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Grasp effects of the Ebbinghaus illusion: Obstacle–avoidance is not the explanation

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Grasp effects of the Ebbinghaus illusion: Obstacle–avoidance is not the explanation

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Abstract. It is often assumed that the primate brain processes visual information 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 provide strong evidence for this perception–versus–action hypothesis. The dichotomy between an action–stream and a perceptual–stream appeared to be 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 was recently suggested (Haffenden & Goodale, 2000; Haffenden, Schiff, & Goodale, 2001). Instead, even subtle variations of the Ebbinghaus illusion affect grasping in the same way as 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 has often been counted as being especially strong in favor of the perception–versus–action hypothesis.

1 Introduction

Goodale and Milner (1992, 1995) proposed that visual information is processed in two functionally distinct systems which they identified anatomically with the dorsal and ventral cortical streams. 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. (For sake of simplicity, we follow the nomenclature of Milner & Goodale, 1995 who use the term "perception" to refer to visual awareness. In other contexts, the word "perception" is used to refer to any processing of sensory input). The perception–versus–action hypothesis has been highly influential in the cognitive neuroscience.

One reasons for the impact of the perception–versus–action hypothesis is based on the fact that it 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, Milner, Jakobson, & Carey, 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, Held, & Frost, 1973; Weiskrantz, Warrington, Sanders, & Marshall, 1987). Both symptoms could be explained by selective impairment of the ventral stream and an intact dorsal stream.

A second reason for the impact of the perception–versus–action hypothesis is the elegant integration of anatomical and functional levels of description. At the *anatomical* level, the perception–versus–action hypothesis is based on the physiological differences between projections from the primary visual cortex to the posterior parietal cortex (dorsal stream) and to the inferior temporal cortex (ventral stream). At the *functional* level, the perception–versus–action hypothesis states that the processing of visual information for the guidance of motor acts poses very different computational requirements than the processing of visual information for perception such that it is adaptive to have two distinct systems. The perception–versus–action hypothesis *integrates* the functional and anatomical levels of description by identifying the vision–for–action system with the dorsal stream and the vision–for–perception system with the ventral stream. Note, however, that the perception–versus–action hypothesis is not the first attempt to integrate anatomical and functional aspects of the visual system. A number of earlier accounts proposed different functional or anatomical subdivisions (e.g., Trevarthen, 1968; Schneider, 1969; Ungerleider & Mishkin, 1982; Livingstone & Hubel, 1988). For example, Ungerleider and Mishkin (1982) suggested that the dorsal stream is mainly concerned with spatial information, while the ventral stream is concerned with space–invariant object recognition. In their view, perception (or visual awareness) as well as motor acts could be based equally well on information from both streams.

A third reason for the impact of the perception–versus–action hypothesis can be seen in findings that

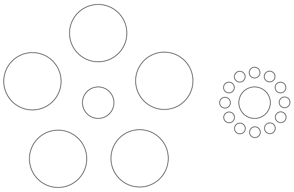

Figure 1: The Ebbinghaus / Titchener illusion: A circle surrounded by larger circles is perceived as being smaller than if surrounded by smaller circles (and vice versa).

even the overt behavior of healthy, non–neurological humans seemed to reflect the functional dichotomy of vision–for–action and vision–for–perception. One of the most influential studies in this respect was conducted by Aglioti, DeSouza, and Goodale (1995) who reported that the Ebbinghaus / Titchener illusion (Figure 1) deceived the perceived size of an object, while grasping was mostly refractory to the illusion. This finding that the Ebbinghaus illusion affects perception but not grasping (or as Aglioti et al. put it: "Size–contrast illusions deceive the eye but not the hand"; title of Aglioti et al., 1995) has often been counted as compelling evidence for the perception–versus–action hypothesis (Koch & Braun, 1996; Jackson & Husain, 1997; Carey, 2001; Plodowski & Jackson, 2001).

However, we (Franz, Gegenfurtner, Bülthoff, & Fahle, 2000) criticized this finding and showed that in the Aglioti paradigm the perceptual task and the motor task were not sufficiently matched (Figure 2). Studies which avoided this problem (Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999; Franz et al., 2000), found motor effects of the same size as the perceptual effects (cf. Figure 3a). In our view, 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; Franz, Fahle, Bülthoff, & Gegenfurtner, 2001).

