



Registered report

The functional subdivision of the visual brain: Is there a real illusion effect on action? A multi-lab replication study



Karl K. Kopiske ^{a,f,*}, Nicola Bruno ^b, Constanze Hesse ^c,
Thomas Schenk ^d and Volker H. Franz ^{a,e}

^a University of Hamburg, Department of Psychology, Hamburg, Germany

^b Dipartimento di Neuroscienze, Università di Parma, Unità di Psicologia, Parma, Italy

^c University of Aberdeen, School of Psychology, Kings College, Old Aberdeen, United Kingdom

^d Ludwig-Maximilians Universität München, Department of Psychology, Munich, Germany

^e University of Tübingen, Department of Computer Science, Experimental Cognitive Science, Tübingen, Germany

^f Center for Neuroscience and Cognitive Systems@UniTn, Istituto Italiano di Tecnologia (IIT), Rovereto, TN, Italy

ARTICLE INFO

Article history:

Protocol Received 11 March 2014

Protocol Accepted 02 September 2014

Received 29 September 2015

Reviewed 12 December 2015

Revised 10 February 2016

Accepted 14 March 2016

Action editor Rob McIntosh

Published online 6 April 2016

Keywords:

Action perception

Visual processing

Illusions

Grasping

Manual size estimation

ABSTRACT

It has often been suggested that visual illusions affect perception but not actions such as grasping, as predicted by the “two-visual-systems” hypothesis of Milner and Goodale (1995, *The Visual Brain in Action*, Oxford University press). However, at least for the Ebbinghaus illusion, relevant studies seem to reveal a consistent illusion effect on grasping (Franz & Gegenfurtner, 2008. Grasping visual illusions: consistent data and no dissociation. *Cognitive Neuropsychology*). Two interpretations are possible: either grasping is not immune to illusions (arguing against dissociable processing mechanisms for vision-for-perception and vision-for-action), or some other factors modulate grasping in ways that mimic a vision-for-perception effect in actions. It has been suggested that one such factor may be obstacle avoidance (Haffenden Schiff & Goodale, 2001. The dissociation between perception and action in the Ebbinghaus illusion: nonillusory effects of pictorial cues on grasp. *Current Biology*, 11, 177–181). In four different labs (total $N = 144$), we conducted an exact replication of previous studies suggesting obstacle avoidance mechanisms, implementing conditions that tested grasping as well as multiple perceptual tasks. This replication was supplemented by additional conditions to obtain more conclusive results. Our results confirm that grasping is affected by the Ebbinghaus illusion and demonstrate that this effect cannot be explained by obstacle avoidance.

© 2016 Elsevier Ltd. All rights reserved.

* Corresponding author. Center for Neuroscience and Cognitive Systems@UniTn, Istituto Italiano di Tecnologia, Corso Bettini, 31, 38068 Rovereto, TN, Italy.

E-mail addresses: karl.kopiske@iit.it (K.K. Kopiske), nicola.bruno@unipr.it (N. Bruno), c.hesse@abdn.ac.uk (C. Hesse), thomas.schenk@psy.lmu.de (T. Schenk), volker.franz@uni-tuebingen.de (V.H. Franz).

<http://dx.doi.org/10.1016/j.cortex.2016.03.020>

0010-9452/© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

1.1. Visual illusions and the two-visual-streams hypothesis (TVSH)

Current theories on the fundamental architecture of the primate brain suggest that there are two functionally and anatomically distinct cortical processing routes for visual information: the dorsal vision-for-action route and the ventral vision-for-perception route. This two-visual-streams hypothesis (TVSH, Goodale & Milner, 1992; Milner & Goodale, 1995, 2006, 2008) is supported by multiple lines of evidence, including evidence from neuropsychology (e.g., action perception-double dissociations after brain damage) and from psychophysics (e.g., action-perception double dissociations in healthy participants responding to visual illusions). Neuropsychological evidence has come from patients with blindsight (Weiskrantz, 1990), optic ataxia (Milner et al., 2001), as well as visual form agnosia (Goodale & Milner, 1992; Goodale, Milner, Jakobson, & Carey, 1991). However, there is an ongoing debate on the question to which degree the neuropsychological data support the TVSH (Milner, Ganel, & Goodale, 2012; Milner & Goodale, 2008; Whitwell, Milner, Cavina-Pratesi, Byrne, & Goodale, 2014), or allow for alternative interpretations (Himmelbach, Boehme, & Karnath, 2012; Schenk, 2006, 2010, 2012). For recent reviews, see Schenk, Franz, and Bruno (2011), Schenk and McIntosh (2010), and Westwood and Goodale (2011). This debate suggests that patient studies may not provide conclusive evidence for the TVSH, so that evidence from healthy participants becomes especially important.

