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Effects of Visual Illusions on Grasping

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In 2 experiments, the Müller-Lyer illusion (F. C. Müller-Lyer, 1889; $N = 16$) and the parallel-lines illusion (W. Wundt, 1898; $N = 26$) clearly affected maximum preshape aperture in grasping (both $ps < .001$). The grasping effects were similar but not perfectly equal to the perceptual effects. Control experiments show that these differences can be attributed to problems in matching the perceptual task and the grasping task. A model is described stating the assumptions that are needed to compare the grasping effects and the perceptual effects of visual illusions. Further studies on the relationship between perception and grasping are reviewed. These studies provide no clear evidence for a dissociation between perception and grasping and therefore do not support the action versus perception hypothesis (A. D. Milner & M. A. Goodale, 1995).

It has been claimed that grasping an object is not at all or hardly at all affected by visual illusions (Aglioti, DeSouza, & Goodale, 1995). Such a dissociation between perceiving the size of an object and estimating it for the purposes of grasping would not only be surprising but also would provide strong evidence of two different pathways for processing visual information, one for action and a separate one for perception (Goodale & Milner, 1992; Milner & Goodale, 1995).

The first study to investigate this question used the Ebbinghaus (or Titchener) illusion. Aglioti et al. (1995) reported a smaller illusion for grasping a disk than for perceiving its size, a result later replicated by Haffenden and Goodale (1998). Contrary to these findings, we argued (Franz, Gegenfurtner, Bülthoff, & Fahle, 2000) that the results of Aglioti et al. were caused by an incomplete match between the perceptual task and the motor task. The problem is as follows. In the perceptual task participants had to directly compare two disks, each being embedded in one Ebbinghaus figure. In the grasping task, however, they grasped only one disk at a time (Figure 1a).

To compare the illusion effects, one has to assume that it is irrelevant for the size of the illusion whether participants operate on both disks simultaneously (as in the perceptual task) or successively (as in the grasping task). We showed that this is not the case. Even in a purely perceptual task the illusion is stronger if participants operate on both disks simultaneously (Figure 1a, and 1b). Therefore, the perceptual task and the grasping task were not adequately matched in the study of Aglioti et al. (1995). We eliminated this problem by presenting only one Ebbinghaus figure at a time (Figure 1c) and found almost identical effects of the Ebbinghaus illusion on perception and on grasping (Franz, Fahle, Gegenfurtner, & Bülthoff, 1998; Franz et al., 2000), as did other researchers who used a similar paradigm (Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999). We concluded from these studies that the Ebbinghaus illusion does influence the motor system and that its effect on action is similar to the effect on perception.

What about other visual illusions? Some studies indicated a dissociation between perception and grasping in other visual illusions as well. Given our results regarding the Ebbinghaus illusion, it might be necessary to reexamine these results.

Brenner and Smeets (1996) and Jackson and Shaw (2000) investigated the Ponzo illusion. Both studies measured the maximum preshape aperture, the same measure that was used in the Aglioti et al. (1995) study and which we discuss in this study. Furthermore, Brenner and Smeets and Jackson and Shaw investigated the forces that were applied to lift the target objects. Brenner and Smeets measured lift force, whereas Jackson and Shaw measured grip force. Lift force and grip force were affected by the Ponzo illusion: Participants exerted more force in the condition in which the target object appeared enlarged. This result seems to indicate an influence of the Ponzo illusion on the motor system. However, Brenner and Smeets as well as Jackson and Shaw did not find an effect of the illusion on maximum preshape aperture, a result that seems to indicate that the Ponzo illusion does not influence the motor system. This contradiction could be resolved if different aspects of the grasping movement were controlled inde-

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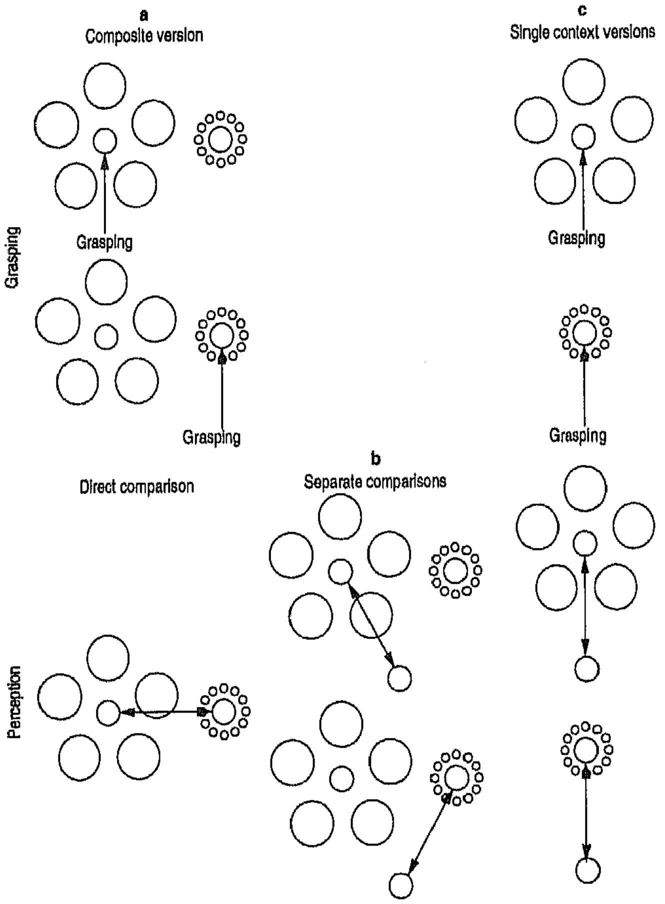

Figure 1. (a) Model of the perceptual task and the motor task of the Aglioti et al. (1995) study. Two Ebbinghaus figures were presented (composite version of the illusion). In the motor task, participants successively grasped one of the central disks. In the perceptual task, they compared the two central disks. Note the asymmetry in this procedure: To grasp, participants had to calculate only the size of one of the central disks at a time. In the perceptual task, however, participants had to compare the two central disks directly, both being subjected to the illusion at the same time. (b) A perceptual task similar to the grasping task in (a). Participants successively compared one of the central disks to a neutral disk. Franz et al. (1998, 2000) showed that in this task, the perceptual illusion is only about ⅔ of the perceptual illusion measured in (a). (c) In the studies of Franz et al. (1998, 2000) and of Pavani et al. (1999), 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 disks, and in the perceptual task they compared the central disk to a neutral disk. In these studies, no difference between the perceptual illusion and the motor illusion was found. From "Grasping Visual Illusions: No Evidence for a Dissociation Between Perception and Action," by V. H. Franz, K. R. Gegenfurtner, H. H. Bülthoff, and M. Fahle, 2000, *Psychological Science, 11,* p. 21. Copyright 2000 by Blackwell Publishers. Reprinted with permission.

pendently by different aspects of the visual information, as argued by Brenner and Smeets and by Jackson and Shaw. It also seems possible that the conditions were not optimal to detect an effect of the illusion on maximum preshape aperture. This view is supported by the fact that both studies used a paradigm similar to the one used in the Aglioti et al. study (i.e., simultaneous presentation in the perceptual task and successive presentation in the grasping task), suggesting that the perceptual illusion was enlarged as a result of the differences between perceptual and motor task. In Brenner and Smeets's study, the perceptual illusion was rather small (in the study of Jackson and Shaw the size of the perceptual illusion was not reported), and in both studies the number of participants was low, which leads to little statistical power to detect an effect of the illusion on maximum preshape aperture.

Daprati and Gentilucci (1997) and Otto-de Haart, Carey, and Milne (1999) investigated the Müller-Lyer illusion. Whereas Daprati and colleagues reported a clear effect of the illusion on grasping, Otto-de Haart and colleagues found only an effect on grasping if the illusion was viewed monocularly. With binocular viewing the grasping effect did not reach significance. In both studies the grasping effect was smaller than the effect on perception. However, nonstandard perceptual measures were used: Either participants blindly drew a line to match the length of the shaft of the Müller-Lyer figure (Daprati & Gentilucci, 1997), or they indicated the length of the shaft using their index finger and thumb (Daprati & Gentilucci, 1997; Otto-de Haart et al., 1999). Both measures are not well established as measures for perception, and therefore it seems beneficial to compare the motor illusion to a classical perceptual measure (e.g., Coren & Girgus, 1972a).

In the present study we tried to overcome these drawbacks and to investigate whether grasping is influenced by visual illusions other than the Ebbinghaus illusion. We investigated the Müller-Lyer illusion (Müller-Lyer, 1889) as well as the parallel-lines illusion (Wundt, 1898), which might be interpreted as a variant of the Müller-Lyer illusion. We put special emphasis on matching the perceptual task and the grasping task as much as possible in order to validly detect a dissociation between perception and grasping. Before describing our experiments, we sketch the reasoning that lies behind the idea that one can compare the perceptual effects of a visual illusion with its effects on grasping.

Maximum Preshape Aperture: Assessing Size Information in the Motor System

The assessment of the perceptual effect of a visual illusion has been well established (e.g., Coren & Girgus, 1972a). For example, this can be achieved by having participants adjust a comparison object to match the size of a target object. For the motor effect of a visual illusion this is not as obvious. The trick is that while reaching to grasp an object the index finger and thumb open to a maximum aperture that is linearly related to the object's size (Jeannerod, 1981, 1984). This maximum preshape aperture (MPA) is formed well before the hand has any contact with the object. Therefore, the MPA is usually interpreted as reflecting the size estimate being used by the motor system. (See, however, Smeets & Brenner, 1999, for a new and different interpretation of the MPA. They assume that MPA is not based on a size estimate but on two estimates of the positions at which index finger and thumb touch the object.) If an individual grasps a three-dimensional object that is affected by a visual illusion, it is possible to determine whether the motor system is influenced by the illusion. As a result, MPA was used as dependent variable in most studies investigating the influences of visual illusions on grasping.

Separate Representation Model Versus Common Representation Model

Three possible explanations for the influence of visual illusions on grasping are discussed. The first is that grasping is not at all influenced by visual illusions. This is the strong version of the action versus perception hypothesis (Milner & Goodale, 1995). In the following this model is referred to as the *strong separate representation model* because it assumes two different representations of object size for the purposes of perception and action. It is easy to test this hypothesis. One simply has to probe whether MPA is influenced by visual illusions. We think this model already is questionable because most researchers did find significant effects of visual illusions on grasping (cf. the General Discussion section).

To account for these influences on grasping in the framework of the separate representation model, one has to allow for some cross talk between the two representations. In fact, this is what has been proposed by several researchers (Aglioti et al., 1995; Daprati & Gentilucci, 1997; Milner & Goodale, 1995). This cross talk leads to the weak version of the separate representation model. It is assumed here that two separate representations of object size exist for the purposes of perception and action and that there is some small effect of the perceptual representation on the motor representation. The prediction is that the motor illusion is decreased relative to the case that only one representation of object size exists. Here, the methodological problem arises to predict the size of the full motor illusion given that a common representation of object size exists.

Most researchers solved this problem by predicting that the full motor illusion should have the same numerical magnitude as the perceptual illusion (e.g., if perception were deceived by 1 mm, the full motor illusion would be predicted to be 1 mm). Although we think that this is a valid solution to the problem, it is not trivial to use this prediction. To justify this prediction, one must have some (plausible) assumptions and use the fact that MPA is a very well-behaved dependent variable. In the following we describe a mathematical model, the common representation model, which explicitly states these assumptions.

The common representation model posits the existence of a single representation of object size. This representation is influenced by the visual illusion and is used to generate the percept of size as well as to guide grasping. Given that MPA as well as perceived size depend linearly on physical size, it is possible to use a linear model that can be tested easily (see Figure 2).

We assume that the visual information is transformed linearly into an internal representation of object size. This internal representation is deceived by the illusion. We model the deception by changing the slope and the intercept of the linear function that relates physical size to the internal representation. The internal representation is then transformed linearly either to the perception of object size (i.e., to the response in the perceptual task) or to MPA in the grasping task.[1] These later transformations are assumed to be unaffected by the illusion. Given this very simple model, it is possible to calculate the influence the visual illusion has on MPA from the influence it has on the perceptual measure (see Appendix A). The model predicts that for each size of the object the motor illusion is proportional to the perceptual illusion

$$\Delta_G(S) = f \times \Delta_P(S), \qquad (1)$$

where $\Delta_G(S)$ is the effect of the illusion on grasping for an object of size S, and $\Delta_P(S)$ is the perceptual illusion for an object of size S. The factor f is equal to $b_G(k)/b_P(k)$, where $b_G(k)$ is the slope with which the grasp measure depends on physical size in illusion condition k, and $b_P(k)$ is the slope with which the perceptual measure depends on physical size in illusion condition k. Note that the model predicts the same value of f for all illusion conditions. The data of this study as well as the data of Franz et al. (2000) conform well to this prediction. If the factor f equals 1, Equation 1 can be simplified as

$$\Delta_G(S) = \Delta_P(S). \qquad (2)$$

In this case, the model predicts that for each size of the object the motor illusion equals the perceptual illusion. In the present study and in the study of Franz et al. (2000), f was close to 1 such that it is possible to work with this simplified formula. Furthermore, we use the simplified formula for our comparison between studies (cf. the General Discussion section) because most studies did not investigate the slopes with which the perceptual measure and the grasping measure depended on physical size. Note, however, that f could deviate from 1 and therefore it is necessary to test the size of f by varying physical size of the objects, especially if unusual (perceptual) measures are used.

