system and an intact vision-for-action system. However, this is not the only possible explanation and therefore additional, independent evidence for the perception-versus-action hypothesis seems needed.

The finding of Aglioti et al. (1995) that the Ebbinghaus/Titchener illusion (Fig. 1) affects perception but not grasping (or only marginally so) has often been accepted as compelling evidence for the perception-versus-action hypothesis (Koch and Braun 1996; Jackson and Husain 1997; Carey 2001; Plodowski and Jackson 2001). It seemed that even the overt behavior of non-neurological humans reflected a fundamental property of the visual system, namely that visual information is processed in

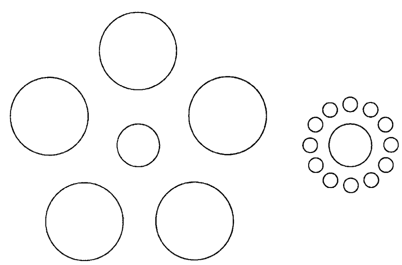

Fig. 1 The Ebbinghaus/Titchener illusion. A circle surrounded by larger circles is perceived as being smaller than if surrounded by smaller circles (and vice versa)

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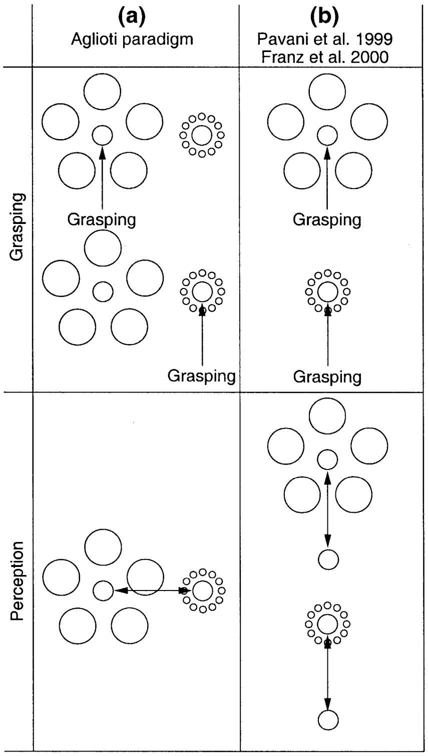

Fig. 2a,b Presentation of perceptual and motor tasks in different studies of the Ebbinghaus illusion. **a** Perceptual task and motor task of the Aglioti et al. (1995) paradigm. Two Ebbinghaus figures were presented and the central circles were replaced by discs which could be grasped. In the perceptual task, participants compared the sizes of the two central discs directly, while in the motor task they successively grasped one of the two central discs. Note the asymmetry in this procedure: in order to grasp, participants had to calculate only the size of one of the central discs at a time. In the perceptual task, however, participants had to compare the two central discs directly, both being subjected to the illusion at the same time. Franz et al. (2000) showed that the task demands of this direct comparison selectively increase the illusion by about 50%. **b** In the studies of Pavani et al. (1999) and of Franz et al. (2000), motor task and perceptual task were matched more closely. Only one Ebbinghaus figure was presented at a time. In the motor task participants grasped the central discs and in the perceptual task they compared the central disc to a neutral comparison stimulus. In these studies, no difference between the perceptual effects and the motor effects of the Ebbinghaus illusion were found (figure adapted from Franz 2001)

two different and parallel streams for the purposes of perception and action.

However, Franz et al. (2000) criticized this finding, and argued that in the Aglioti paradigm the perceptual task and the motor task were not sufficiently matched (Fig. 2). Studies that avoided this problem (Pavani et al. 1999; Franz et al. 2000) found motor effects of the same size as the perceptual effects (cf. Fig. 3a). This suggests that a common source is responsible for the illusion effects in perception and in grasping (common source model, cf. Franz et al. 2000, 2001).