Aglioti, DeSouza, and Goodale (1995) conducted a seminal study that is often cited as key evidence that the TVSH also holds for healthy human observers. In this study they investigated how perception and action are affected by size contrast illusions (i.e., the Ebbinghaus or Titchner illusion). In this illusion, a central disc is surrounded by larger (or smaller) context circles, which creates a size-contrast illusion, meaning that the central disc is perceived as being smaller (or larger) than without context circles. Aglioti et al. (1995) found that this illusion only affected the perceptual judgements of the central disc, but not the maximum grip aperture (MGA) when grasping the central disc. They argued that this dissociation between perceptual and visuomotor tasks is best explained by assuming that the Ebbinghaus illusion is generated in the vision-for-perception stream, whereas the vision-for-action stream processes size independent of the context. They further suggested that, when performing an action such as grasping, our vision-for-action stream calculates a veridical and metrically accurate representation of the target object that is not accessible to our perceptual awareness. This notion has been dubbed a “motoric zombie” (Ramachandran & Blakeslee, 1999). In consequence, the perception-action dissociation as observed in the Ebbinghaus illusion was considered a strong argument in support of the TVSH (Carey, 2001).

However, since then other researchers have reported different results based on which they have argued that the effect of Ebbinghaus illusion displays on grasping may be comparable to the effects observed in perceptual tasks (Franz,

Gegenfurtner, Bülthoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999). This seems contradictory at first sight, but a closer look at the data across different illusion studies suggests that the findings are relatively consistent. In summary, the two key findings are that (a) perceptual measures show large differences between illusion effects (see Fig. 1a), and (b) grasping shows a consistent illusion display effect across all studies (see Fig. 1b). We will first discuss (a) and then (b). Furthermore, we will argue that after careful analysis, the dissociation between perceptual measures and grasping disappears (Franz & Gegenfurtner, 2008).

1.2. Illusion effects on perception

The question of why perceptual measures yield such inconsistent effects was investigated in several studies by Franz and colleagues (for a review, see Franz & Gegenfurtner, 2008). In a nutshell, their main argument was that perceptual measures have varying response functions. Most importantly, manual size estimation (ME), which has been used in many studies, has been shown to differ from most other measures (see Franz, 2003). When performing ME, participants indicate the size of an object using their index finger and thumb. Proponents of the TVSH have interpreted this as a ‘manual “read-out” of what participants perceive’ (Haffenden & Goodale, 1998, p. 125), i.e., a form of cross-modal matching (Stevens, 1959). In consequence, ME has been widely used in studies on perception-action dissociations.

However, ME will typically exaggerate a physical change of object size. For example, in the study by Haffenden and Goodale (1998), a physical increase in object size of 1 mm led to an increase of app. 1.6 mm in ME. We can therefore expect that an illusory increase in object size of 1 mm would also result in a 1.6 mm (and not 1 mm) increase in ME. This is different from more classic perceptual measures such as a size adjustment task in which a physical increase in object size of 1 mm typically also leads to app. 1 mm increase in a size adjustment task (Franz, 2003). In consequence, we cannot interpret raw illusion effects found in a ME¹-task. We first have to correct ME for the steeper response function. Because ME depends linearly on object size, the correction can be done by simply dividing the measured illusion effect by the slope of the response function (this corresponds to a calibration in metrology, see also Bruno & Franz, 2009; Franz, Fahle, Bülthoff, & Gegenfurtner, 2001; Franz, Scharnowski, & Gegenfurtner, 2005; Glover & Dixon, 2002; Schenk et al., 2011 for details). Although correction may not be as necessary for other measures, as the slopes of their response functions are typically closer to one, we nevertheless performed such a correction for all measures (for a detailed discussion of when calibration is necessary and when it is optional, see Franz et al., 2001). Once the correction is performed, the

¹ It should be noted that ME does not always seem to exaggerate a physical change of size. If ME is performed closed-loop such that the hand is seen all the time the exaggeration seems to vanish. For an example, see de Grave et al. (2005). Because this has not been investigated systematically, we include two ME conditions in our experiment: One open-loop and one closed-loop.