Another fact that can be exploited to distinguish between the different models is that participants show interindividual differences in the strength of the perceptual illusion and of the motor illusion. The question arises whether these differences are correlated across participants (e.g., whether a participant showing a large perceptual effect also shows a large motor effect). The strong version of the separate representation model predicts that there is no correlation between the perceptual illusion and the motor illusion across participants; the model does not predict any motor illusion at all. The common representation model on the other hand clearly predicts an across-subjects correlation between the motor illusion and the perceptual illusion. How big should this correlation be? This question is important for the interpretation of small and nonsignificant correlations. Are these correlations not significant because of a lack of statistical power, or can they be taken as evidence against the common representation model? The problem here is that the interindividual differences can be small compared to the overall noise level.

Fortunately, it is possible to derive an upper bound for the expected value of the correlation. The idea is as follows. Assume the perceptual measure reflected the internal representation without any noise. In this case, it would perfectly measure the interindividual differences between participants. Furthermore, assume that the MPA suffered from some noise that is added between internal representation and grasping (an assumption that is necessary to account for the larger variance of the motor data). Given this model, the idealized expected correlation (IEC; i.e., between perceptual illusion and motor illusion) equals the ratio of their standard deviations (see Appendix B):

$$\mathrm{IEC} = \frac{\sigma_{\Delta_P}}{\sigma_{\Delta_G}}, \qquad (3)$$

where IEC is the correlation between the mean grasping illusion and the mean perceptual illusion; σ_{Δ_P} is the standard deviation of

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[1] One might ask why we allow for two different functions for perception and grasping here. The reason is that MPA and perception are in principle differently related to the physical size of the object. For example, MPA always is larger than the physical size of the object; the fingers open wider than the object actually is.

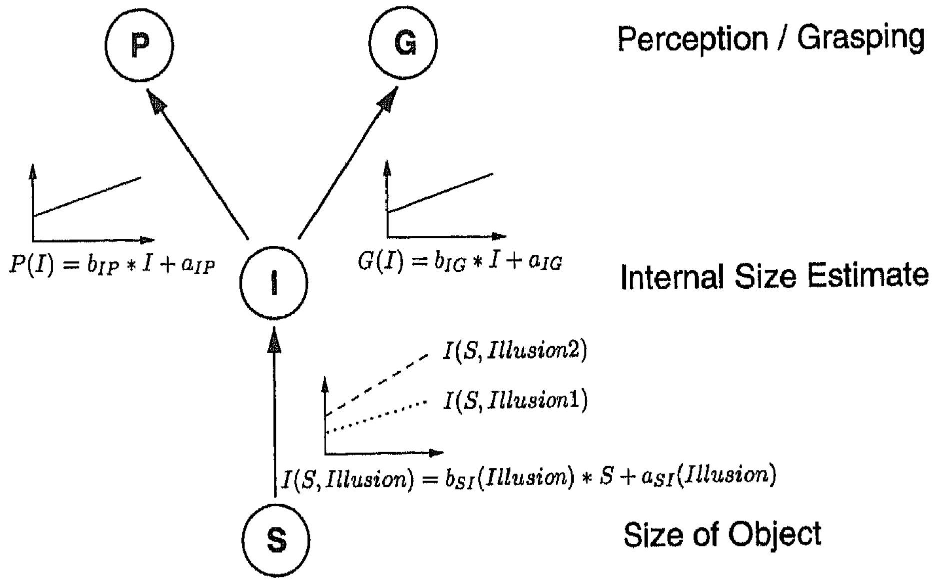

Figure 2. An explicit version of the common representation model. See the introduction and the appendixes for more details on this model.

the mean perceptual illusion; and σ_{Δ_G} is the standard deviation of the mean grasping illusion. This is an idealized model; it is assumed that no noise is added in the transformation from the internal representation to the perceptual measure. Any such noise reduces the expected value of the correlation. Note that the IEC is, statistically speaking, the upper bound of a population parameter. That is, the measured values in a sample fluctuate around its expected value and can, according to the laws of probability, very well be larger than its expected value as well as larger than the IEC.

The IEC gives a rough idea of what size of correlation can be expected and what sample sizes are required to provide enough statistical power to reliably detect these correlations. For example, in the study on the Ebbinghaus illusion (Franz et al., 2000), we found an IEC of .32, whereas the empirical correlation was ρ = .34. Expecting a similar relationship in future research, one can calculate the optimal sample sizes to reliably detect such an effect. Cohen (1988) gave an optimal sample size of $N = 68$ for an expected correlation of $\rho = .30$ and of $N = 37$ for $\rho = .40$ (one-tailed test, $\alpha = .05$, $\beta = .20$). This shows that in general large sample sizes are needed, at least to show that there is no correlation between perceptual effect and grasping effect (typically, studies used smaller sample sizes of 8 to 18 participants; cf. the General Discussion section).

The IEC mainly discriminates between the strong separate representation model on one side and the weak separate representation model and the common representation model on the other side. This is because the IEC is only an upper bound for the expected value of the correlation, and both the weak separate representation model and the common representation model predict a smaller correlation than the IEC. The common representation model does so because of noise in the perceptual system. The separate representation model does so because of the incomplete crosstalk between the perceptual representation and the motor representation.

In summary, two measures can be used to distinguish between the models (see Table 1): (a) The size of the perceptual illusion and of the motor illusion discriminates between the strong separate representation model, the weak separate representation model, and the common representation model. The strong separate representation model predicts that there is no motor illusion at all. The common representation model predicts that the motor illusion equals the perceptual illusion (if the factor f equals 1), and the weak separate representation model predicts that the motor illusion is smaller than the perceptual illusion. (b) The across-subjects correlation between the perceptual illusion and the motor illusion can give some insights about the validity of the strong separate representation model versus the weak separate representation model and the common representation model. The strong separate representation model predicts no correlation between the perceptual illusion and the motor illusion. The weak separate representation model as well as the common representation model both predict a positive correlation. For these models it is possible to give an upper bound for the expected value of the correlation, the IEC.

In the following we use these different predictions of the competing models to evaluate the Müller-Lyer illusion and the parallel-

Table 1
Predictions of the Competing Models

Model	Illusion effects	Across-subjects correlation
Strong separate representation model	$\Delta_G(S) = 0$	$\rho_{\Delta_P,\Delta_G} = 0$
Weak separate representation model	$0 < \Delta_G(S) < \Delta_P(S)$	$0 < \rho_{\Delta_P,\Delta_G} \ll \text{IEC}$
Common representation model	$\Delta_G(S) = \Delta_P(S)$	$0 < \rho_{\Delta_P,\Delta_G} \leq \text{IEC}$

Note. The predictions rest on specific assumptions that are described in the introduction and in the appendixes. Specifically, we assume that $f = 1$ (Equation 1 in the text). Moreover, $\Delta_G(S)$ is the grasping illusion for an object of size S, $\Delta_P(S)$ is the perceptual illusion for an object of size S, and ρ_{Δ_P,Δ_G} is the expected value of the correlation between the mean perceptual illusion and the mean grasping illusion. IEC = idealized expected correlation.

lines illusion. We also report control experiments ensuring that the perceptual task and the motor task were adequately matched.

Investigating the Müller-Lyer Illusion

Experiment 1: Grasping the Illusion

We conducted this experiment to test how the Müller-Lyer illusion influences grasping. It is similar to an experiment reported by Daprati and Gentilucci (1997). However, we used an adjustment procedure as perceptual measure (Coren & Girgus, 1972a) to assess the perceptual effect of the illusion.

Method

Participants. Students of the University of Tübingen participated in all our experiments. In return for their participation, they received a payment of 13 DM ($6.50) per hour. Participants in all experiments had normal or corrected-to-normal vision (Snellen equivalent of 20/25 or better; Ferris, Kassoff, Bresnick, & Bailey, 1982). They had normal stereopsis of 60 s of arc or better (Stereotest-circles, Stereo Optical, Chicago). The participants of the grasping experiments (Experiments 1 and 4) were right-handed (Oldfield, 1971). Sixteen people (10 women and 6 men) participated in Experiment 1; they ranged in age from 18 to 31 years (M = 25.5 years).

Apparatus and stimuli. The apparatus is shown in Figure 3a. The participants sat on a stool. They used a chin rest to keep the position of the head constant throughout the experiment. Participants looked down, as if looking at the top of a table. At a distance of approximately 65 cm from the eyes, a 21-in. (53.3-cm) monitor (effective screen diagonal of 48.5 cm) was positioned. The screen of the monitor served as table for the presentation of the target stimuli. The screen was not horizontal; it was slightly tilted to be oriented perpendicular to gaze direction.

On top of the screen, a black plastic bar (7 mm wide; 5 mm high; and 40, 43, 46, or 49 mm long) was positioned as target. At each end of the target, two black fins were displayed on the monitor. The fins pointed either outward or inward, thus creating the Müller-Lyer figure. The outward-pointing fins were 31 mm long and formed an angle of 30° with the main axis of the target bar. The inward-pointing fins were 19 mm long and had an angle of 150° to the main axis of the target bar. The fins were constructed in such a way that the end of the bar was clearly distinguishable from the fins (Figure 3c). This separation was also emphasized by the fact that the fins were slightly further away from the eyes; this is because any CRT image is created behind the glass of the monitor screen.

In the perceptual task, a comparison bar was displayed on the monitor. The comparison bar was parallel to the target bar at a distance of 80 mm. For each trial, the position of the comparison was randomly chosen to be left or right, with a parallel displacement of ±7 mm (Figure 3b). The comparison bar was 7 mm wide, as were all elements of the Müller-Lyer figure.

Procedure. Participants wore liquid-crystal (LC) shutter glasses (Milgram, 1987). The glasses were opaque while the stimuli for each trial were set up by the experimenter. Thereafter, the glasses became transparent and the participant performed the required task.

In the grasping task, participants grasped the target bar with their right hand. As soon as they started to move their hand away from the starting position (i.e., as soon as they had moved both fingers more than 20 mm; the distance between starting position and target bar was 250 mm), the glasses became opaque again. Therefore, the participants could see neither their hand nor the stimulus during grasping (open loop condition; Haffenden & Goodale, 1998; Jeannerod, 1981; Post & Welch, 1996). The participants grasped the target bar, lifted it, moved it to a goal area that was close to the starting position, and finally moved their hand back to the starting position. Then the experimenter recollected the bar and prepared the next trial. The grasp trajectory was recorded using an Optotrak system: Three infrared light emitting diodes (LEDs) were rigidly attached to thumb and index finger (Figure 3c). In a pretest, the participants were able to grasp the target bars, and the approximate midpoints of the contact surfaces of thumb and index finger with the target bars were determined. After the experiment, the trajectories of these points were calculated from the trajectories of the LEDs. The sampling rate was 100 Hz.

In the perceptual task, participants adjusted the comparison bar to match the size of the target bar. The initial length of the comparison bar differed randomly from the length of the target bar within a range of ±10 mm. The adjustment was done by pressing the buttons of a computer mouse (one button to increase the size and the other button to decrease the size of the comparison bar). After the participants finished their adjustment, the glasses became opaque again and the experimenter prepared the next trial.

The grasping task and the perceptual task were done in separate blocks, and the succession of the tasks was counterbalanced across participants. Before the beginning of the grasping task, 10 practice trials were per-

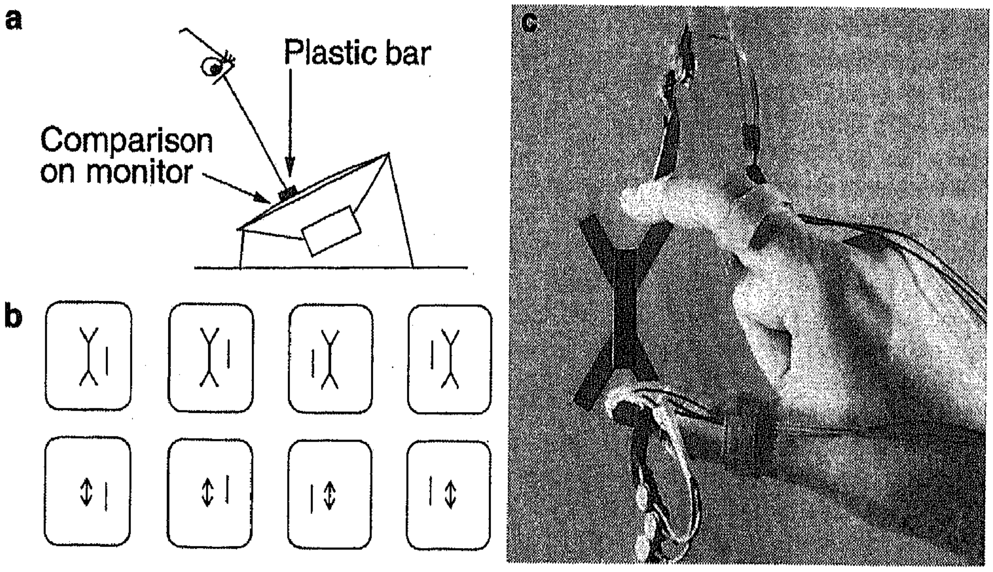

Figure 3. (a) Apparatus used in Experiment 1. (b) Stimulus conditions in the perceptual task. The comparison bar was displayed on the monitor at different positions relative to the target (left vs. right and up vs. down). (c) A participant grasping the target bar. The fins of the Müller-Lyer figure are displayed on the monitor.

formed. In the perceptual task, 5 practice trials were performed. Subsequently, each participant performed 72 grasps and 24 adjustments. Given eight different trial types (4 sizes of the target bar × 2 contexts), participants performed nine grasps per trial type and three adjustments per trial type.