Recently, Haffenden and colleagues (Haffenden and Goodale 2000; Haffenden et al. 2001) proposed that the motor effects of the Ebbinghaus illusion might be

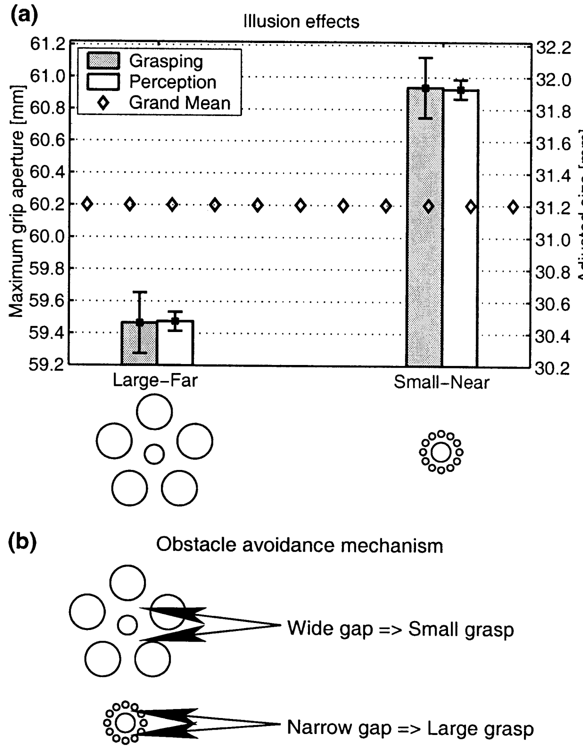

Fig. 3a,b Effects of the Ebbinghaus illusion on perception and on grasping. **a** Effects found by Franz et al. (2000). The effects on perception and on grasping are virtually identical. A similar result was obtained by Pavani et al. 1999. Labels *Large* and *Small* refer to the size of the context circles and labels *Near* and *Far* to the eccentricity of the context circles. The effects were calculated in exactly the same way as in the present study (cf. Methods section and Fig. 5). **b** Explanation for the illusion effects as suggested by Haffenden and colleagues (Haffenden and Goodale 2000, Haffenden et al. 2001) who assume that the effects of the Ebbinghaus illusion on grasping are caused by mechanisms other than those involved in the perceptual effects. According to their obstacle avoidance hypothesis, the context circles are treated by the vision-for-action system as potential obstacles that affect the trajectories of the fingers. Haffenden and coworkers suggested that a wide gap between the context circles and the target disc leads to *smaller* grasping, while a narrow gap leads to *wider* grasping

generated independent of the perceptual effects in the vision-for-action system. Haffenden and Goodale argued that the context circles of the Ebbinghaus illusion could be treated as potential obstacles for the fingers and therefore might affect the trajectories of the grasp movements. Accordingly, the finding of equal effects of the Ebbinghaus illusion on grasp and perception could simply be a coincidence.

How could such an obstacle avoidance mechanism work? In principle, we see three possibilities of which, however, only one can explain the effects of the Ebbinghaus illusion on grasping. The possibilities are as follows. (1) Humans might use a larger grasp if the overall size of the Ebbinghaus illusion, i.e., the outline of all context circles that surround the grasp disc, is larger. In this case, the "Large–Far" condition of Franz et al. (2000) should yield larger grasping than the "Small–

Near" condition (Fig. 3a). However, this is not the case, and hence this mechanism can not explain the grasp effects we found with the Ebbinghaus illusion. (2) Humans might use a larger grasp if the gap between the central grasp disc and the surrounding context circles is wider. Again, this mechanism predicts larger grasping in the Large–Far condition than in the Small–Near condition, which is not the case (Fig. 3a). Finally, (3) humans might use a *smaller* grasp if the gap between grasp disc and context circles is wider (cf. Fig. 3b). This is the only mechanism that conforms to the grasp effects of the Ebbinghaus illusion and this is the mechanism that was proposed by Haffenden and colleagues (Haffenden and Goodale 2000; Haffenden et al. 2001). Note, that (a priori) it is not very plausible that humans should open the hand less if the gap is wider. To explain this, Haffenden and colleagues (Haffenden and Goodale 2000; Haffenden et al. 2001) argued that the motor system interprets the wide gap (Large–Far condition) as a hole in which to fit the fingers, and that the narrow gap (Small–Near condition) is not wide enough to do this.

In two studies, Haffenden and colleagues (Haffenden and Goodale 2000, Haffenden et al. 2001) tried to demonstrate this obstacle avoidance mechanism. However, both studies had drawbacks. The first study failed to show significant effects of the distance of the context elements on grasping (Fig. 6, p 1603 of Haffenden and Goodale 2000). The second study (Haffenden et al. 2001) added a third illusion condition to the Ebbinghaus illusion, whereby the gap for the small context circles was the same as for the large context circles (see the Small–Far and the Large–Far conditions in Fig. 4a). According to the obstacle avoidance mechanism, this manipulation should eliminate the grasp effect of the Ebbinghaus illusion because now the gap was the same for both conditions. On the other hand, the common source model still predicts some effect on grasping because matching the gaps decreases (but does not eliminate) the perceptual effect (cf. Girgus et al. 1972). The results of Haffenden and coworkers conform to the prediction of the obstacle avoidance mechanism: there was no significant difference in grasping between the Large–Far and the Small–Far conditions.