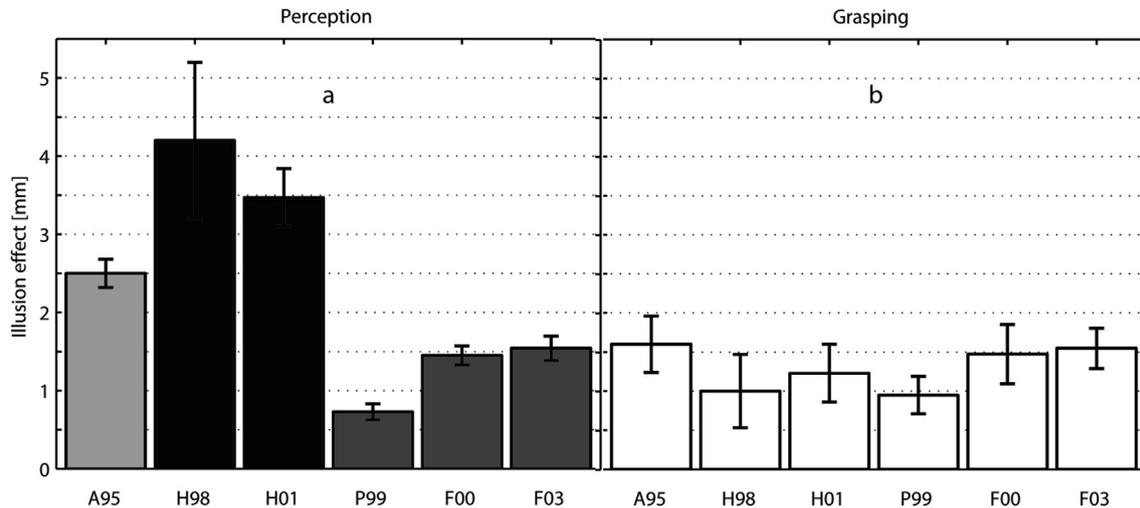


Fig. 1 – Results of previous studies on the Ebbinghaus/Titchener illusion with configurations identical to the original study by Aglioti et al. (1995): (a) Illusion effects on perceptual measures. These are colour-coded as black: Manual size estimation (ME) (open-loop). Dark grey: Perceptual comparison of a central target disc surrounded by illusion inducing circles to a neutral comparison element; light grey: Perceptual comparison of a central target disc surrounded by small illusion inducing circles to another central target disc surrounded by large illusion inducing circles, as used by Aglioti et al. (1995). This method was criticised by Franz et al. (2000) because it overestimates the relevant part of the illusion for grasping by app. 50%. It was therefore not used by subsequent studies and hence we will not discuss this measure in further detail here. (b) Illusion display effects on MGA in grasping. A95: Aglioti et al. (1995), H98: Haffenden and Goodale (1998), H01: Haffenden, Schiff, and Goodale (2001), P99: Pavani et al. (1999), F00 and F03: Franz et al. (2000; 2003). Error bars depict the SEM of the illusion effect.

perceptual effects become very consistent and can now be compared to the (equally consistent) illusion display effects on grasping (Franz & Gegenfurtner, 2008).

1.3. Illusion effects on grasping

For the Ebbinghaus illusion, reported effects on grasping range from not significantly different from 0 (e.g., Haffenden & Goodale, 1998) to significantly different from 0, but still smaller than the perceptual effect (e.g., Aglioti et al., 1995; Glover & Dixon, 2002) to significantly different from 0 and comparable to the perceptual effect (e.g., Franz et al., 2000; Pavani et al., 1999). However, unlike the perceptual effects discussed above (see Fig. 1a), the absolute size of the motor effect has not varied much between studies (Fig. 1b). This gives a very consistent picture of the effect of illusion displays on grasping. Since grasping shows a response function slope that is similar to the slopes found for classic perceptual measures, we can compare the raw illusion display effects between these measures.² Visual inspection shows that while statistical significance varies, these illusion display effects are actually quite

² More specifically: Grasping has been found to have a response function slope of app. .82 (Smeets & Brenner, 1999). If we perform the correction discussed above, the raw illusion display effects will be multiplied by roughly $1/.82 = 1.22$, to result in the corrected illusion effects. For classic perceptual measures the correction has hardly any effect (slope is close to 1), such that overall the match between perceptual illusion and grasping illusion is even better if we perform the correction. This better comparison was done in the present study but is omitted for the sake of brevity here.

similar in size between studies (Fig. 1b; see also Franz, 2003 and Franz & Gegenfurtner, 2008). In conclusion, it seems that the effects of the Ebbinghaus illusion displays on grasping might be very similar to the observed perceptual effects. However, the cause of the effect on grasping has been much debated.