Data analysis. In all experiments, we used a significance level of .05 for the statistical analyses. *P* values above .001 are given as exact values. Some parameters are given as A ± the standard error (*SE*). If not stated otherwise, we performed repeated measures analysis of variance (ANOVA) using the Greenhouse–Geisser correction (Greenhouse & Geisser, 1959) if a factor had more than two levels. This corrects for possible violations of the sphericity assumption in repeated measure data. For the Greenhouse–Geisser correction, the parameter ϵ is estimated as $0 < \epsilon_{\min} \leq \epsilon \leq 1$, which is used to adjust the degrees of freedom of the F distribution. If $\epsilon = 1$, no violation of sphericity was detected and the Greenhouse–Geisser correction has no effect. If $\epsilon < 1$, the resulting test is more conservative than if no correction was performed (Greenhouse & Geisser, 1959; Jennings, 1987; Vasey & Thayer, 1987).

For each grasping movement, the following parameters were determined: Start of the movement was defined as the time the LC-shutter glasses were opened until the velocities of both fingers first exceeded a threshold of 100 mm/s. Movement time was measured from start of the movement until the velocities of both fingers had once fallen below a threshold of 30 mm/s. MPA and peak velocities were determined during movement time. Time to MPA was measured from start of the movement.

Results

Illusion effects. Figure 4a shows the mean adjusted length of the comparison bar and the mean MPA as functions of the length of the target bar and of the illusion-inducing context. In the perceptual task the main effects of illusion-inducing context, $F(1, 15) = 70.0$, $p < .001$, and of length of target bar, $F(3, 45) = 394.0$, $\epsilon = 0.75$, $p < .001$, were highly significant. The interaction between the two factors was not significant, $F(3, 45) = 0.8$, $\epsilon = 0.87$, $p = .47$. Similarly, in the grasping task the main effects of illusion-inducing context, $F(1, 15) = 66.0$, $p < .001$, and of length of target bar, $F(3, 45) = 136.0$, $\epsilon = 0.59$, $p < .001$, were highly significant. The interaction was not significant, $F(3, 45) = 0.3$, $\epsilon = 0.75$, $p = .8$.

Slopes. For the fin-out configuration, MPA depended on physical size with a slope of 0.90 ± 0.07, and the perceptual measure depended on physical size with a slope of 0.87 ± 0.04. The relationship of these slopes is $f(1) = b_G(1)/b_P(1) = 1.03 \pm 0.09$ (see Appendix A and the introduction for a description of f). For the fin-in configuration, the slope of MPA was 0.93 ± 0.07. The slope of the perceptual measure was 0.90 ± 0.04. The relationship of the slopes is $f(2) = b_G(2)/b_p(2) = 1.04 \pm 0.08$. As predicted by the common representation model, the values for $f(1)$ and $f(2)$ are very similar. Estimating f with the mean of the two f values gives $\bar{f} = 1.03$. This value is close enough to 1 to work with the simplified Equation 2. That is, we are justified in comparing the absolute values of the motor illusion to the absolute values of the perceptual illusion.

Comparing motor illusion with perceptual illusion. The overall illusion effects averaged across all lengths of the target bar are shown in Figure 4b. The overall effect of the illusion on grasping was significantly larger than on perception, $F(1, 15) = 9.5$, $p = .008$. This difference was not affected by the factor length of target bar ($p > .99$).

The overall illusion effects calculated for each participant individually are shown in Figure 5a. The grasping illusion is predicted by the perceptual illusion with a slope of 0.3. The corresponding correlation is not significant, $\rho = .19$, $t(14) = 0.7$, $p = .24$, one-tailed, and IEC $= \sigma_{\Delta_p}/\sigma_{\Delta_G} = 0.97/1.67 = .58$.

Development of the illusion across trials. To test whether the repeated presentation of the Müller-Lyer figure caused a decrement of illusion strength (for discussion of this topic, see Coren & Girgus, 1972b; Day, 1962; Predebon, 1998; Schiano & Jordan,

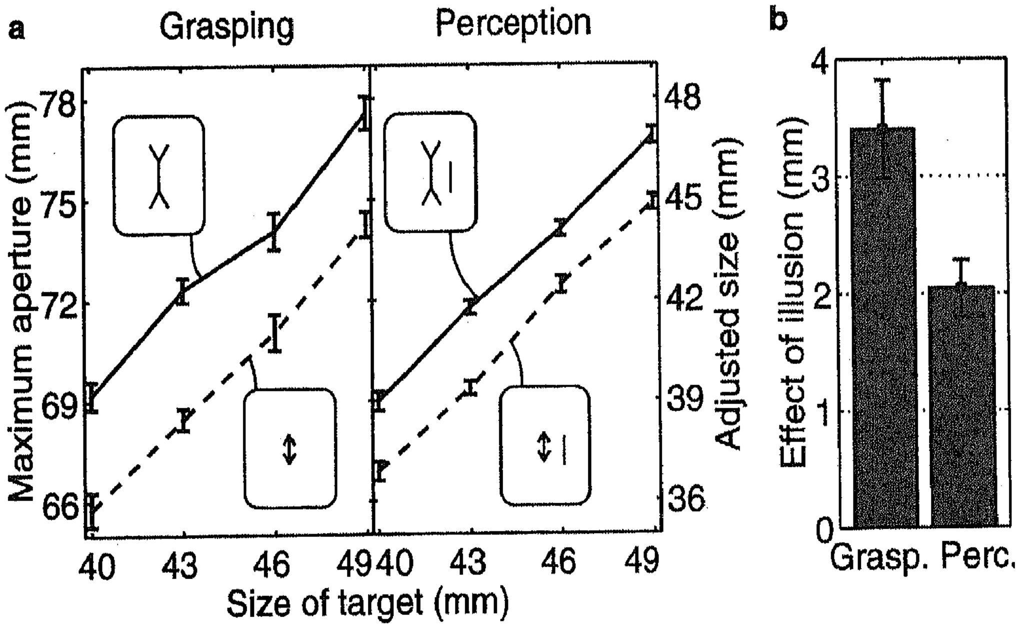

Figure 4. Results of the perceptual (Perc.) task and of the grasping (Grasp.) task in Experiment 1. (a) Mean adjusted length of the comparison bar and mean maximum preshape aperture as functions of the length of the target bar and of the illusion-inducing context. Error bars depict ±1 *SEM*. (Data are normalized to account for absolute differences in hand sizes and aperture sizes between the participants.) (b) Overall illusion effects averaged across all lengths of the target bar. Error bars depict ±1 *SEM*.

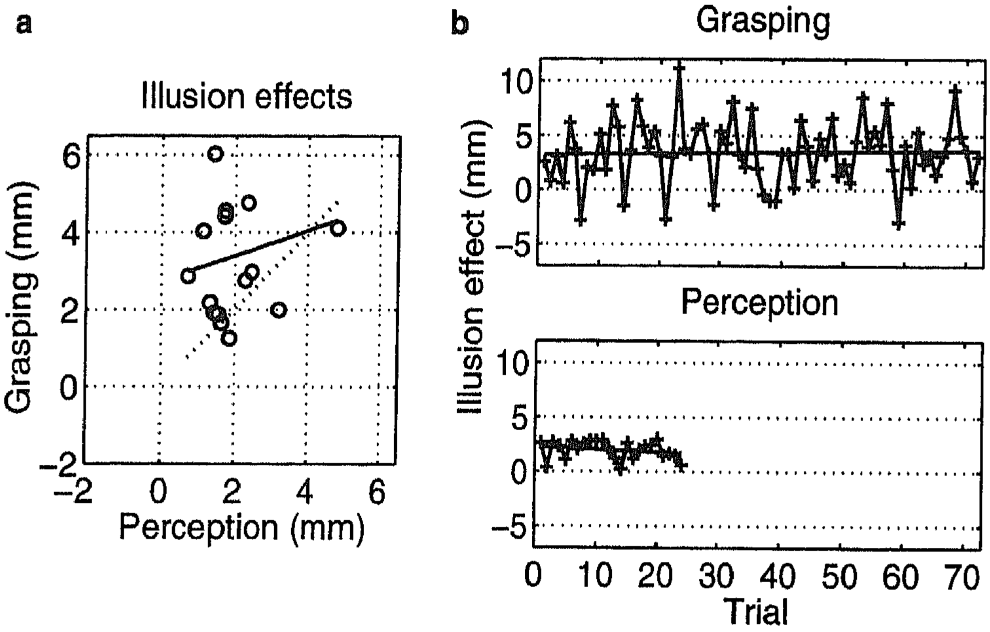

Figure 5. Further analyses of the results of Experiment 1. (a) Overall illusion effects calculated separately for each participant and correlated across participants. The solid line indicates the regression, and the dashed line indicates a proportional relationship. (b) Illusion effects calculated separately for each trial. The solid line indicates the regression.

1990), we calculated the illusion effects separately for each trial. This was done in the framework of a multiple regression analysis: The measured values of each trial were corrected for the effects of the factor participant and the factor length of the target bar. The illusion effect was then calculated as the difference between the values for the outward pointing fins and the values for the inward pointing fins. Results are shown in Figure 5b. We fitted a linear regression to these data. Neither in the perceptual task nor in the grasping task did the regression show a decrement of the illusion effect with the number of trials: perception, IE = $-0.03 \times$ TN + 2.3 (mm), $t(22) = -1.0, p = .32$; grasping, IE = $+0.01 \times$ TN + 3.2 (mm), $t(70) = 0.4, p = .73$. (IE stands for illusion effect and TN for trial number. The t-value tests the slope of the regression.)

Time and velocity parameters for grasping. We tested whether the grasping movements differed in speed for the different illusion conditions. This was done because faster movements can lead to a larger MPA (e.g., Wing, Turton, & Fraser, 1986; for a review, see Smeets & Brenner, 1999). We found no difference in movement speed between the conditions of the experiment.

The average start time of the grasping movements after opening of the LC glasses was 628 ms, the average time when the LC glasses closed was 685 ms, the average time from start time to MPA was 582 ms, and the average movement time was 869 ms. None of these parameters was significantly affected by the factors illusion-inducing context and length of target bar or by the interaction between these factors. Only the time to MPA showed a small, nonsignificant trend for the factor illusion-inducing context: For the fin-in configuration, the time to MPA was 7 ms shorter than for the fin-out configuration, $F(1, 15) = 3.2, p = .09$. All other p values were larger than .10.

The mean values of the maximum velocities of index finger and thumb during the reach movement were 627 mm/s and 584 mm/s, respectively. These parameters were not affected by the factors illusion-inducing context and length of target bar or by the interaction between these two factors (all $ps > .10$).

Discussion

We found a clear and highly significant effect of the Müller-Lyer illusion on grasping. This result replicates the study of Daprati and Gentilucci (1997), who also reported an effect of the Müller-Lyer illusion on grasping (see Table 2). Stimuli were not identical in the two studies. For example, the target bar was much longer in the Daprati and Gentilucci study, and the fins were not presented on a monitor but were drawn on a board. Moreover, grasping was performed open loop in our experiment, whereas in the Daprati and Gentilucci experiment, full vision of both the hand and the stimuli was allowed during grasping. Both facts suggest that the effect of the Müller-Lyer illusion on grasping is robust across different stimulus conditions. Only in a study by Otto-de Haart et al. (1999) was there no significant effect of the Müller-Lyer on grasping, and only in the binocular vision condition. However, the effect was close to being significant and was very similar to the effect found in the monocular viewing condition of this study (see Table 2). Therefore, we think the Otto-de Haart et al. result is not a strong argument against an effect of the Müller-Lyer illusion on grasping.

In the perceptual task of Experiment 1, the adjusted length of the comparison bar was always smaller than the physical size of the target bar. This might be interpreted to mean that we did not succeed in inducing the normal perceptual Müller-Lyer illusion because the fin-out configuration should lead to an overestimation. However, such a bias relative to the absolute size of the target is common in illusion studies (e.g., Coren & Girgus, 1972b; Girgus, Coren, & Agdern, 1972; Massaro & Anderson, 1971). These studies interpret such biases as constant errors caused by differ-

Table 2
Effects of Visual Illusions on Perception and Grasping

		Grasping		Perception (standard)		Perception (nonstandard)		
Study	*N*	*M* (*SE*)	*p*	*M* (*SE*)	*p*	*M* (*SE*)	*p*	Comp. version
				Ebbinghaus illusion				
Aglioti et al. (1995)	14	1.6 (0.4)[a,b]	<.05	2.5 (0.2)	<.05			Yes
Haffenden and Goodale (1998)	18	1.0 (0.5)[a,c]	*ns*	2.4 (0.2)	<.05	4.2 (1.0)[a,c,d]	<.05	Yes
Pavani et al. (1999)	18	1.0	<.05	0.7	<.05			No
Franz et al. (1998, 2000)	26	1.5 (0.38)	<.05	1.5 (0.12)	<.05			No
				Ponzo illusion				
Brenner and Smeets (1996)	8	0.3	.18[e]	0.8	<.05			Yes
Jackson and Shaw (2000)[f]	8	−0.7	.07					
				Müller-Lyer illusion				
Daprati and Gentilucci (1997)	8	1.0	<.05			3.7[g]	<.05	
						2.4[h]	<.05	
Otto-de Haart et al. (1999)								
Binocular	14	1.7	.08			9.0[g]	<.05	
Monocular	14	2.1	<.05			12.6[g]	<.05	
Experiment 1, present study	16	3.4 (0.42)	<.05	2.0 (0.24)	<.05			No
				Parallel-lines illusion				
Experiment 4, present study	26	1.2 (0.32)	<.05	2.3 (0.26)	<.05			No

Note. All illusion effects are the differences between an enlarging version of the illusion and a shrinking version. The grasping effects are based on maximum preshape aperture. Available standard errors of the means are presented in parentheses. One study (Marotta, DeSouza, Haffenden, & Goodale, 1998) did not report sizes of the effects and is not included. Comp. = composite; this column indicates whether the composite version of the illusion was used.