Recently, Haffenden et al. (2000, 2001) suggested that the motor effects of the Ebbinghaus illusion might be 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 grasp and perceptual effects of the Ebbinghaus illusion could simply be a coincidence.

How could such an obstacle–avoidance mechanisms 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:

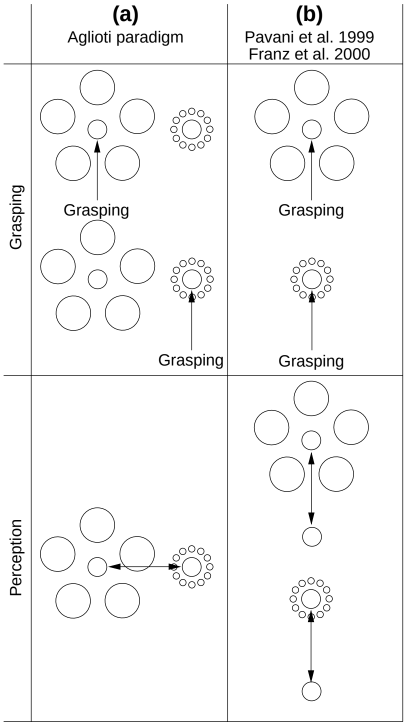

Figure 2: **(a)** Perceptual task and motor task of the Aglioti paradigm (Aglioti et al., 1995). Two Ebbinghaus figures were presented and the central circles were replaced by discs which could be grasped. In the perceptual task, participants compared the sizes of the two central discs directly, while 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. We (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).

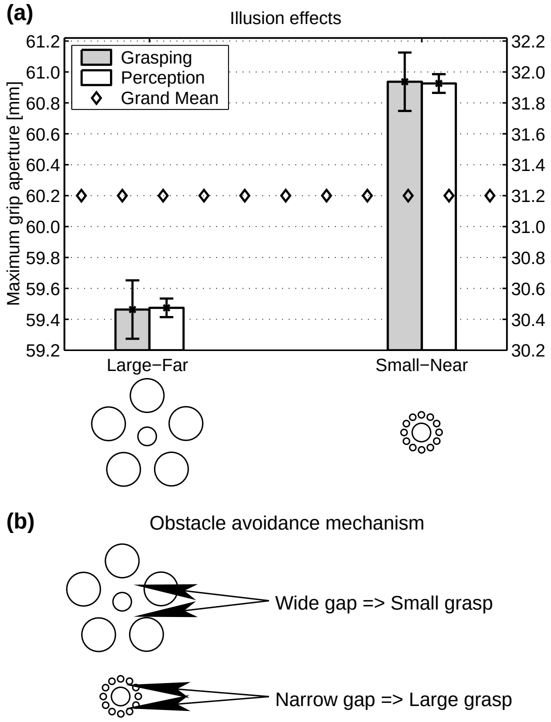

Figure 3: **(a)** Effects of the Ebbinghaus illusion on perception and on grasping as found by Franz et al. (2000). The effects on perception and on grasping are virtually identical. A similar result was obtained by Pavani et al. (1999). The labels "Large" and "Small" refer to the size of the context circles and the labels "Near" and "Far" to the eccentricity of the context circles. The effects were calculated in exactly the same way as in the present study (cf. Method section and Figure 5). **(b)** Explanation for the illusion effects, as suggested by Haffenden et al. (2000, 2001): Haffenden et al. assume that the effects of the Ebbinghaus illusion on grasping are caused by other mechanisms than the perceptual effects. According to their obstacle–avoidance hypothesis, the context circles are treated by the vision–for–action system as potential obstacles which affect the trajectories of the fingers. Haffenden et al. 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.

(a) Humans might grasp larger if the overall size of the Ebbinghaus illusion, that is the outline of all context circles which 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 (Figure 3a). However, this is not the case, hence this mechanism can not explain the grasp effects we found in the Ebbinghaus illusion. (b) Humans might grasp larger 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 (Figure 3a). (c) Finally, humans might grasp *smaller* if the gap between grasp disc and context circles is wider (cf. Figure 3b). This is the only mechanism which conforms to the grasp effects of the Ebbinghaus illusion and this is the mechanism which was proposed by Haffenden et al. (2000, 2001). Note, that (a–priori) it is not very plausible why humans should open the hand less if the gap is wider. To explain this, Haffenden et al. (2000, 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 any case, independent of the plausibility of this mechanism, it is an empirical question whether this mechanism is effective in grasping. Here, we tested this obstacle–avoidance mechanism in a more extensive way than has been done before.