1.4. Why do Ebbinghaus displays influence grasping?

If it was true that the Ebbinghaus illusion affects perception and action similarly, then this would directly contradict the notion of Aglioti et al. (1995) that grasping is immune to the Ebbinghaus illusion as predicted by the TVSH. However, this conclusion may be premature for two reasons.

First, Goodale (2008) suggested that some studies have measured grasping in ways that are so intrusive that the movement becomes awkward (Gonzalez, Ganel, & Goodale, 2006; Gonzalez, Ganel, Whitwell, Morrissey, & Goodale, 2008). According to the TVSH, awkward movements are controlled by the vision-for-perception system and therefore it would be no surprise that those studies found illusion display effects on grasping. Although this argument has been tested and refuted (Franz, Hesse, & Kollath, 2009), we took great care in our study to measure grasping in exactly the same way as done in the original study of Aglioti et al. (1995) such that this concern cannot apply.

Second, Haffenden and Goodale (2000) argued that in the Ebbinghaus display used by all studies in this field (starting with the first study by Aglioti et al., 1995 and as used in all the studies in Fig. 1), the context circles caused unexpected motor effects on grasping. Specifically, they argued that, even

though these motor effects look like illusion effects, they are in fact unrelated. Data supporting this notion was provided in a subsequent study (Haffenden et al., 2001). The main idea of Haffenden et al. (2001; Haffenden & Goodale, 2000) is that in some conditions the context circles of the Ebbinghaus display are treated as obstacles by the vision-for-action system. Such an obstacle avoidance effect may look like a perceptual effect, but would in fact be a motor effect. If obstacle avoidance can indeed explain the effects of Ebbinghaus displays on grasping, then the finding that grasping is affected by the illusion could be reconciled with the TVSH. There is, however, some contradictory data on this topic (Franz, Bühlhoff, & Fahle, 2003; Franz et al., 2001; Haffenden & Goodale, 1998; Pavani et al., 1999). In the following section, we will discuss the suggestion that obstacle avoidance may be the cause of illusion effects on grasping in more detail.

1.5. Can obstacle avoidance explain the effects of the Ebbinghaus display on grasping?

According to the obstacle avoidance hypothesis by Haffenden and Goodale (2000), the traditional distance between the target and the large context circles (approx. 9.5...14 mm in Aglioti et al., 1995, and Haffenden & Goodale, 1998) is just big enough for participants to fit their fingers between the annulus and the target, which reduces the in-flight aperture size. Conversely, the traditional distance between the targets and the small context circles (approx. 2...5 mm) is assumed to be not big enough to fit the fingers in between. As a consequence, participants tend to adjust their aperture size to fit around the whole stimulus, including annulus (see Fig. 2 for details). Thus, according to the obstacle avoidance hypothesis, the size of the MGA in grasping for Ebbinghaus illusion displays depends on annulus distance, rather than context circle size.

Haffenden et al. (2001) tested the obstacle avoidance hypothesis by comparing three grasp responses: targets surrounded by small context circles that were far away (Fig. 3: *small-far*), targets surrounded by the traditional small-context configuration (Fig. 3: *small-near*), and the traditional large-context configuration (Fig. 3: *large-far*). They found that the small-far responses were markedly different from small-near responses, but almost identical to large-far responses, which

is precisely what the obstacle avoidance hypothesis would predict.

Franz et al. (2003) repeated the study by Haffenden et al. (2001) and added another condition (*large-near*: large context circles, small distance; see Fig. 3). In this study, they found that participants grasped smaller in conditions with large context circles than in conditions with small context circles, regardless of context circle distance, contradicting the predictions of the obstacle avoidance account. Instead, the effects on grasping followed the same pattern as the perceptual effects. In conclusion, two studies (Franz et al., 2003; Haffenden et al., 2001) obtained opposite results using the same conditions. Importantly, this is the only case of obvious data inconsistency in the visual illusions and grasping literature on the Ebbinghaus illusion. Proponents of the obstacle avoidance account argue that the results of Haffenden et al. (2001) are more in line with results from other studies (Goodale, 2008; Westwood & Goodale, 2011), while sceptics argue that the study by Franz et al. (2003) had more statistical power due to a larger sample size, as well as clearer predictions due to an additional illusion condition (Franz & Gegenfurtner, 2008; Schenk et al., 2011).