[a] Effects are calculated from only 50% of the trials (for which the calculations are comparable to other studies). [b] Values are estimated from Figure 5 (p. 683) of this study. [c] Values are from A. Haffenden (personal communication, August 1998). [d] Manual estimation: Participants indicated target size by opening index finger and thumb without seeing hand and stimulus. [e] Values are from E. Brenner (personal communication, January 2000). [f] For technical reasons, this study did not assess the size of the perceptual effect. [g] Manual estimation: Participants indicated target size with full vision of hand and stimulus. [h] Participants indicated target size by drawing a line of the length of the target without seeing hand and paper but with seeing the stimulus.

ences in stimulus presentation between target and comparison. The constant error only poses a problem when comparing the differential contributions of the two illusion configurations. In this case one has to introduce a neutral condition in which the target is not influenced by the illusion. However, because we did not intend in this study to compare the differential effects of the two illusion versions, such a constant error does not pose a problem for the interpretation of the illusion effects.

According to the common representation model we had to compare the slopes that relate MPA and the perceptual measure to physical size. Our results have three aspects: (a) The slopes of MPA in both illusion conditions were approximately 10% smaller than 1. This is similar to the results of previous studies. For example, Smeets and Brenner (1999) reviewed a large number of studies and found an average slope of 0.82. (b) The slopes of the perceptual measure were also approximately 10% smaller than 1. Given that length comparison (the perceptual measure we used) is usually accurate, one might expect a slope of 1 here. However, the slight decrease might be caused by the size of the target object, which was not varied in isolation, but in the context of the perceptual illusion. This view is strengthened by the similar slopes we obtained in the perceptual control experiments (Experiments 2 and 3). (c) According to the common representation model, the relationships of the MPA slope and the perceptual slope should be constant for the two illusion conditions. Our data conform well with this prediction. Moreover, the factor f, which relates the motor illusion to the perceptual illusion in the common representation model, was close to 1 (cf. Equation 1). In this case, the common representation model predicts the same absolute size for the perceptual illusion as for the motor illusion. To the contrary, the strong separate representation model predicts no motor illusion, whereas the weak separate representation model predicts an effect for the motor illusion, which is between zero and the size of the perceptual illusion.

Interestingly, the motor illusion was even larger than the perceptual illusion in this experiment. In contrast, Daprati and Gentilucci (1997), using other perceptual measures, reported a larger perceptual than motor illusion (cf. Table 2). In the following control experiments, we investigated whether the reason for this larger perceptual effect can be found in an insufficient match between perceptual task and motor task.

A second reason for the control experiments is that the across-subjects correlation between perceptual illusion and motor illusion was small ($\rho = .19$) compared to the IEC (.58) and did not reach significance. Although the nonsignificant result does not allow one to conclude that there is no correlation (to decide this question one needed a larger sample size; cf. the introduction), it might indicate an insufficient match between the perceptual task and the motor task.

Experiment 2: Effects of Presentation Time?

In the perceptual task of Experiment 1, participants had unlimited time to adjust the comparison bar. By contrast, presentation time was limited in the grasping task. As soon as the reach started, vision was suppressed by closing the shutter glasses in order to have open loop grasping conditions. In Experiment 2 we tested whether the perceptual effect of the illusion changes for shorter presentation times.

Method

Six people (3 women and 3 men) participated in Experiment 2; their ages ranged from 20 to 28 years ($M = 23.5$ years). Participants sat on a chair at a viewing distance of approximately 65 cm to a standard 21-in. (53.3 cm) computer monitor.

All stimuli were now presented on the monitor; that is, in contrast to the first experiment no real objects were presented. The monitor stood in a normal, upright position (unlike in Experiment 1, where the monitor was tilted in such a way that its screen could serve as a table for the real objects). The target bar had lengths of 43, 44, 45, and 46 mm. The comparison bar was shifted relative to the target bar along the main axis of the target bar by 160 mm. In all other respects, stimuli were identical to the stimuli of Experiment 1.

In the long inspection task, participants adjusted the comparison bar to match the size of the target bar. After they finished their adjustment, the stimuli disappeared from the screen. This procedure is similar to the perceptual task of Experiment 1. Each participant performed five practice trials first and then two blocks of 24 trials each. Given eight different trial types (4 sizes of the target bar × 2 contexts), participants performed six adjustments per trial type.

In the short inspection task, the stimuli were displayed only for a duration of 1,600 ms. Participants had to decide whether the comparison bar was longer or shorter than the target bar (two alternative forced choice task). We chose the presentation time to be roughly twice as large as the mean presentation time in the grasping task of Experiment 1, because participants had to calculate the size of two stimuli (the target bar and the comparison bar). Because of the distance between the stimuli (14° of visual angle), participants probably made at least one saccade between the stimuli. In contrast, in the grasping task of Experiment 1 participants had to calculate only the size of one stimulus (the target).

Each participant performed 15 practice trials first and then six blocks of 80 trials each. Given eight different trial types, participants performed 60 judgments per trial type. The size of the comparison bar was determined through an adaptive up–down procedure: For each block and each trial type, separate staircases were used with the comparison bar, initially being either 5 mm larger or 5 mm smaller than the target. If the participant responded "larger" ("smaller"), the comparison was presented 1 mm smaller (larger) the next time this trial type was displayed. For data analysis, cumulative gaussians were fitted to the data, and the point of subjective equality was determined. The succession of the long and the short inspection tasks was counterbalanced over participants.

Results

Figure 6a shows the mean illusion effects of the long and short inspection tasks. There was a highly significant main effect of the illusion factor, $F(1, 5) = 27.0$, $p = .003$. The illusion effect was larger for the short inspection task than for the long inspection task, $F(1, 5) = 21.0$, $p = .006$. The different sizes of the target bar had no differential effect on the size of the illusion, $F(3, 15) = 2.2$, $\epsilon = .50$, $p = .18$. Furthermore, the interaction between target size and task was not significant, $F(3, 15) = 1.1$, $\epsilon = .63$, $p = .37$.

We also computed a linear regression of the perceptual measure as a function of the size of the target bar. We did this to compare the slope to the slope obtained in Experiment 1. Because the ANOVA showed no significant interaction of the size of the target bar with any of the other factors (all $ps > .18$), we pooled all conditions to obtain one estimate for the slope. The slope was 0.98 ± 0.37.

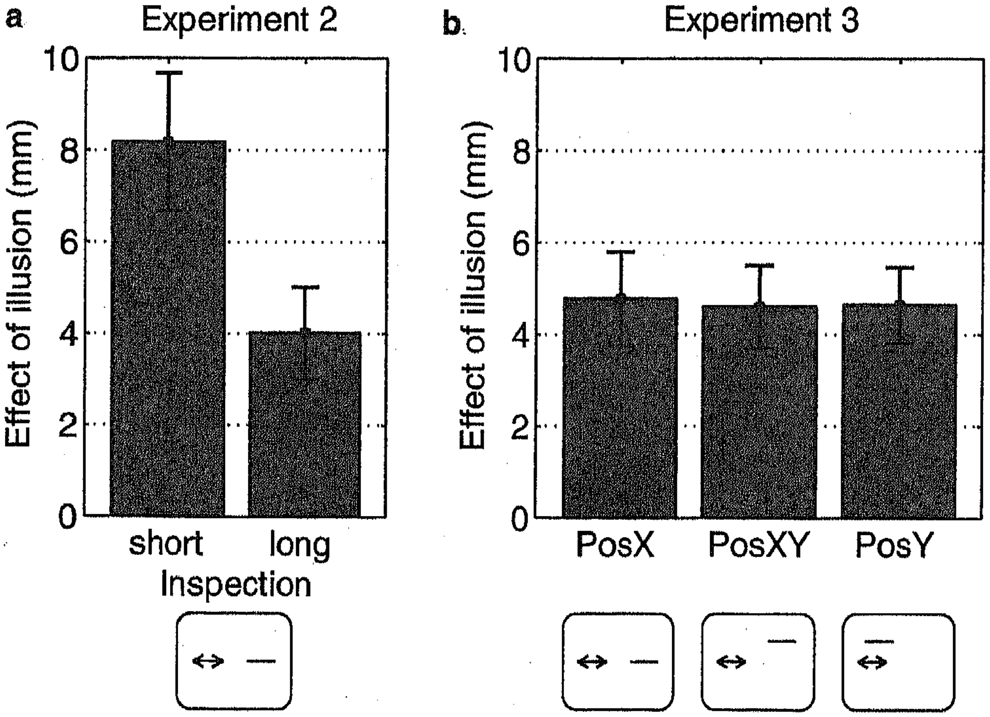

Figure 6. Overall illusion effects averaged across all lengths of the target bar for Experiment 2 (a) and Experiment 3 (b). Error bars depict ±1 *SEM*.

Discussion

In the Müller-Lyer illusion, short presentation times lead to a larger illusion than longer presentation times. Because presentation times were shorter in the motor task of Experiment 1, this fact could account for the larger motor illusion in this experiment.

Experiment 3: Effects of Comparison Position?

We tested one more possible source of differences between the perceptual task and the motor task of Experiment 1. We hypothesized that in the perceptual task of Experiment 1, the comparison bar might have been so close to the target bar that the illusion influenced the comparison as well as the target. If so, the comparison would no longer be neutral, and this could have changed the measured perceptual effect. If this were the case, then varying the position of the comparison would yield different perceptual measures for the illusion.

Method

Eight people (4 women and 4 men) participated in Experiment 3; their ages ranged from 16 to 30 years (M = 23.0 years). Procedure and stimuli were similar to the long inspection task of Experiment 2 and to the perceptual task of Experiment 1. The only difference was that the comparison was now presented at three different locations. For easier description, imagine an x-axis parallel to the main axis of the target bar and a y-axis perpendicular to this. In the PosX condition the comparison was shifted along the x-axis by 160 mm. In the PosY condition the comparison was shifted along the y-axis by ± 80 mm and along the x-axis by ± 8 mm, with the signs of the shifts being determined randomly from trial to trial. Finally, in the PosXY condition the comparison was shifted along the x-axis by 160 mm and along the y axis by ± 80 mm. Note that the PosY condition corresponds to the stimulus arrangement of Experiment 1 and that the PosX condition corresponds to the stimulus arrangement of Experiment 2.

Each participant performed five practice trials first and then six identical blocks of 24 trials each. Given 24 different trial types (4 sizes of the target bar × 2 contexts × 3 positions of the comparison), participants performed six adjustments per trial type.

Results

Figure 6b shows the mean illusion effects measured at the different positions of the comparison bar. Although the main effect of the illusion inducing context was highly significant, $F(1, 7) = 29$, $p = .001$, there was no difference of the illusion effects between the different positions of the comparison bar, $F(2, 14) = 0.07$, $\epsilon = .61$, $p = .84$; no difference in illusion effects for the different sizes of the target bar, $F(3, 21) = 2.7$, $\epsilon = .61$, $p = .11$; and no significant interaction between the last two factors, $F(6, 42) = 1.6$, $\epsilon = .34$, $p = .24$.

We also computed a linear regression of the perceptual measure as a function of the size of the target bar. This was done to compare the slope to the slope obtained in Experiment 1. Because the ANOVA showed no significant interaction of the size of the target bar with any of the other factors (all $ps > .10$), we pooled all conditions to obtain one estimate for the slope. The slope was 0.80 ± 0.18.

Discussion

The results of Experiment 3 suggest that the position of the comparison bar was not critical for the measurement of the perceptual effect in Experiment 1.

Taken together, the perceptual control experiments revealed one plausible reason for the increased motor illusion in Experiment 1: the shorter presentation time in the motor task. A second cause for the increased motor illusion could be a fundamental confound in the Müller-Lyer illusion: The overall size of the fin-out figure (that enlarges the perceived size of the target bar) is larger than the size of the fin-in figure. It is possible that participants were influenced in grasping by this overall size and that this caused an additional increase in measured illusion size. We minimized this problem by clearly separating the target bar and the fins (see the *Method* section of Experiment 1). Nevertheless, this problem is always present in the standard version of the Müller-Lyer illusion, and therefore we used another variant of the Müller-Lyer illusion: the parallel-lines illusion.

Investigating the Parallel-Lines Illusion

The parallel-lines illusion might be the simplest of all visual distortions: A long line causes a shorter, parallel line to be perceived as longer (and vice versa). It has been argued (Pressey, 1983, as cited in Jordan & Schiano, 1986) that the parallel-lines illusion may serve as a prototype for more complex visual illusions like the Müller-Lyer illusion. In the context of our grasping experiments, the parallel-lines illusion has the advantage that there are no fins that might distort grasping. To obtain a strong illusion, we presented two context lines with one target bar in between (see Figure 7c). With the parallel-lines illusion, we performed the same set of experiments as we performed for the Müller-Lyer illusion.