However, we see two problems with this result. Firstly, the result is a null effect (no difference between Large–Far and Small–Far in grasping; cf. Fig. 4a). An important issue here is the sample size needed to detect reliably the effect predicted by the common source model. We found that the 18 participants used by Haffenden and colleagues were not enough to detect this effect with sufficiently high probability. A power analysis shows that the probability of *missing* the effect predicted by the common source model was high (see Methods section for details). In consequence, the null effect found by Haffenden et al. (2001) could very well be due to random, statistical fluctuations. Secondly, Haffenden et al. (2001) also looked at the difference between the Small–Far and the Small–Near conditions (cf. Fig. 4a). The problem here is that both models predict differences: the obstacle avoid-

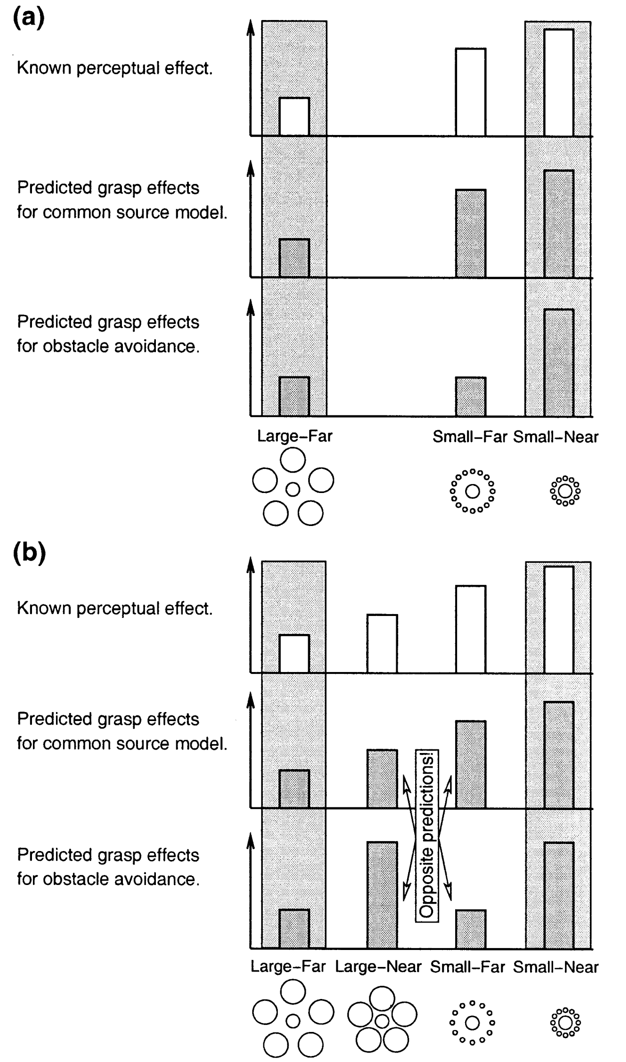

Fig. 4a,b Predictions of the common source model and of the obstacle avoidance mechanism for the study of Haffenden et al. (2001) and for the present study. Labels *Large* and *Small* refer to the size of the context circles and the labels *Near* and *Far* to the eccentricity of the context circles. *Shaded areas* indicate the data for which the obstacle avoidance mechanism was postulated (post hoc). Therefore these conditions cannot serve as a test for the obstacle avoidance mechanism. **a** In the study of Haffenden et al. (2001), the gap between central disc and context circles was the same for the two *Far* conditions. In consequence, the obstacle avoidance mechanism predicts no difference in grasping between these two conditions. On the other hand, the common source model predicts a difference in grasping because there should still be a (slightly decreased) perceptual illusion effect between these two conditions. **b** In the present study, the two *Far* and the two *Near* conditions had the same gap. In consequence, the obstacle avoidance mechanism predicts no difference in grasping between the two *Far* and between the two *Near* conditions, while the common source model predicts difference in grasping, which should follow the perceptual effects of the illusion. Note, that the predictions in the *Large–Near* and *Small–Far* conditions are in the opposite direction for the common source model than that for the obstacle avoidance mechanism. All stimuli are drawn approximately to scale (note the small but unimportant difference between the *Small–Far* conditions of the two studies). In the study of Haffenden et al. (2001), the *Large–Far* and *Small–Near* conditions were named "Traditional Large" and "Traditional Small", respectively. The *Small–Far* condition was named "Adjusted Small" ance mechanism predicts a large difference, and the common source model predicts a small difference, which should correspond to the perceptual difference. In consequence, the predictions are quite similar and, to assess which model conforms better to the data, we have to know exactly what the perceptual effect is. This is problematic because the perceptual measures usually reported in the literature typically do not yield exactly the same magnitude of perceptual effects of the Ebbinghaus illusion. Thus, there has been some debate regarding which perceptual measure is most appropriate for comparison with grasping (Carey 2001; Franz 2001).