In two studies, Haffenden et al. (2000, 2001) tried to demonstrate this obstacle–avoidance mechanism. However, both studies had drawbacks. The first study (Haffenden & Goodale, 2000) failed to show significant effects of the distance of context elements on grasping (Figure 6, p. 1603). The second study (Haffenden et al., 2001) added a third illusion–condition to the Ebbinghaus illusion. In this condition, 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 Figure 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 in both conditions. On the other side, the common–source model still predicts some effect on grasping because matching the gaps does decrease (but not eliminate) the perceptual effect (cf. Girgus, Coren, & Agdern, 1972). The results of Haffenden et al. 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: (a) The result is a null effect (no difference between "Large–Far" and "Small–Far" in grasping; cf. Fig-

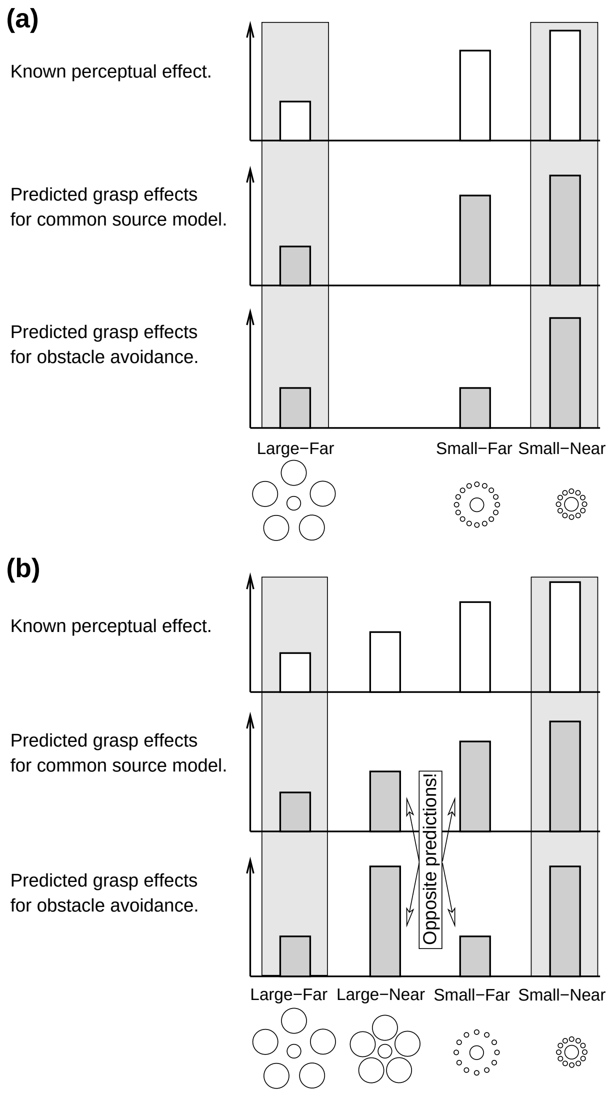

Figure 4: Predictions of the common–source model and of the obstacle–avoidance mechanism for the study of Haffenden et al. (2001) and for the present study. The labels “Large” and “Small” refer to the size of the context circles and the labels “Near” and “Far” to the eccentricity of the context circles. 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 side, 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. 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 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”.

ure 4a). This rises the question, how large the sample size needed to be in order to reliably detect the effect predicted by the common–source model. We found that the 18 participants used by Haffenden et al. were not enough to detect this effect with sufficient high probability. A power–analysis shows that the probability to *miss* the effect predicted by the common–source model was high (see Method section for details). In consequence, the null effect found by Haffenden et al. (2001) could very well be due to random, statistical fluctuations. (b) Haffenden et al. (2001) also looked at the difference between the "Small–Far" and the "Small–Near" conditions (cf. Figure 4a). The problem here is that both models predict differences: The obstacle–avoidance mechanism predicts a large difference, and the common–source model 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 employed in the literature usually do not yield exactly the same size for the perceptual effects of the Ebbinghaus illusion and there has been some debate on the question which perceptual measure is most appropriate to be compared to grasping (Carey, 2001; Franz, 2001).