Experiment 4: Grasping the Illusion

In this experiment we compared the effects of the parallel-lines illusion on grasping and perception. The experiment is similar to Experiment 1, except that the parallel-lines illusion was used.

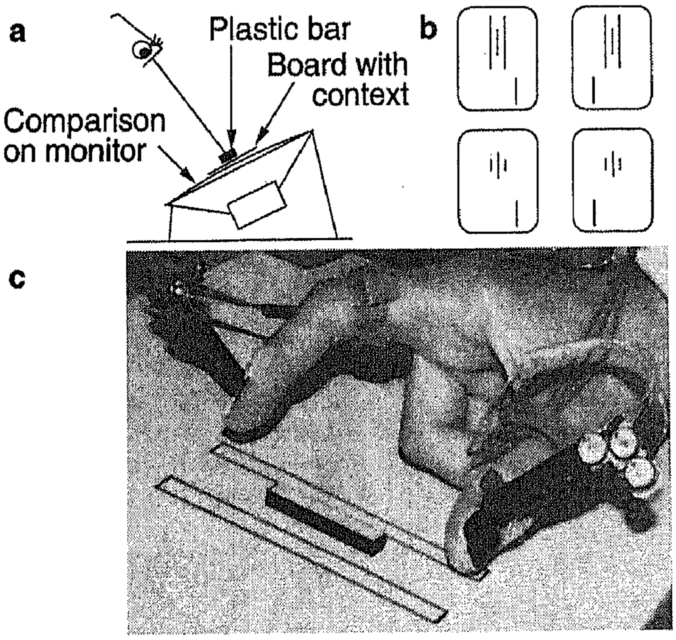

Figure 7. (a) Apparatus of Experiment 4. (b) Stimulus conditions in the perceptual task of Experiment 4. The comparison bar was displayed on the monitor either left or right of the target. (c) A participant grasping the target bar. The illusion context was drawn on a board.

Method

Twenty-six people (15 women and 11 men) participated in Experiment 4; they ranged in age from 17 to 36 years ($M = 24.7$ years). The apparatus of Experiment 4 is shown in Figure 7.

Stimuli, apparatus, and procedure were identical to Experiment 1 except for the following: Instead of adding fins to the target bars, the target bars were now accompanied by two parallel lines that had a distance of 11 mm to the midline of the target bar and were either 100 mm long (the enlarging version of the illusion) or 22 mm long (the shrinking version of the illusion). As in Experiment 1, all elements of the parallel-lines figure were 7 mm wide. Moreover, the target bars were 7 mm wide; 5 mm high; and 40, 43, 46, or 49 mm long. Because in the parallel-lines illusion the parallel lines do not touch the target bar, it was no longer necessary to adapt the illusion-inducing context to each length of the target bar. Therefore, instead of presenting the illusion-inducing context on the monitor, we decided to use two boards on which the long and the short parallel lines were drawn and positioned them behind the target bars (see Figure 7a and 7c). As one final difference to Experiment 1, we added for exploratory purposes a group factor: 10 of the participants viewed the whole stimulus configuration as 1-mm thick outlines, whereas the other 16 participants saw the stimuli configuration filled black.

Results

Outlines versus filled stimuli. For both dependent variables, the adjusted length of the comparison bar and MPA, we did not find any difference between stimuli that were drawn only as outlines or as filled stimuli. This is reflected by the fact that ANOVAs for both dependent variables (within-subjects factors: length of target bar and illusion inducing context; between-subjects factor: outlines) did not show any significant main effect or interaction of the factor outlines (all $ps > .12$). Moreover, adding or removing the factor outlines only minutely changed the results of the ANOVAs. For ease of presentation we therefore pooled the two groups.

Illusion effects. Figure 8a shows the mean adjusted length of the comparison bar and the mean MPA as functions of the length of the target bar and of the illusion-inducing context. In the perceptual task the main effects of length of target bar, $F(3, 75) = 377.0$, $\epsilon = 0.61$, $p < .001$, and of illusion-inducing context, $F(1, 25) = 82.0$, $p < .001$, were highly significant. The interaction between the two factors was also highly significant, $F(3, 75) = 5.5$, $\epsilon = 0.83$, $p = .004$. Similarly, in the grasping task the main effects of length of target bar, $F(3, 75) = 135.0$, $\epsilon = 0.89$, $p < .001$, and of illusion-inducing context, $F(1, 25) = 16.0$, $p < .001$, were highly significant. There was no interaction between these two factors, $F(3, 75) = 0.2$, $\epsilon = 0.96$, $p = .87$.

Slopes. For the long parallel lines MPA depended on physical size with a slope of 0.87 ± 0.06, and the perceptual measure depended on physical size with a slope of 0.98 ± 0.03. The relationship of these slopes is $f(1) = b_G(1)/b_P(1) = 0.89 \pm 0.07$ (see Appendix A and the introduction for a description of f). For the short parallel lines the slope of MPA was 0.89 ± 0.05. The slope of the perceptual measures was 0.85 ± 0.04. The relationship of the slopes is $f(2) = b_G(2)/b_P(2) = 1.04 \pm 0.07$. Estimating f with the mean of the two f values gives $\bar{f} = 0.97$. This value is close enough to 1 to work with the simplified Equation 2. That is, we are justified in comparing the absolute values of the motor illusion to the absolute values of the perceptual illusion.

Comparing motor illusion with perceptual illusion. The overall illusion effects averaged across all lengths of the target bar are shown in Figure 8b. The overall effect of the illusion on grasping was significantly smaller than that on perception, $F(1, 25) = 17$, $p < .001$. This difference was not affected by the factor length of target bar ($p > .20$).

The overall illusion effects calculated for each participant separately and correlated across participants are shown in Figure 9a. The grasping illusion is predicted by the perceptual illusion with a slope 0.7. The corresponding correlation is highly significant, $\rho =$

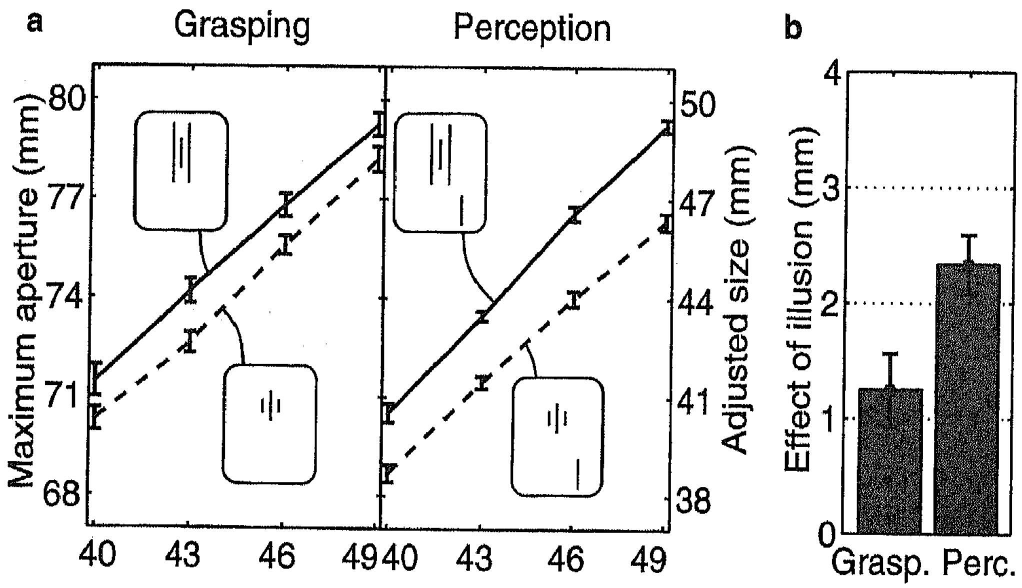

Figure 8. Results of the perceptual (Perc.) task and of the grasping (Grasp.) task in Experiment 4. (a) Mean adjusted length of the comparison bar and mean maximum preshape aperture as functions of the length of the target bar and of the illusion-inducing context. Error bars depict ±1 *SEM*. (Data are normalized to account for absolute differences in hand sizes and aperture sizes between the participants.) (b) Overall illusion effects averaged across all lengths of the target bar. Error bars depict ±1 *SEM*.

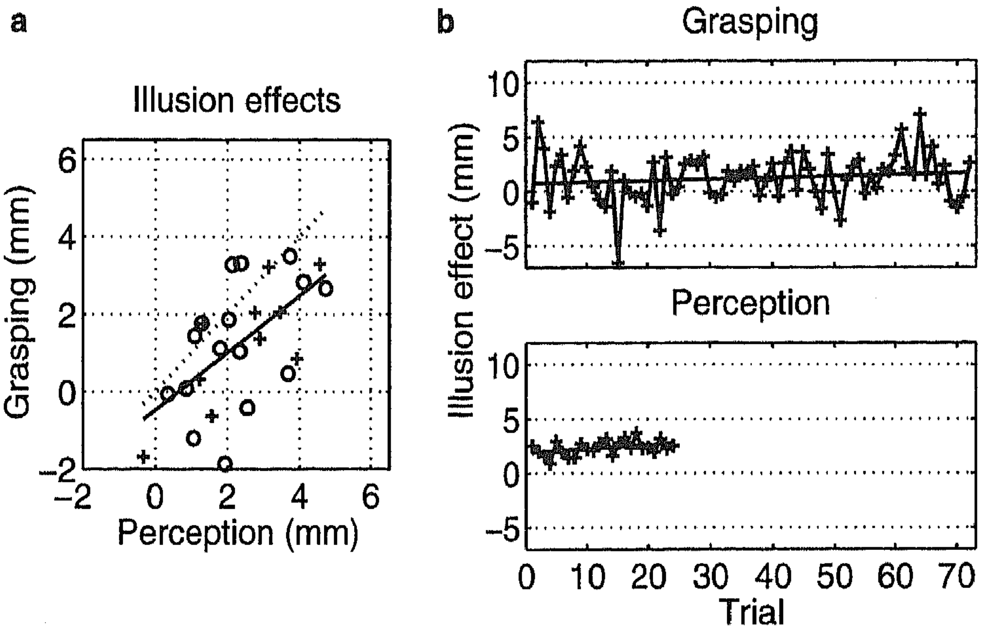

Figure 9. Further analyses of the results of Experiment 4. (a) Overall illusion effects calculated separately for each participant and correlated across participants. Illusion effects of participants who saw outlines are shown as crosses, and data for those who saw filled bars are shown as circles. The solid line indicates the regression, and the dashed line indicates a proportional relationship. (b) Illusion effects calculated separately for each trial. The solid line indicates the regression.

.61, $t(24) = 3.8$, $p < .001$, one-tailed. The IEC (cf. description in the introduction) is $\sigma_{\Delta_P}/\sigma_{\Delta_G} = 1.32/1.60 = .82$.

Development of the illusion across trials. To test whether the repeated presentation of the parallel-lines figure causes a decrement of illusion strength, we calculated the illusion effects separately for each trial, as we did in Experiment 1. Results are shown in Figure 9b. The linear regression of illusion effect as a function of trial number showed in the perceptual task a small, barely significant increase of the illusion over time. In the grasping task no change of the illusion effect over time was found: perception, IE = 0.04 × TN + 1.9 (mm), $t(22) = 2.1$, $p = .048$; grasping, IE = 0.01 × TN + 0.7 (mm), $t(70) = 1.1$, $p = .28$, where IE stands for illusion effect and TN for trial number. The t value tests the slope of the regression.

Time and velocity parameters for grasping. As in Experiment 1, we tested whether the grasping movements differed in speed for the different illusion conditions. We found that if the short parallel lines were presented, the grasping movements were faster than if the long parallel lines were presented: The average start times were 684 ms versus 710 ms; for short versus long parallel lines, $F(1, 25) = 7.9$, $p = .009$. The average times when the LC glasses closed were 726 ms versus 752 ms, $F(1, 25) = 7.7$, $p = .01$; the average times from start time to MPA were 588 ms versus 598 ms, $F(1, 25) = 9.5$, $p = .005$; and the average movement times were 870 ms versus 888 ms, $F(1, 25) = 14.9$, $p = .001$. Neither the factor length of target bar nor the interaction between length of target bar and illusion-inducing context showed significant effects on these parameters (all $ps > .16$).

The mean values of the maximum velocities of index finger and thumb during the reach movement were 830 mm/s and 687 mm/s, respectively. These parameters were not affected by the length of target bar, the illusion-inducing context, or the interaction between these two factors (all $ps > .39$).

Discussion

As in our study of the Müller-Lyer illusion, we found clear and highly significant effects of the parallel-lines illusion on grasping. The motor illusion as well as the perceptual illusion stayed the same irrespective of whether the stimuli were presented as outlines or filled, indicating that results are consistent for different ways of stimulus presentation.

Furthermore, we found similar results as in the Müller-Lyer illusion for the factor f that relates the motor illusion to the perceptual illusion in the common representation model. For both illusion conditions the factor f was close to 1, such that the common representation model predicts the same size for the perceptual illusion as for the motor illusion. However, the strong separate representation model predicts no motor illusion, whereas the weak separate representation model predicts an effect for the motor illusion between zero and the size of the perceptual illusion.