In the present study we tried to overcome these shortcomings in two ways. Firstly, we used more stimulus conditions and arranged them in such a way that the predictions of the obstacle avoidance mechanism and of the common source model were in *opposite* directions (see the Large–Near and Small–Far conditions in Fig. 4b). In consequence, we do not rely on null effects for our decision between the two models, but contrast two opposing predictions. Also, the problem of the exact size of the perceptual effects is diminished, because now it is sufficient to know the direction of the perceptual effects instead of their exact sizes. Secondly, we used a much larger sample size (52 participants, see Methods section for a power analysis on this sample size). This large sample size enabled us to discriminate reliably between the predictions of the common source model and of the obstacle avoidance mechanism.

In summary, we contrast two hypotheses in this study. One hypothesis states that the motor effects of the Ebbinghaus illusion have their origin at the same source as the perceptual effects (common source model; Franz et al. 2000, 2001). The other hypothesis states that the motor effects of the Ebbinghaus illusion are generated independent of the perceptual effects (obstacle avoidance mechanism; Haffenden and Goodale, 2000; Haffenden et al. 2001). In our experimental design (Fig. 4b), the common source model predicts that participants use a larger grasp in the Small–Far than in the Large–Near condition, while the obstacle avoidance mechanism predicts that participants use a *smaller* grasp.

Methods

Power analyses for sample sizes

In order to discriminate reliably between the predictions of the obstacle avoidance mechanism and of the common source model, we have to ensure that if an effects exists in reality it will be detected with sufficient probability (or "statistical power"). Such a power analysis (Cohen 1988) can easily be performed for the Ebbinghaus illusion because we already have ample data on the effects of the illusion on grasping. In consequence, we can estimate the sample size that is needed to detect reliably the effects predicted by the different models. We performed two power analyses, one for the study of Haffenden et al. (2001) and one for the present study. Both power analyses are based on the effects found by Franz et al. (2000), which are also depicted in Fig. 3a. These grasp effects are similar to those found in a number of other studies (for an overview see Franz 2001) and are the effects for which the obstacle avoidance mechanism was postulated by Haffenden and colleagues (Haffenden and Goodale 2000; Haffenden et al. 2001).

Franz et al. (2000) found a grasp effect for the illusion of δ= MGA(Small,Near)−MGA(Large,Far) =1.47 mm (MGA representing maximum grip aperture). In the following, this effect will be called the "original effect". The standard deviation of the original effect was σ=1.93 mm. This corresponds to an effect size of $d = \frac{\delta}{\sigma} = \frac{1.47}{1.93} = 0.76$.

In the Haffenden et al. (2001) study, the common source model predicted a somewhat smaller illusion effect between the Small–Far and Large–Far conditions than the original effect, while the obstacle avoidance mechanism predicted no effect (cf. Fig. 4a). If we assume that the common source model is true and that we still want to detect an effect of 80% of the original effect (i.e., d=0.76×80%=0.61), this results in a statistical power of 64% for the 18 participants used in the study of Haffenden et al. (two-tailed test, α=5%). In other words, the probability of *missing* this illusion effect if it exists in reality was as high as β=100−64%=36%. In consequence, it is very possible, that Haffenden et al. (2001) missed an existing effect (conforming with the common source model) simply due to random, statistical fluctuations.