In the present study we tried to overcome these shortcomings by two measures: (a) 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 Figure 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. (b) We used a much larger sample size (52 participants, see Method section for a power–analysis on this sample size). This large sample size enabled us to reliably discriminate between the predictions of the common–source model and of the obstacle–avoidance mechanism.

In short: We contrast two hypotheses in this study. One hypothesis states that the motor effects of the Ebbinghaus illusion origin in 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 & Goodale, 2000; Haffenden et al., 2001). In our experimental design (Figure 4b), the common–source model predicts that participants grasp larger in the "Small–Far" than in the "Large–Near" condition, while the obstacle–avoidance mechanism predicts that participants grasp *smaller*.

2 Results and Discussion

Participants performed a perceptual and a grasping task on the stimuli shown in Figure 4b. In the perceptual task, they adjusted an isolated comparison circle to match the size of the target disc. Results show the well–known perceptual illusion (Figure 5): The target disc appears larger if the context circles are smaller (and vice versa). Also, the target disc appears slightly larger if the small or the large context circles are 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 maximum grip aperture (MGA) between index finger and thumb was determined (see Method section for further details on this measure). In the "Large–Far" and "Small–Near" conditions results replicated our previous finding of an approximately 4.5% illusion effect (to see this, compare Figure 5b with Figure 3a). In 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, $p < .001$).

Finally, comparing the illusion effects of grasping to those of perception, shows that grasping responded to the Ebbinghaus illusion in exactly the same way as perception (Figure 5). Even with our large sample size, we found no differences in the magnitudes of perceptual and motor effects of the Ebbinghaus illusion.

These findings present strong evidence against the notion that the motor effects might be generated independent of the perceptual effects in the action system: The obstacle–avoidance mechanism proposed by Haffenden et al. (2001) can not explain the pattern of results we found.

Note, that the predictions of the obstacle–avoidance mechanism are independent of any perceptual effect. If this mechanism were true, it should predict (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 no matter what the perceptual effects were. This result is important in the context of the debate which perceptual measure is most appropriate to be compared to grasping. Proponents of a dissociation between perception and action focus mainly on a perceptual measure which has been named "manual estimation": Participants indicate the target size by opening index fin-