In contrast to the results for the Müller-Lyer illusion, the parallel-lines illusion exerted a larger perceptual illusion than motor illusion. This outcome is consistent with the assumption that in the Müller-Lyer illusion the fins might have exerted an additional effect on the motor system. Also in contrast to the Müller-Lyer illusion, we found a strong and highly significant across-subjects correlation between perceptual illusion and motor illusion, suggesting that the same signal is responsible for the illusion effects in perception and in grasping.

Another difference between the results of the parallel-lines illusion study and the Müller-Lyer illusion study is that the speed of the grasping movements varied with the illusion condition. Participants grasped slightly faster if the short parallel lines were presented than if the long parallel lines were presented. It is known that faster movements can lead to an increase in MPA (e.g., Wing et al., 1986; for a review, see Smeets & Brenner, 1999). This effect counteracts the effect of the visual illusion: Movements were faster for the short parallel lines and therefore MPA should be increased, whereas because of the illusion the target bar was perceived as being shorter and therefore MPA should be decreased. That is, the effect of movement speed could contribute to the smaller size of the motor illusion in this experiment.

In an attempt to find further possible reasons for the (again) different sizes of the perceptual illusion and the motor illusion, we performed the same control experiments as for the Müller-Lyer illusion.

Experiment 5: Effects of Presentation Time?

As in Experiment 2, we perceptually tested whether the different presentation times in the perceptual task and in the grasping task can cause different illusion strengths.

Method

Eight people (3 women and 5 men) participated in Experiment 5; they ranged in age from 21 to 26 years ($M = 23.3$ years). Stimuli, apparatus, and procedure were almost identical to Experiment 2. The only difference was the use of the parallel-lines illusion instead of the Müller-Lyer illusion.

Results

Figure 10a shows the mean illusion effects of the long and the short inspection tasks. We found a highly significant main effect of the factor illusion, $F(1, 7) = 25.0$, $p = .002$. The illusion effect was almost the same for the short inspection task and for the long inspection task, $F(1, 7) = 0.1$, $p = .77$. The different sizes of the target bar had no differential effect on the size of the illusion, $F(3, 21) = 0.4$, $\epsilon = .76$, $p = .71$. Moreover, the interaction between target size and task was not significant, $F(3, 21) = 0.3$, $\epsilon = .73$, $p = .74$.

We also computed a linear regression of the perceptual measure as a function of the size of the target bar. This was done to compare the slope to the slope obtained in Experiment 4. Because the ANOVA showed no significant interaction of the size of the target bar with any of the other factors (all $ps > .72$), we pooled all conditions to obtain one estimate for the slope. The slope was 0.84 ± 0.22.

Discussion

Presentation time did not seem to have an influence on illusion strength in the parallel-lines illusion. This is different from the Müller-Lyer illusion and might indicate that the influence of short presentation times on the Müller-Lyer illusion is caused by a decrement in the ability to separate the fins from the target. For the purposes of our comparison of motor illusion and perceptual illusion in the parallel-lines illusion, this means that presentation time likely does not bias the results in one of the two measures.

Experiment 6: Effects of Comparison Position?

As in Experiment 3, we tested whether the comparison bar might have been influenced by the illusion-inducing context. If this were the case, then varying the position of the comparison would yield different perceptual measures for the illusion.

Method

Six people (3 women and 3 men) participated in Experiment 6; they ranged in age from 17 to 25 years ($M = 22.3$ years). Stimuli, apparatus, and procedure were almost identical to those used in Experiment 3. The only

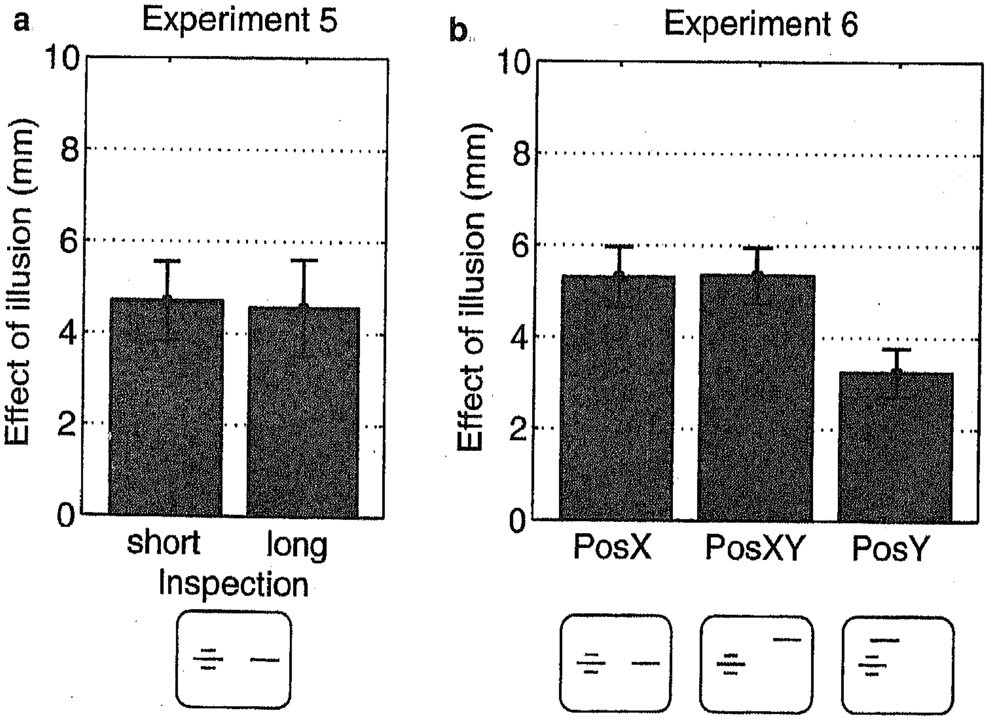

Figure 10. Overall illusion effects averaged across all lengths of the target bar for Experiment 5 (a) and Experiment 6 (b). Error bars depict ±1 *SEM*.

difference was the use of the parallel-lines illusion instead of the Müller-Lyer illusion.

Results

Figure 10b shows the mean illusion effects measured at different positions of the comparison bar. The main effect of the illusion inducing context was highly significant, $F(1, 5) = 70.0, p < .001$, and the different positions of the comparison bar had a highly significant influence on the illusion effect, $F(2, 10) = 18.3$, $\epsilon = .82$, $p < .001$. Illusion effects were similar for the different sizes of the target bar, $F(3, 15) = 3.9$, $\epsilon = .57$, $p = .07$, and the interaction between the last two factors also was not significant, $F(6, 30) = 0.1$, $\epsilon = .41$, $p = .95$.

Post hoc analyses show that there is no difference between the illusion effects in the PosX and PosXY conditions (Tukey test, $p > .10$). However, there were highly significant differences between the illusion effects in the PosX and PosXY conditions on one side and the illusion effect in the PosY condition on the other side (Tukey test, all $ps < .01$).

We also computed a linear regression of the perceptual measure as a function of the size of the target bar. This was done to compare the slope to the slope obtained in Experiment 4. Because the ANOVA showed no significant interaction between the size of the target bar and any other factor (all $ps > .06$), we pooled all conditions to obtain one estimate for the slope. The slope was 1.07 ± 0.19.

Discussion

The position of the comparison bar had a strong influence on the measured strength of the parallel-lines illusion. This suggests that the illusion-inducing context influences not only the target but also the comparison. In other words, spatial separation does not seem to be sufficient in the parallel-lines illusion to keep the comparison uninfluenced. This, however, is a prerequisite to accurately measure the size distortion of the target.

Jordan and Schiano (1986) described an effect that could account for these results. They found that the parallel-lines illusion reverses from assimilation (the target is perceived as being longer if the context is longer) to contrast (the target is perceived as being shorter if the context is longer), with large spatial separation between target and context.

Applying this finding to the comparison bar could account for the data found in our experiment. Assume the case in which the context lines were long and the comparison had a large distance to the parallel-lines figure. In this configuration one expects the target to be perceived longer (assimilation effect, short distance) and the comparison to be perceived shorter (contrast effect, long distance). If participants now match target and comparison, they have to change the length of the comparison by a larger amount than if the comparison were unaffected by the context elements. This leads to a larger value of the measured illusion.

For our purposes this is an unwanted effect. For a valid comparison to the grasping task, the perceptual task should only measure an illusionary change induced in one stimulus because only one stimulus can be grasped. The other stimulus, the comparison, should be uninfluenced by the illusion.

In other words, grasping is inherently a unipolar measure of size information, because only the size of one stimulus needs to be computed to guide grasping. In contrast, the perceptual measures we used so far were all bipolar measures because two sizes had to be computed, the size of the target and the size of the comparison. This procedure does not lead to any problem as long as the comparison can be assumed to be unaffected by the illusion. In the parallel-lines illusion, however, this is not the case.

A solution to this problem would be to find a unipolar perceptual measure that requires only that individuals compute the size of one stimulus, the target. For this purpose, we trained participants in Experiment 7 to estimate the length of stimuli in millimeters and then asked them to estimate the length of the target in the parallel-lines illusion.

Experiment 7: Using a Unipolar Perceptual Measure

To obtain a unipolar perceptual measure of the illusion effect in the parallel-lines illusion, we replicated Experiment 6 and used a magnitude estimation method in which participants were first trained to estimate the length of bars in millimeters and subsequently had to estimate the length of the target in the parallel-lines illusion. (Cf. Coren & Girgus, 1972a, for a similar estimation method in which, however, no training was performed. See also Vishton, Rea, Cutting, & Nunez, 1999.)

Method

Eight people (4 women and 4 men) participated in Experiment 7; they ranged in age from 16 to 30 years ($M = 24.4$ years). The experiment consisted of two tasks. The adjustment task was almost identical to Experiment 6. However, we reduced the number of blocks from six to four. Given 24 different trial types (4 sizes of the target bar × 2 contexts × 3 positions of the comparison), participants performed four adjustments per trial type. To be as comparable as possible to Experiment 4, the target bar had lengths of 40, 43, 46, and 49 mm (instead of 43, 44, 45, and 46 mm).

In the magnitude estimation task, participants were first trained to give absolute estimates of the length of a single bar. The bar had lengths between 33 mm and 56 mm (in increments of 1 mm). Participants viewed the bar without any context elements on the monitor and set a number (by pressing the buttons of a computer mouse) that should reflect the length of the bar in millimeters. After the participants had set the number, a feedback was provided that gave the true length of the bar and displayed scores depending on the performance of the participant. Participants did this training for 48 trials and were instructed to be as precise as possible. After the training, they performed the experimental condition. Exactly the same stimuli as in the adjustment task were presented for 48 trials, and the participants were requested to estimate their length. No feedback was given in the experimental condition. Given eight different trial types (4 sizes of the target bar × 2 contexts), participants performed six estimates per trial type. After the experimental condition, participants performed the training again for 24 trials to control for changes in response during the experimental condition.

Results

Figure 11 shows the mean adjusted lengths of the comparison bar and the mean estimated lengths as functions of the length of the target bar and of the illusion-inducing context. All dependent measures showed linear relationships to physical size. Most important, magnitude estimation showed a similar relationship as the other dependent measures, indicating that participants reacted to physical size differences in the magnitude estimation condition as they did in the other conditions. This fact allows us to compare the illusion effects between the different dependent measures.

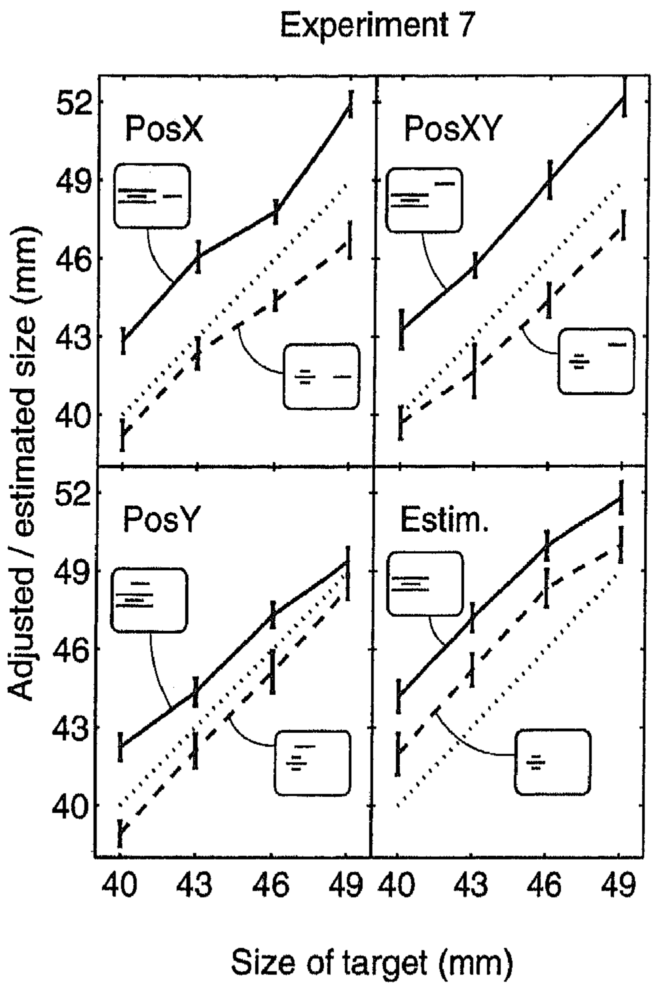

Figure 11. Results of Experiment 7. Mean adjusted length of the comparison bar for the different positions of the comparison bar in the adjustment task and mean estimated (Estim.) size in the estimation task. Error bars depict ±1 *SEM*. The dashed line indicates a proportional relationship.