In the present study, the common source model predicted a smaller illusion effect between the Small–Far and Large–Near conditions than the original effect, while the obstacle avoidance mechanism predicted the original effect, but in opposite direction (cf. Fig. 4b). If we assume that the common source model is true and that we still want to detect an effect at 70% of the original effect (i.e., d=0.76×70%=0.53), this results in a statistical power of 94% for the 52 participants used in this study (two-tailed test, α=5%). In other words, the probability of *missing* the effect predicted by the common source model if it exists in reality was β=100−94%=6%. On the other hand, if we assume that the obstacle avoidance mechanism is true, the power to detect the reversed original effect between Small–Far and Large–Near conditions is greater than 99%. That is, the probability of *missing* the effect predicted by the obstacle avoidance mechanism if it exists in reality was less than 1%. In consequence, we can be very confident of having minimized the errors due to random, statistical fluctuations.

Participants

Fifty-two volunteers (29 female, 23 male) participated in the experiment, ranging in age from 16 to 47 years (mean 25.4 years). In return for their participation, they received a payment of DM 15 per hour (approximately 7.5, or US$ 7). Participants had normal or corrected-to-normal vision (Snellen equivalent of 20/25 or better; Ferris et al. 1982), normal stereopsis of 60 seconds of arc or better (Stereotest circles, Stereo Optical, Chicago, USA), and all were right-handed (Oldfield 1971). Written, informed consent was obtained from the participants prior to their inclusion in the study and the rights of the participants were protected according to the 1964 Declaration of Helsinki.

Stimuli

The variants of the Ebbinghaus illusion used in our experiment are shown in Fig. 4b. The "Large" and "Small" context circles were 58 and 10 mm in diameter, respectively. In the "Near" and "Far" conditions the distances between the midpoint of the target disc and the nearest point on the context circles was 24 and 31 mm, respectively). All context circles were drawn on a board. The targets were aluminum discs, 31, 34, or 37 mm in diameter (corresponding to 2.7, 3.0, and 3.3 degrees of visual angle) and were 5 mm in height. To maximize the similarity between the three-dimensional target disc and the two-dimensional context circles we minimized shadows and had participants view the stimuli from above. In the perceptual task, an isolated comparator circle was displayed on a computer monitor at a distance of 155 mm (13.8 degrees of visual angle) from the target disc. Note, that the Large–Far and the Small–Near conditions were identical to the conditions used in our previous study on this topic (Franz et al. 2000) and geometrically similar to the conditions used by Aglioti et al. (1995).

Apparatus

Participants sat on a stool and used a chin rest to keep the position of the head constant. They looked down at a 21-inch monitor (effective screen diagonal of 48.5 cm) as if looking at the top of a table. The monitor was positioned at a distance of approximately 65 cm from the eyes. The screen of the monitor served as a table for the presentation of the stimuli. The screen was not horizontal, but tilted so as to be oriented perpendicular to gaze direction. Participants wore liquid-crystal (LC) shutter glasses (Milgram 1987), which allow efficient suppression of vision. The grasp trajectories were recorded using an Optotrak system (sampling rate 100 Hz): six infrared light-emitting diodes (LEDs) were mounted on two little flags (three LEDs per flag). The flags were attached to thumb and index finger. Before starting the experiment, the typical grasp points on the fingers were determined and measured relative to the markers on the flags. This enabled us to calculate the trajectories of the grasp points and to determine the maximum grip aperture (MGA, i.e., the maximum aperture between index finger and thumb during the reach phase of the grasp movement). MGA was used as dependent variable in almost all studies investigating the question of functional dissociation between vision-for-perception and vision-for-action in visual illusions (e.g., Aglioti et al. 1995; Daprati and Gentilucci 1997; Haffenden and Goodale 1998; Pavani et al. 1999; Franz et al. 2000, 2001; Haffenden et al. 2001). MGA has several advantages: (1) it is usually reached before the hand has any contact with the grasp object, excluding possible effects of direct, haptic feedback, and (2) MGA is linearly related to the physical size of objects (Jeannerod 1981, 1984). This allows the reasoning that if a visual illusion affects the size estimate used by the motor system then this should be reflected in the MGA. This reasoning was originally suggested by Aglioti et al. (1995). For a detailed mathematical formulation and discussion see Franz et al. (2001).