Another study that tested the notion of whether obstacle avoidance may influence grasping in Ebbinghaus displays in a slightly different way was conducted by de Grave, Biegstraaten, Smeets, and Brenner (2005). They rotated the 2D context elements of Ebbinghaus figures to manipulate the extent to which the context elements might be perceived as blocking the path between the fingers and the object during a grasping movement and thereby manipulating the extent to which the context elements might act as obstacles. The authors found an effect of context element size on MGA, consistent with an illusion effect on grasping. They also found effects of context element rotation on several grasping parameters (grip orientation, final grip aperture), suggesting that context elements affect grasping movements in several other ways than just by altering perceived size. However, they did not find an effect of context circle rotation on MGA (Fig. 5c of de Grave et al., 2005). This is important, as MGA is the critical dependent variable which has been used in all studies to test for illusion effects on grasping. Moreover, the obstacle avoidance hypothesis has been specifically suggested by

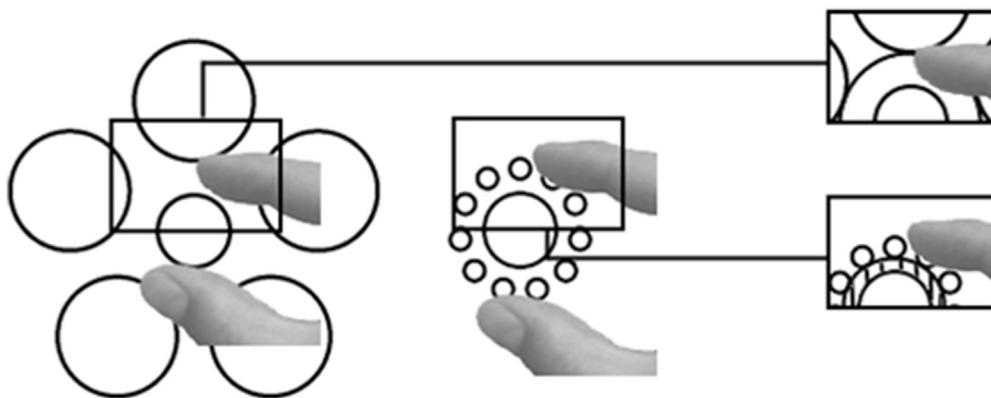


Fig. 2 – Obstacle avoidance as proposed by Haffenden and Goodale (2000) and Haffenden et al. (2001): The gap between the target and the large context circles (left) is just large enough to fit fingers in. Conversely, the gap between the target and the small context circles (right) is assumed to be too small to fit the fingers in and thereby causes a larger grip aperture.