The main effect of the illusion-inducing context was highly significant, $F(1, 7) = 77.0$, $p < .001$, and the different ways of assessing the illusion effects (different positions of the comparison bar and the magnitude estimation task) had a highly significant influence on the illusion effect, $F(3, 21) = 11.6$, $\epsilon = .92$, $p < .001$. There was no difference of the illusion effects for the different sizes of the target bar, $F(3, 21) = 0.4$, $\epsilon = .79$, $p = .72$, and the interaction between the last two factors was not significant, $F(9, 63) = 2.3$, $\epsilon = .31$, $p = .11$.

Overall effects averaged across all lengths of the target bar are shown in Figure 12. Post hoc analyses showed that there was no difference between the illusion effects in the PosX and PosXY conditions and between the illusion effects in the PosY condition and the magnitude estimation task (Tukey test, all *ps* > .10). However, there were highly significant differences between the illusion effects in the PosX and PosXY conditions on one hand and the illusion effects in the PosY condition and in the magnitude estimation task on the other hand (Tukey test, all *ps* < .01).

We also computed a linear regression of the perceptual measure as a function of the size of the target bar. This was done to compare the slope to the slope obtained in Experiment 4. Because the ANOVA showed no significant interaction of the size of the target bar with any of the other factors (all *ps* > .11), we pooled all conditions to obtain one estimate for the slope. The slope was 0.91 ± 0.04.

Because the adjustment task of Experiment 7 was intended to be a replication of the adjustment task of Experiment 6, we compared the illusion effects of the adjustment tasks across the two experiments. An ANOVA showed neither a significant difference between the two experiments, $F(1, 12) = 3.5$, $\epsilon = .97$, $p = .09$, nor an interaction of experiment with position, $F(2, 24) = 0.1$, $\epsilon = .97$, $p = .89$.

Discussion

The results of Experiment 7 have three aspects. First, the results replicate those of Experiment 6, showing that different illusion strengths are obtained if the position of the comparison bar is varied. Second, we succeeded in introducing magnitude estimation as a linear, unipolar measure. Third, magnitude estimation gives a smaller illusion effect than the adjustment task in the conditions in which the distance between target and comparison was large. This is exactly what can be expected if our contrast interpretation is valid: With large distances between the illusion context and the comparison, a contrast effect changes the perceived size of the comparison, and this enlarges the measured illusion. Because this effect is not possible in magnitude estimation, the measured illusion is smaller.

What does this mean with respect to the interpretation of Experiment 4? In Experiment 4, we used a perceptual task that was similar to the PosXY condition of the present experiment. The magnitude estimation as the more appropriate unipolar measure showed an illusion effect that was about half the size of the effect in the PosXY condition. This suggests that the perceptual illusion measured in Experiment 4 was overestimated, because of effects of the illusion context on the comparison. Correcting for this bias,

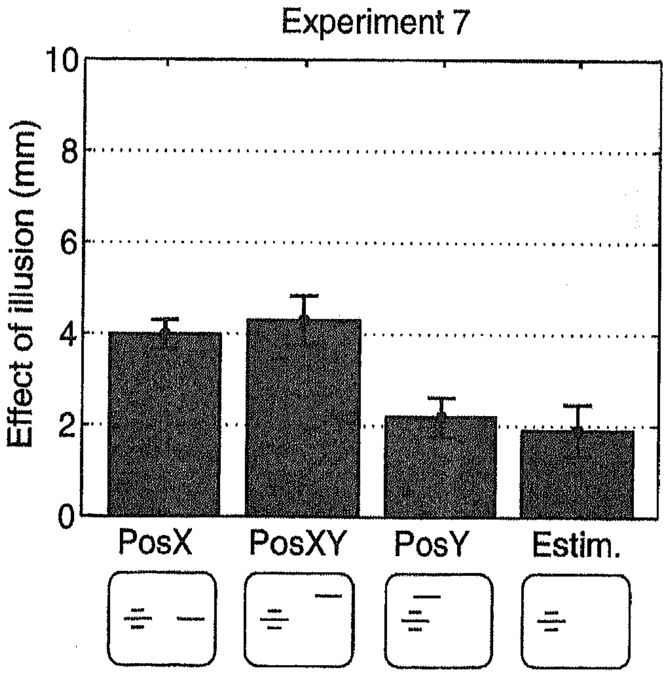

Figure 12. Overall illusion effects averaged across all lengths of the target bar for the different positions of the comparison bar in the adjustment task and for the estimation (Estim.) task of Experiment 7. Error bars depict ±1 *SEM*.

one expects a perceptual illusion of roughly the same size as in grasping.

General Discussion

We found strong and highly significant effects of the Müller-Lyer illusion and the parallel-lines illusion on grasping. In the Müller-Lyer illusion, the motor illusion was larger than the perceptual illusion, and in the parallel-lines illusion it was smaller. The across-subjects correlation between the motor illusion and the perceptual illusion was small in the Müller-Lyer illusion, whereas it was large and highly significant in the parallel-lines illusion.

In the Müller-Lyer illusion there might be two reasons for the stronger motor illusion. First, presentation time was shorter in the motor task than in the perceptual task. We showed that shorter presentation time can increase illusion strength. Second, the illusion effect is confounded with the overall size of the Müller-Lyer figure. This may have selectively influenced grasping and hence increased the motor illusion.

To minimize this confound we investigated the parallel-lines illusion, because here the target is much better separated from the illusion-inducing context than in the Müller-Lyer illusion. In the parallel-lines illusion the motor illusion was smaller than the perceptual illusion. However, we also found a strong and highly significant across-subjects correlation between the perceptual illusion and the motor illusion. That is, a participant showing a large perceptual illusion also tended to show a large motor illusion, suggesting that both illusions have the same origin.

Investigating the reasons for the smaller motor illusion in the parallel-lines illusion, we found that (a) presentation time was not critical and (b) the measured perceptual effect depended strongly on placement of the comparison bar relative to the target bar. Because grasping does not involve a comparison bar (we called this feature *unipolar*), a question arises: Which position of the comparison bar should be used to compare the perceptual illusion with the motor illusion? Using size estimation as a unipolar perceptual measure, we found that the perceptual effect is also smaller for this unipolar measure. This fact suggests correcting the perceptual effect measured in Experiment 4, allowing one to reconcile the smaller motor illusion with the common representation model.

In summary, we found evidence against the strong separate representation model, because the parallel-lines illusion and the Müller-Lyer illusion clearly affect grasping. We see no convincing evidence for the weak separate representation model because the motor effects were not consistently smaller than the perceptual effects but were larger in the Müller-Lyer illusion and smaller in the parallel-lines illusion. Furthermore, we found a strong across-subjects correlation between perceptual effect and motor effect in the parallel-lines illusion. We obtained a relatively good (however not perfect) agreement of the data with the common representation model because the differences between the perceptual illusion and the motor illusion can be attributed to differences between the perceptual task and the grasping task.

The present study shows how difficult it is to adequately match the perceptual task and the grasping task (cf. Post & Welch, 1996; Smeets & Brenner, 1995). This problem might lead to the pessimistic view that an adequate comparison of the tasks and therefore a discrimination between the weak separate representation model and the common representation model is impossible. We think, however, that this endeavor can give insights about subtleties of the cognitive system, as, for example, the influence of the parallel-lines illusion on the comparison bar. In the following section, we relate our findings to the results of previous studies.

Comparison With Previous Studies

Table 2 summarizes the results of all studies that (to our knowledge) were performed on the influences of visual illusions on grasping, using MPA as a dependent measure. It seems clear from these data that visual illusions do influence grasping. Most of the studies found significant effects of visual illusions on grasping. Other studies found effects that were close to being significant (Haffenden & Goodale, 1998; Otto-de Haart et al., 1999). The remaining studies of Brenner and Smeets (1996) and Jackson and Shaw (2000) used relatively small sample sizes, and the study of Brenner and Smeets used a relatively small perceptual illusion (for the Jackson & Shaw study, no values of the perceptual illusion were reported). Brenner and Smeets and Jackson and Shaw found effects of the illusion on other parameters of the grasping movement (lift force and grip force, respectively). With respect to the Ebbinghaus illusion, there is unusual agreement: All four studies, performed in three different laboratories, used almost the same geometry for their stimuli and found similar sizes for the motor illusion. Taken together, the evidence argues against the strong version of the separate representation model, which assumes that there is no influence of visual illusions on grasping.

What about the perceptual effects? In Table 2 we distinguish between standard and nonstandard perceptual measures. By *standard perceptual measures* we mean measures that are typically used to investigate visual illusions. Participants either chose one object out of a series of objects to match the size of the target or adjusted the size of a comparison stimulus (see, e.g., Coren & Girgus, 1972a, for an investigation on these measures). The nonstandard measures are different and are discussed later.

The studies of Aglioti et al. (1995) and Haffenden and Goodale (1998) used the composite version of the Ebbinghaus illusion (indicated in the last column of Table 2). We showed that this can lead to an enlarged perceptual effect (see Figure 1 and Franz et al., 2000). Researchers who avoided this problem found a very good match of perceptual effect and motor effect in the Ebbinghaus illusion (Franz et al., 1998, 2000; Pavani et al., 1999). Moreover, we found a significant across-subjects correlation between the perceptual effects and the motor effects of the Ebbinghaus illusion (Franz et al., 2000).[2]

Brenner and Smeets (1996) also used a composite version and the Aglioti et al. (1995) paradigm to investigate the Ponzo illusion. It is likely that the same problem of an enlarged perceptual effect arises for this illusion as in the Aglioti et al. study. Therefore, it is difficult to interpret the difference between the perceptual illusion and the motor illusion in the study of Brenner and Smeets. Furthermore, the focus of this study was not on MPA but on measuring the force that was applied to lift the objects. This measure was clearly affected by the illusion, indicating an influence of the illusion on the motor system.

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[2] Unfortunately, none of the other studies reported values for the across-subjects correlation of the motor illusion and the perceptual illusion. Because very large sample sizes are needed to reliably detect these correlations (cf. the introduction), it would be of interest to compare the values of the across-subjects correlation across studies.

Finally, Experiments 1 and 4 also used standard perceptual measures and were discussed above. In conclusion, we do not see evidence in the standard perceptual measures to advocate the weak separate representation model: The better the match between perceptual task and motor task, the less the difference between the perceptual illusion and the motor illusion.

Three of the studies listed in Table 2 used different, nonstandard perceptual measures to assess the perceptual effects of the illusion. Haffenden and Goodale (1998) used a manual estimation task. Participants estimated target size by opening index finger and thumb without seeing their hand or the stimulus during performance of the task. Daprati and Gentilucci (1997) and Otto-de Haart et al. (1999) also used a manual estimation task, with the difference that now participants had full vision of stimulus and hand during the task. Finally, Daprati and Gentilucci used a second task in which participants drew a line of the length of the target without seeing hand or paper. All these tasks have potential benefits. The manual estimation tasks are, for example, very similar to the grasping task. Furthermore, all tasks are unipolar measures because participants act on only one object at a time. This is one requirement we found for a perceptual measure to be validly compared to grasping. However, we see the following problems in these measures.

First, it is unclear whether these measures can be interpreted as perceptual measures. On the contrary, one might argue that the motor system is tapped with these tasks (in fact, in the study of Vishton et al., 1999, a similar task was used and interpreted as motor task; see below for a description of this study). This problem is even more pronounced if no visual feedback of the hand is allowed. In this case, participants have to rely heavily on feedback of the motor system. Before being interpreted as perceptual, these measures should be compared to standard perceptual measures. For example, they should yield effects of a similar size as the standard perceptual measures, they should correlate across participants with standard perceptual measures, and the slope of the function relating these measures to physical size of the object should be known in order to validly compare them to grasping as well as to standard perceptual measures (the same situation as we described for the comparison of grasping with standard perceptual measures in the introduction).

Second, Table 2 shows that the nonstandard perceptual measures yield diverging results. In particular, the manual estimations tasks (indicated by superscripts d and g) tend to show very large illusion effects. In the Haffenden and Goodale (1998) study, the difference between the effect in the manual estimation task and in the standard perceptual measure was of about the same size as the difference between the standard perceptual measure and grasping. This is even more the case if one takes into account that in this study the standard perceptual measure might be an overestimate because of the use of the composite version of the illusion in the Aglioti et al. (1995) paradigm (as argued in the introduction and in Franz et al., 2000). A similar situation can be found in the Daprati and Gentilucci (1997) study. The drawing task (indicated by superscript h) differs from the grasping task by about the same amount as from the manual estimation task (indicated by superscript g). This is also reflected in that there was only one significant difference in the post hoc comparisons of this study: The fin-in configuration of the Müller-Lyer figure showed a larger illusion effect in the manual estimation task than in both the grasping task and the drawing task. The grasping illusion and the illusion in the drawing task were not significantly different. In summary, we think that the case of the nonstandard perceptual measures in favor of a dissociation between perception and action is not clear. Moreover, some inconsistencies between the nonstandard perceptual measures and the classical perceptual measures require further investigation.