Procedure

In the perceptual task, participants adjusted an isolated circle that was displayed on the computer monitor until they perceived it to be of the same diameter as the target disc. The initial diameter of the comparison circle was set (pseudo) randomly between 17 and 48 mm (step sizes of 1 mm, uniform distribution). During the adjustments, participants had full vision of the stimuli and there was no time limit for the adjustments. In perceptual control experiments we established that this adjustment method leads to the same measured illusion effects as a constant stimuli method with 800 ms presentation time. The adjustment method has the advantage of being more efficient. The LC shutter glasses suppressed vision as soon as the participant finished the adjustments until the next trial was set up by the experimenter. For each participant, the trials were presented in a different, computer-generated, (pseudo) random order. Each participant performed 36 adjustments (3 sizes of the central disc × 4 illusion conditions × 3 repetitions).

In the motor task, participants grasped the target disc with their dominant, right hand, lifted the disc, and moved it to the side. Then, the experimenter fetched the target disc and prepared the next trial. The LC shutter glasses suppressed vision as soon as the grip started (on average 840±47 ms after stimulus presentation) such that participants could neither see their hand nor the stimulus during grasping. Participants had 4 s to finish the movement (from opening of the shutter glasses until depositing the disc). If this time limit was exceeded, the trial was returned to the set of trials to be performed and repeated later at a randomly determined time. As in the perceptual task, trials were presented in a (pseudo) random order. Each participants performed 72 grasps (3 sizes of the central disc × 4 illusion conditions × 6 repetitions).

In both tasks and before each trial the experimenter selected the current combination of context circles and target disc, positioned the target disc on top of the board with the context circles and mounted the board on top of the monitor. The LC shutter glasses were opaque during this preparation. When finished, the experimenter pressed a button to open the LC shutter glasses and to start the trial. The order of tasks was counterbalanced between participants, such that 26 participants performed the perceptual task first, and the other 26 participants performed the motor task first.

Data analysis

For data analysis, repeated measures analyses of variance (ANOVAs) were performed with the factors diameter of target disc (three levels: 31, 34, 37 mm) and type of context circles (four levels; cf. Fig. 4b). Dependent variables were MGA (motor task), adjusted size of the comparator circle (perceptual task), and the difference between MGA and adjusted size of the comparator circle (comparison of the illusion effects between motor and perceptual task).

We used a significance level of $\alpha=0.05$ for all statistical analyses. *P*-values above 0.000001 are given as exact values. For appropriate parameters values are presented as means ±standard error of the mean (SEM).

Results

Participants performed a perceptual and a grasping task on the stimuli shown in Fig. 4b. In the perceptual task, they adjusted an isolated comparator circle to match the size of the target disc. Results show the well-known perceptual illusion (Fig. 5, Table 1): the target disc appeared larger if the context circles were smaller (and vice versa). Also, the target disc appeared slightly larger if the small or the large context circles were closer to it (to see this, compare the Near conditions with the Far conditions; cf. Girgus et al. 1972).

In the motor task, participants grasped the target disc and the MGA between index finger and thumb was determined. We found highly significant illusion effects on grasping (Table 1). Grasping as well as perception were linearly related to the physical size of the target disc (slope grasping 0.74±0.04; slope perception 0.88±0.02). These slopes were sufficiently similar that we did not need to correct for possible differences in the slopes (cf. Franz et al. 2001; see Franz 2003 for a discussion of this topic). ANOVA on the differences between the perceptual response and grasping shows that the illusion effects in grasping did not differ from the illusion effects in perception (Fig. 5 and Table 1).

In the Large–Far and Small–Near conditions, results replicated our previous finding of an approximately 4.5% illusion effect (to see this, compare Fig. 5b with Fig. 3a). In the two new conditions (the Large–Near and Small–Far conditions), results conformed well with the predictions of the common source model but not with the predictions of the obstacle avoidance mechanism: MGA was *larger* in the Small–Far than in the Large–Near condition ($t_{(51)}=4.5$, $P=0.00004$, two-tailed test), as predicted by the common