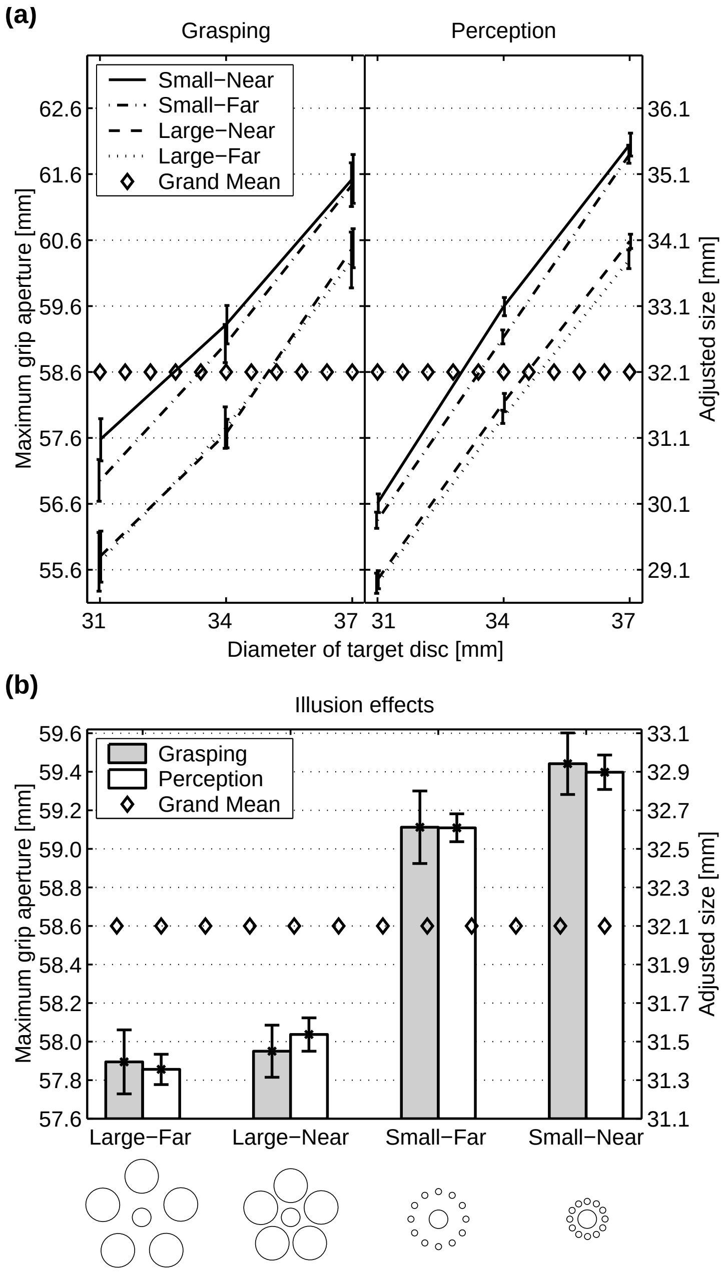

Figure 5: Results for grasping and the perceptual task. **(a)** Maximum grip aperture (MGA) and adjusted size of the comparison circle as functions of the illusion conditions and of the size of the target disc. Grasping as well as perception showed highly significant illusion effects. The illusion effects were not differentially affected by the sizes of the target disc. (ANOVA for grasping: Main effect illusion: $F(3, 153) =$ 17.7, $p < .001$; Main effect size: $F(2, 102) =$ 97.5, $p < .001$; Interaction: $F(6, 306) =$ 0.3, $p = .94$; ANOVA for perception: Main effect illusion: $F(3, 153) =$ 65.9, $p < .001$; Main effect size: $F(2, 102)$ = 854.7, $p < .001$; Interaction: $F(6, 306)$ = 2.1, $p = .053$). 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). The illusion effects did not differ between grasping and perception (ANOVA for difference between MGA and adjusted size: Main effect illusion: $F(3, 153)$ = 0.1, $p = .97$; Main effect size: $F(2, 102)$ = 4.3, $p = .017$; Interaction: $F(6, 306)$ = 0.7, $p = .65$). **(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, (a) and (b), the ordinates are aligned such that the grand means of MGA and of adjusted size are at the same height. Error bars depict ± 1 standard error of the mean (SEs are based on normalized data to account for absolute differences in MGA between participants, cf. Loftus & Masson, 1994).

ger and thumb with (or without) seeing hand or stimulus during performance of the task (e.g., Daprati & Gentilucci, 1997; Haffenden & Goodale, 1998; Haffenden et al., 2001). Proponents of a common source of the illusion for perception and 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 argued (Franz, 2001) that manual estimation leads to larger illusion effects than both, grasping as well as standard perceptual measures.

Of course, the failure of the obstacle–avoidance mechanism suggested by Haffenden et al. (2000, 2001) does not rule out the possibility that other non–perceptual 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 origin in a common source.

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 removes one piece of evidence which has been counted as being especially strong for the perception–versus–action hypothesis because it seemed to demonstrate 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 this 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: (a) The Ebbinghaus illusion could be generated *before* the vision–for–action and the vision–for–perception systems separate, an assumption which could reconcile the perception–versus–action hypothesis with our findings. A problem of 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 & Enns, 1993). (b) The Ebbinghaus illusion could be generated in the vision–for–perception system, but there could be enough crosstalk between the two systems such that the illusion "leaked" 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). (c) 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 & Mishkin, 1982). A problem of this view is that it has to explain the other evidence which has been compiled in favor of the perception–versus–action hypothesis (e.g., the dissociation found in patient D.F.). Certainly, our data *alone* cannot warrant a decision of this question. A much wider base of evidence has to be taken into account as, for example, lesion studies on monkeys, electrophysiological studies, imaging studies, and studies on neurological patients.

3 Conclusions

We found that grasping is deceived by the Ebbinghaus illusion in the same way as perception. The recently proposed non–perceptual mechanisms (Haffenden & Goodale, 2000; Haffenden et al., 2001; Plodowski & 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. Either 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 as suggested by the perception–versus–action hypothesis. The first two possibilities show that the perception–versus–action hypothesis can be reconciled with our findings. However, the Ebbinghaus illusion can no longer be counted as strong and compelling evidence for the perception–versus–action hypothesis and against alternative accounts which assume a different functional subdivision of the visual system (e.g., Ungerleider & Mishkin, 1982).

4 Materials and Methods

4.1 Power analyses for sample sizes

In order to reliably discriminate 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 which is needed to reliably detect 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 us (Franz et al., 2000), which are also depicted in Figure 3a. These grasp effects are similar to the effects found in a number of other studies (for an overview see Franz, 2001) and these are the effects for which the obstacle–avoidance mechanism was postulated by Haffenden et al. (2000, 2001).