As a final issue, we want to discuss one study that comes to very similar conclusions as the present study, although it used a different approach and is therefore not listed in Table 2. Vishton et al. (1999) investigated the horizontal–vertical illusion. Participants did not grasp three-dimensional objects; instead, they reached for two-dimensional objects that were printed on paper. They were instructed to perform this movement as if they were grasping the objects. The dependent measure was the opening of the fingers at the moment when the paper was touched (not MPA). In our opinion this measure needs further validation. The potential problem is that participants did not get any haptic feedback. It is known that reach movements change if no haptic feedback is provided. Participants start to perform stereotyped movements that are different from normal grasp movements when no haptic feedback is presented as compared to when it is (Opitz, Gegenfurtner, & Bülthoff, 1996).

Nevertheless, it is interesting to compare the results of Vishton et al. (1999) to ours. In a first experiment, Vishton and colleagues compared the effect of the horizontal–vertical illusion on the (mimicked) grasping with the effect on perception and found a smaller effect on grasping as on perception. However, they argued that in the perceptual task a relative judgment was required because participants compared the horizontal line with the vertical line, both being part of the horizontal–vertical illusion figure (this is the same problem as with the composite version in the Aglioti et al., 1995, paradigm). They argued that contrary to the perceptual task, participants operated on only one of the two lines in the grasping task, and therefore an absolute judgment of size was required. (We called this a *unipolar measure.*) In further experiments they introduced absolute (or unipolar) measures of perception, one of which was a task similar to the magnitude estimation task of Experiment 7. Using these measures, the differences between grasping and perception vanished. This result is congruent with our findings.

Consequences for the Action Versus Perception Hypothesis

The action versus perception hypothesis (Goodale & Milner, 1992; Milner & Goodale, 1995) is an attempt to integrate evidence from lesion studies on monkeys (e.g., Ungerleider & Mishkin, 1982), neuropsychological studies (e.g., Goodale et al., 1994; Goodale, Milner, Jakobson, & Carey, 1991), and psychophysical studies (e.g., Bridgeman, Lewis, Heit, & Nagle, 1979; Goodale, Pélisson, & Prablanc, 1986; Hansen & Skavenski, 1985). Goodale and Milner proposed that the two systems of the primate brain, the dorsal stream and the ventral stream, are used selectively for perception and action. They suggested that the function of the dorsal stream is to guide the manipulation of objects, whereas the function of the ventral stream is to perform computations necessary for object recognition and conscious perception. They argued that these computations have to fulfill different requirements. Computations for the guidance of actions have to be fast, they only need short-term memory because the position of the object can change quickly, and they have to code the position of the object relative to the effector (egocentric coding). In contrast, computations for the purposes of object recognition do not need to be as fast, and long-term memory is needed for object constancy. Finally, it is not as important to code the objects relative to an effector, but the object should be coded relative to other objects (allocentric coding).

The most prominent evidence for the action versus perception hypothesis is a dissociation between perception and action found in the patient D.F. (Goodale et al., 1994, 1991). This patient had a profound visual form agnosia caused by carbon monoxide poisoning. MRI scans showed that the major focus of cortical damage was in the ventrolateral region of the occipital cortex, an area that can be seen as the human homologue of the ventral stream. The primary visual cortex, however, seemed to be largely intact. D.F. showed poor perception of shape and orientation, while having relatively intact basic visual abilities (Milner et al., 1991). Despite these deficits, she performed normally if she was asked for motor actions that required her to take into account the shape or orientation of objects. For example, Goodale et al. (1991) showed that D.F. was not able to report the orientation of a slot verbally or by manually orienting a card to match its direction (cf. Milner et al., 1991). However, she was able to reach out and place her hand (or a hand-held card) in the slot. These data are the cornerstone of the action versus perception hypothesis. The idea is that input to the ventral stream (and thus perception) is impaired, whereas the primary visual cortex is still able to convey information to the dorsal stream (and the motor system).

There are caveats to this conclusion: The diffuse nature of the brain damage of D.F. requires some caution in drawing strong conclusions. Plasticity and learning might have changed the pattern of deficits such that straightforward interpretations can be problematic. Finally, a dissociation between perception and action is not the only possible cause for the pattern of deficits in D.F. For example, the deficits could also be caused by a damage to one of two output systems that both use the same representation of object size (cf. Smeets & Brenner, 1995).

It would provide strong support for the theory if one found a dissociation between perception and action in the healthy visual system. In fact, this is a necessary condition because Milner and Goodale (1995) assumed that the two streams create different representations of an object as a result of different output requirements for motor acts and visual perception. If the output behavior does not reflect a difference in the representations, then the assumed cause for the existence of the two systems is in doubt. Some studies seemed to provide evidence for a dissociation between pointing movements and perception (cf. Bridgeman et al., 1979; Bridgeman, Peery, & Anand, 1997; Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996). However, this issue is under review because of serious questions of method (cf. Post & Welch, 1996; Smeets & Brenner, 1995).

The original finding of Aglioti et al. (1995) was interpreted to suggest that there is hardly any influence of visual illusions on grasping, as indicated by the title of the study, "Size–Contrast Illusions Deceive the Eye but Not the Hand." This conclusion fits the action versus perception hypothesis. The action system should work in egocentric coordinates and should represent a grasp object relative to the hand, independent of other objects. Because visual illusions such as the Ebbinghaus illusion are created by special arrangements of objects, the theory predicts that the motor system should hardly be deceived by the illusion, and this is what Aglioti et al. (1995) found.

On the basis of the evidence presented here, we think this strong claim should be questioned. This challenges the action versus perception hypothesis, but our findings do not necessarily disprove the hypothesis. The idea of two distinct systems for perception and action could be sustained if visual illusions are relatively early phenomena created before the two systems separate. Future research might reveal whether this is a feasible assumption. However, there is evidence suggesting that visual illusions (and especially the Ebbinghaus illusion) are dependent on higher cognitive functions (e.g., Coren & Enns, 1993; Deni & Brigner, 1997; Zanuttini, Zavagno, & Agostini, 1996), which casts doubt on this proviso.

Our results suggest directions for future research. There is a need to discriminate between unipolar and bipolar measures. We call perceptual measures that rely on a comparison between two simuli (the target and the comparison stimulus) *bipolar,* because two sizes have to be computed to perform the task. In bipolar measures, both the target stimulus and the comparison stimulus can be affected by the illusion context. This can lead to ambiguous measures of the perceptual illusion. Therefore, we used size estimation as a unipolar perceptual measure because only one size (the size of the target) has to be computed. We think that such unipolar perceptual measures are more adequate for comparison with grasping.

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Appendix A

Perceptual Illusion Versus Motor Illusion

In this Appendix we derive from our explicit version of the common representation model the two relationships between perceptual illusion and motor illusion, which are expressed in the Equations 1 and 2 of the introduction.

Figure 2 shows the explicit version of the common representation model. The model is fully linear, an assumption that is justified by the fact that both the perceptual measure and the MPA are linearly related to object size. We assume that an internal estimate (I) of object size (S) is affected by the illusion:

$$I(S, k) = b_{SI}(k) \times S + a_{SI}(k),$$

where $k = 1, 2$ stands for two versions of the illusion that are going to be compared. We do not need any further assumptions, except for the trivial assumption that the slopes differ from zero: $b_{SI}(k) \neq 0$; $k = 1, 2$.

The linear functions that relate the internal estimate to the perceptual measure (P) and to grasping (G) are assumed to be unaffected by the illusion:

$$P(I) = b_{IP} \times I + a_{IP}$$

and

$$G(I) = b_{IG} \times I + a_{IG}.$$

Again, we set $b_{IP} \neq 0$ and $b_{IG} \neq 0$. Simple calculations yield the differences between the two illusion versions:

$$\Delta_G(S) = G(I(S, 2)) - G(I(S, 1)) = b_{IG} \times (I(S, 2) - I(S, 1))$$

and

$$\Delta_P(S) = P(I(S, 2)) - P(I(S, 1)) = b_{IP} \times (I(S, 2) - I(S, 1)).$$

Combining the two equations yields

$$\Delta_G(S) = \frac{b_{IG}}{b_{IP}} \times \Delta_P(S).$$

In the following we relate the fraction b_{IG}/b_{IP} to the perceptual measure and to grasping. Both are linear functions of object size:

$$\begin{aligned} G(S, k) = G(I(S, k)) &= b_{SI}(k) \times b_{IG} \times S + a_{SI}(k) \times b_{IG} + a_{IG} \\ &=: b_G(k) \times S + a_G(k) \end{aligned}$$

and

$$\begin{aligned} P(S, k) = P(I(S, k)) &= b_{SI}(k) \times b_{IP} \times S + a_{SI}(k) \times b_{IP} + a_{IP} \\ &=: b_P(k) \times S + a_P(k). \end{aligned}$$

The slopes of these functions are $b_P(k) = b_{SI}(k) \times b_{IP}$ and $b_G(k) = b_{SI}(k) \times b_{IG}$. Dividing $b_G(k)$ by $b_P(k)$ gives

$$\frac{b_G(k)}{b_P(k)} = \frac{b_{SI}(k) \times b_{IG}}{b_{SI}(k) \times b_{IP}} = \frac{b_{IG}}{b_{IP}}.$$

Note that the model predicts for all illusion conditions k a constant value of $b_G(k)/b_P(k)$. (The data of this study as well as the data of Franz et al., 2000, conform to this prediction.) Using this relationship we get Equation 1 in the text:

$$\Delta_G(S) = f \times \Delta_P(S),$$

with

$$f = \frac{b_G(k)}{b_P(k)}.$$

If $b_G(k)$ and $b_P(k)$ are equal, this simplifies to Equation 2 in the text:

$$\Delta_G(S) = \Delta_P(S).$$

To obtain a single measure for the illusion effect, we used the mean illusion effect, averaged across all sizes. Because of the linear relationships of the model, this is equal to the illusion effect for the mean size:

$$\begin{aligned} \frac{1}{n}\sum_{i=1}^{n} \Delta_P(S_i) &= \frac{1}{n}\sum_{i=1}^{n} P(S_i, 2) - P(S_i, 1) \\ &= \frac{1}{n}\sum_{i=1}^{n} b_P(2) \times S_i + a_P(2) - b_P(1) \times S_i - a_P(1) \\ &= b_P(2) \times \frac{1}{n}\sum_{i=1}^{n} S_i + a_P(2) - b_P(1) \times \frac{1}{n}\sum_{i=1}^{n} S_i - a_P(1) \\ &= b_P(2) \times \bar{S} + a_P(2) - b_P(1) \times \bar{S} - a_P(1) \\ &= P(\bar{S}, 2) - P(\bar{S}, 1) \\ &= \Delta_P(\bar{S}). \end{aligned}$$

The calculation for $\Delta_G(\bar{S})$ is analogous. For simplicity of notation we renamed the mean illusions effects to Δ_P and Δ_G throughout this article:

$$\Delta_P := \Delta_P(\bar{S})$$

and

$$\Delta_G := \Delta_G(\bar{S}).$$

(*Appendixes continue*)

Appendix B

The Idealized Expected Correlation

The common representation model allows an idealized prediction of the across-subjects correlation between the motor illusion and the perceptual illusion. We assume for simplification that the perceptual measure of the illusion (Δ_P) is noise-free. That is, we assume that all variation in Δ_P reflects differences in the internal size estimates across participants and that there is no noise added in the transformation from internal size estimate to the perceptual measure. This is a strongly idealized assumption. However, it helps estimate the statistical power of our studies because it yields a larger expected value than if we took into account the noise in the perceptual system. If we find that the power is insufficient to detect the IEC, we cannot expect to detect any actual correlation.

A second assumption is related to the noise in the motor system. To account for the larger variation in grasping than in the perceptual measure, we assume additional noise in the transformation from internal size estimate to grasping. Using Equation 2 in the introduction, we set

$$\Delta_G = \Delta_P + N,$$

with Δ_P and Δ_G being random variables describing the mean perceptual effect and the mean grasping effect of the illusion for each participant individually. N reflects the added motor noise, which is assumed to be uncorrelated to the perceptual effect: $Cov(\Delta_P, N) = 0$. The covariance of Δ_P and Δ_G is

$$Cov(\Delta_P, \Delta_G) = E(\Delta_P \times \Delta_G) - E(\Delta_P) \times E(\Delta_G).$$

Replacing Δ_G with $\Delta_P + N$ gives

$$\begin{aligned} Cov(\Delta_P, \Delta_G) &= E(\Delta_P \times (\Delta_P + N)) - E(\Delta_P) \times E(\Delta_P + N) \\ &= E(\Delta_P^2) - E^2(\Delta_P) + E(\Delta_P \times N) - E(\Delta_P) \times E(N). \end{aligned}$$

To simplify this expression, we use the equations $\sigma_A^2 = E(A^2) - E^2(A)$ and $\sigma_{A,B} = E(A \times B) - E(A) \times E(B)$, which are true for any random variables A and B. We get

$$Cov(\Delta_P, \Delta_G) = \sigma_{\Delta_P}^2 + Cov(\Delta_P, N).$$

We assume $Cov(\Delta_P, N)$ to be zero. This gives

$$Cov(\Delta_P, \Delta_G) = \sigma_{\Delta_P}^2.$$

Using this equation we can calculate the IEC:

$$\text{IEC} = \frac{Cov(\Delta_P, \Delta_G)}{\sigma_{\Delta_P} \times \sigma_{\Delta_G}} = \frac{\sigma_{\Delta_P}^2}{\sigma_{\Delta_P} \times \sigma_{\Delta_G}} = \frac{\sigma_{\Delta_P}}{\sigma_{\Delta_G}}.$$

This is Equation 3, which we used in the introduction.

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