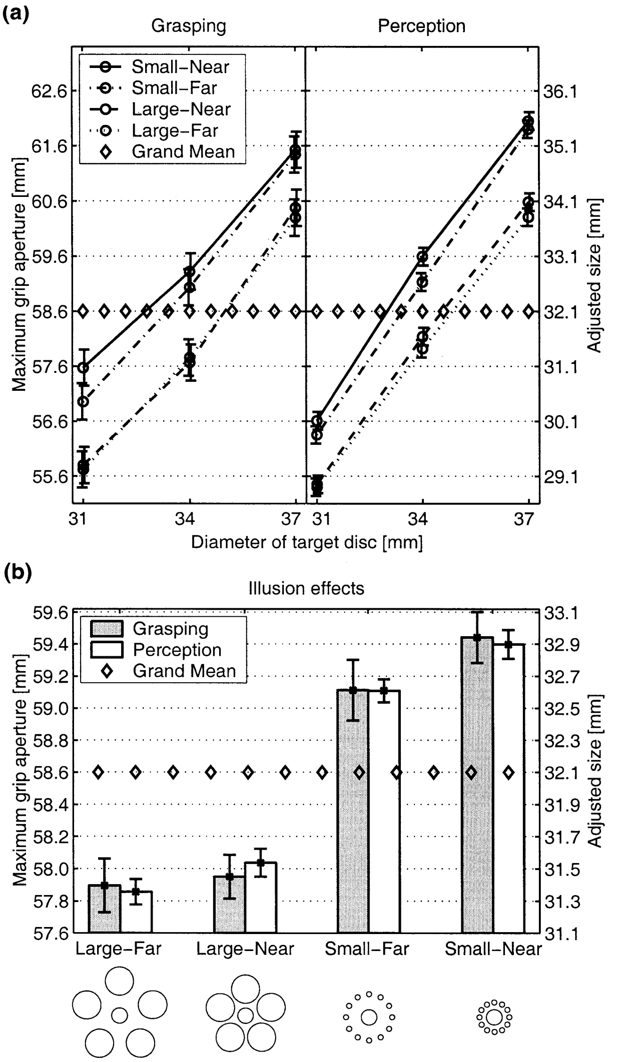

Fig. 5a,b Results for grasping and for the perceptual task. **a** Maximum grip aperture (MGA) and adjusted size of the comparator circle as functions of the illusion conditions and of the size of the target disc. **b** Graphic depiction of the illusion effects. For each illusion condition, MGA and adjusted size are averaged across the different sizes of the target disc. In both plots, the *ordinates* are aligned such that the grand means of MGA and of adjusted size are at the same height. Data depict means ±SEM. In **a**, the SEMs are calculated from the subject × context error term in order to correct for between-subject variability (cf. Loftus and Masson 1994)

source model, and not smaller, as would be expected if the obstacle avoidance mechanism were correct.

Discussion

These findings present strong evidence against the notion that the motor effects of the Ebbinghaus illusion might be generated independent of the perceptual effects in the action system: the obstacle avoidance mechanism proposed by Haffenden et al. (2001) cannot explain the current pattern of results.

Note that the predictions of the obstacle avoidance mechanism are independent of any perceptual effect. If this mechanism were true, it should have predicted (at least approximately) the pattern of results we found in our grasp data. The fact that this is not the case provides strong evidence against this obstacle avoidance mechanism. This result is important in the context of the debate concerning which perceptual measure is most appropriate to be compared with grasping. Proponents of a dissociation between perception and action focus mainly on a perceptual measure that has been named manual estimation: participants indicate the target size by opening index finger and thumb with (or without) seeing hand or stimulus during performance of the task (e.g., Daprati and Gentilucci 1997; Haffenden and Goodale 1998; Haffenden et al. 2001). Proponents of a common source of the illusion for perception and for action focus mainly on "standard" perceptual measures. For example, participants adjust a reference to match the size of the target (adjustment procedure; e.g., Pavani et al. 1999; Franz et al. 2000). We have argued elsewhere (Franz 2001) that manual estimation leads to larger illusion effects compared with both grasping and standard perceptual measures. In the present study, however, this is not a problem because we just need to compare the *directions* of the illusion effects in order to discriminate between the common source model and the obstacle avoidance mechanism.