We (Franz et al., 2000) found a grasp effect for the illusion of $\delta = MGA(Small, Near) - MGA(Large, Far) = 1.47$ mm. In the following, this effect will be called the "original effect". The standard deviation of the original effect was $\sigma = 1.93$ 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. Figure 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 power of 64% for the 18 participants used by Haffenden et al. (two–tailed test, $\alpha = 5\%$). In other words, the probability to *miss* this illusion effect if it exists in reality, was as high as $\beta = 100\% - 64\% = 36\%$. In consequence, it is well 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. Figure 4b). If we assume that the common–source model is true and that we still want to detect an effect of 70% of the original effect (i.e., $d = 0.76 * 70\% = 0.53$), this results in a power of 94% for the 52 participants used in this study (two–tailed test, $\alpha = 5\%$). In other words, the probability to *miss* the effect predicted by the common–source model if it exists in reality, was $\beta = 100\% - 94\% = 6\%$. 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", was larger than 99%. That is, the probability to *miss* the effect predicted by the obstacle–avoidance mechanism if it exists in reality, was less than 1%. In consequence, we can be very confident to have minimized the errors due to random, statistical fluctuations.

4.2 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 15 DM per hour (approximately 7 US$). Participants had normal or corrected–to–normal vision (Snellen–equivalent of $20/25$ or better; Ferris, Kassoff, Bresnick, & Bailey, 1982), normal stereopsis of 60 seconds of arc or better (Stereotest–circles, Stereo Optical, Chicago), and were right–handed Oldfield, 1971.

4.3 Stimuli

The variants of the Ebbinghaus illusion used in our experiment are shown in Figure 4b. The "Large" ("Small") context circles were 58 mm (10 mm) in diameter. In the "Near" ("Far") condition the distance between the midpoint of the target disc and the nearest point on the context circles was 24 mm (31 mm). All context circles were drawn on a board. The targets were aluminum disc, 31, 34, or 37 mm in diameter (corresponding to 2.7, 3.0, and 3.3 degrees of visual angle) and 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 comparison 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 by us in our previous study on this topic (Franz et al., 2000) and geometrically similar to the conditions used by Aglioti et al. (1995).

4.4 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 table for the presentation of the stimuli. The screen was not horizontal, but tilted to be oriented perpendicular to gaze direction. Participants wore liquid-crystal (LC) shutter glasses (Milgram, 1987) which allow to efficiently suppress vision. The grasp trajectories were recorded using an Optotrak^{TM} 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 start of the experiment, the typical grasp points on the fingers were determined and measured relatively to the markers on the flags. This enabled us to calculate the trajectories of the grasp points and to determine the 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 by almost all studies investigating the question of a functional dissociation between vision–for–perception and vision–for–action in visual illusions (e.g., Aglioti et al., 1995; Daprati & Gentilucci, 1997; Haffenden & Goodale, 1998; Pavani et al., 1999; Franz et al., 2000, 2001; Haffenden et al., 2001). MGA has several advantages: (a) MGA is usually reached before the hand had any contact with the grasp object. This excludes possible effects of direct, haptic feedback. (b) 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).

4.5 Procedure

In the perceptual task, participants adjusted an isolated circle which 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 mm 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 msec presentation time. The adjustment method has the advantage to be more efficient. The LC shutter glasses suppressed vision as soon as the participant finished the adjustments and 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 x 4 illusion conditions x 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 msec after stimulus presentation) such that participants could neither see their hand nor the stimulus during grasping. Participants had 4 sec time 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 at a randomly determined, later 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 x 4 illusion conditions x 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.

4.6 Data analysis

For data analysis, repeated measures ANOVAs were calculated with the factors diameter of target disc (3 levels: 31, 34, 37 mm) and type of context circles (4 levels, cf. Figure 4b). Dependent variables were MGA (motor task), adjusted size of the comparison circle (perceptual task), and the difference between MGA and adjusted size of the comparison circle (comparison of the illusion effects between motor and perceptual task).

We used a significance level of $\alpha = .05$ for all statistical analyses. P–values above $.001$ are given as exact values. For parameters which are given as $X \pm Y$, X is the mean and Y is the standard–error of the mean.

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