Of course, the failure of the obstacle avoidance mechanism suggested by Haffenden and coworkers (Haffenden and Goodale 2000; Haffenden et al. 2001) does not rule out the possibility that other non-perceptual

Table 1 ANOVAs for grasping and perception in the Ebbinghaus illusion. For each task (grasping and perception) individual repeated measures ANOVAs were calculated. To determine whether grasping was affected by the illusion in a different way to perception, an additional repeated measures ANOVA was calculated on the difference between the grasp responses and the perceptual responses. In all ANOVAs, the factors were illusion condition (four levels; cf. Fig. 4b), size of the target disc (three levels: 31, 34, and 37 mm), and their interaction. Dependent variables were maximum grip aperture (MGA, grasping), adjusted size of the comparison circle (perception), and the difference between MGA and adjusted size

Task	Main effects				Interaction Illusion × size	
	Illusion		Size of target disc			
	$F_{(3,153)}$	P	$F_{(2,102)}$	P	$F_{(6,306)}$	P
Grasping	17.7	<0.000001***	97.5	<0.000001***	0.3	0.941
Perception	65.9	<0.000001***	854.7	<0.000001***	2.1	0.053
Difference	0.1	0.965	4.3	0.017*	0.7	0.653

* P<0.05, *** P<0.001

mechanisms are responsible for the grasp effects of the Ebbinghaus illusion. However, no such mechanism has yet been proposed or tested. Given the surprisingly similar effects of the Ebbinghaus illusion on perception and on grasping, it seems parsimonious to assume that the effects originate from a common source.

Another possibility is that the dissociation can only be detected with different time requirements from those we employed. For example, Carey (2001) suggested that the dorsal stream dominates motor actions only if they are fast. In contrast, Glover and Dixon took an opposite view and suggested that the dorsal stream only dominates motor actions after a certain time delay (Glover 2002; Glover and Dixon 2002). Therefore the dissociation should only show up in the very final stages of a grasp movement (but see Franz 2003). Given these contradictory notions to modify the perception-versus-action hypothesis, it seems that more research is needed to clarify these issues.

What are the consequences for the perception-versus-action hypothesis if we adopt the view that grasp effects and perceptual effects of the Ebbinghaus illusion have the same source? First of all, this view removes one piece of evidence that has been considered as being especially strong for the perception-versus-action hypothesis. It seemed that the functional distinction between a vision-for-action system and a vision-for-perception system is fundamental enough to be reflected in the overt behavior of healthy, non-neurological humans.

But does our finding disprove the perception-versus-action hypothesis? This is not necessarily the case. We see three possibilities to explain our findings and not all of them are incompatible with the perception-versus-action hypothesis. (1) The Ebbinghaus illusion could be generated *before* the vision-for-action and the vision-for-perception systems separate, an assumption that would reconcile the perception-versus-action hypothesis with our findings. A problem with this view is the fact that the Ebbinghaus illusion seems to depend partially on higher cognitive functions which are related to object recognition and should be performed in the vision-for-perception system (Coren and Enns 1993). (2) The Ebbinghaus illusion could be generated in the vision-for-perception system, but there could be enough crosstalk between the two systems for the illusion to "leak" to the vision-for-action system. The problem with this view is that if there is too much crosstalk between the systems, the notion of two separate systems becomes problematic (for a discussion of this possibility see also Franz et al. 2001). (3) The functional separation between vision-for-action and vision-for-perception as proposed by the perception-versus-action hypothesis could be wrong and alternative accounts might be more appropriate (e.g., Ungerleider and Mishkin 1982). A problem with this view is that it must explain the other evidence that has been compiled in favor of the perception-versus-action hypothesis (e.g., the dissociation found in patient D.F. of Goodale et al. 1991). Certainly, our data *alone* cannot provide the final solution to this question. A much wider base of evidence has to be taken into account, for example, from lesion studies, electrophysiological studies, imaging studies, and studies on neurological patients.

Conclusions

We found that grasping is deceived by the Ebbinghaus illusion in the same way as perception. The recently proposed non-perceptual mechanisms (Haffenden and Goodale 2000; Haffenden et al. 2001; Plodowski and Jackson 2001) cannot account for the motor effects of the Ebbinghaus illusion. This suggests that the same source is responsible for the perceptual effects and for the motor effects of the Ebbinghaus illusion. We see three possibilities to explain our findings. It is possible that the Ebbinghaus illusion is generated before the perceptual stream and the action stream separate, or information is exchanged between the two streams, or the primate visual system is not subdivided in the way suggested by the perception-versus-action hypothesis. The first two possibilities show that the perception-versus-action hypothesis could be reconciled with our findings. However, the Ebbinghaus illusion can no longer be included as strong and compelling evidence for the perception-versus-action hypothesis and against alternative accounts that assume a different functional subdivision of the visual system (e.g., Ungerleider and Mishkin 1982).

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