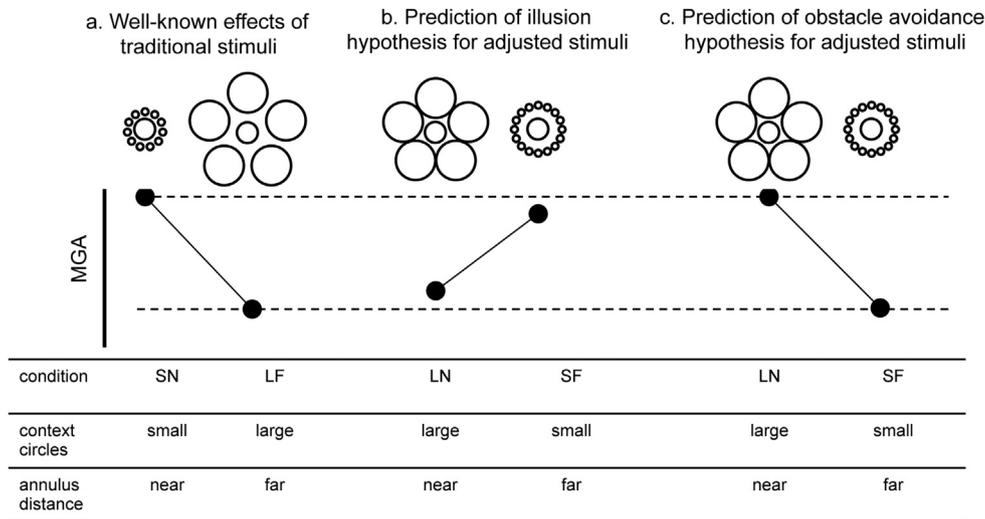


Fig. 3 – Stimuli and predictions of our study by context circle size and distance: small-near (SN), small-far (SF), large-near (LN), large-far (LF). (a) Traditional Ebbinghaus configurations create a known effect: larger grasping (MGA) in the SN condition than in the LF condition. This can be explained either by a single mechanism creating the illusion in grasping and in perception (illusion effect hypothesis: IEH) or by an obstacle avoidance mechanism operating independently of the perceptual illusion in grasping (obstacle avoidance hypothesis). We used a new set of conditions with oppositional predictions for the competing hypothesis: (b) According to the IEH, varying the distance and size of the context circles should have similar effects on grasping and on perception: large context circles lead to a smaller perceived size of the central circle. Larger context circle distance also leads to a slightly smaller perceived size (cf. the quantitative model of Roberts, Harris, & Yates, 2005,³). (c) According to the obstacle avoidance hypothesis, the gap between context circles and central circle is the critical parameter for grasping, not the size of the context circles. Consequently, a small gap should always lead to a large MGA, independent of the size of the context circles (compare SN and LN conditions), because the gap is too small to fit the fingers in. A larger gap, about finger-width, should lead to relatively small MGA due to finger-fitting, again independent of the size of the context circles (compare SF and LF conditions). Note the opposite pattern of predictions in (b) and (c).

Haffenden and Goodale (2000) to account for the illusion effect on MGA that was found in some studies. Given the fact that de Grave et al. (2005) did not find an effect of context-rotation on MGA, their results cannot be used to support the Haffenden and Goodale (2000) claim that obstacle avoidance processes account for illusion effects in grasping.

To summarise: according to de Grave et al. (2005) there are obstacle avoidance effects of context elements on certain grasping parameters, but not on MGA. Therefore, the question of whether obstacle avoidance can reconcile the TVSH with the effects of Ebbinghaus displays on grasping remains unresolved. At the core of this issue is an inconsistency in the empirical data (Franz et al., 2003; Haffenden et al., 2001). Resolving this issue is the main goal of our study.

³ For our figure, we fit the data from Franz et al. (2003) to the decay function proposed by Roberts et al. (2005): Illusion magnitude in mm = $-.07883 + .37616 \exp(-x/2.3076)$, where x = distance (in mm) from center of target to center of inducers. Plotted are the best linear fits. For large context circles: Illusion magnitude = $.02527 + 2.0983 \cdot f(x)$, small context circles: illusion magnitude = $.2004 + 2.1475 \cdot f(x)$. Note that there is a typing error in the published version of the original model, as it says $-.7883$ for parameter a , instead of $-.07883$. This being a typing error has been confirmed by Brian Roberts and Mike Harris (personal communication, January 10, 2014).

1.6. How to test for a dissociation: the issue of perceptually matched stimuli

Testing for a dissociation between perception and grasping requires comparing the effects of the illusion on different dependent variables. This is not trivial and is somewhat unusual. Illusion studies have employed three approaches to solve this problem (of which we employed the first two in our study).

The most common approach is to use different illusion displays and keep the physical size of the target object constant (“physically-matched condition”). The illusion effect is calculated by subtracting responses to the two different illusion configurations with the same target size (cf. Fig. 1). Although simple and straightforward, this approach has one major drawback: since the TVSH predicts grasping to be unaffected by the illusion, it predicts a null-effect (H0), which raises the problem of how to argue in favour of a statistical null-hypothesis (Westwood & Goodale, 2011; but see Schenk et al., 2011; Schenk & McIntosh, 2010). Some remedies can be used to tackle this issue, such as the use of Bayes factors or methods that test the predictions of the TVSH as the alternative hypothesis (H1). A prominent method to achieve the latter is described in the following paragraph and was employed together with Bayes factors and the physically-matched condition in our study.

To create a situation in which the TVSH predicts the H1 and not the H0, some studies (Aglioti et al., 1995; Haffenden &

Goodale, 1998) used a perceptual nulling method. Perceptual nulling is done by selecting two targets that look perceptually equal when embedded in different illusion configurations, although they differ in physical size (“perceptually-matched condition”). Because the TVSH assumes grasping to be veridical, it should follow the physical size of the targets such that the TVSH now predicts an effect (H1) between conditions with different context circles, while the IEH predicts a null-effect. Therefore, Westwood and Goodale (2011) argued that this nulling procedure provides a better test of the TVSH. Nevertheless, it also has its drawbacks: (a) because physical size and illusion are confounded it is difficult to quantify the illusion display effect if there is some effect on grasping that needs to be compared quantitatively to the perceptual effect, and (b) matching two targets in figure-surround configurations to be perceptually equal is in principle very difficult to do, especially when the surrounds have opposite effects (incremental vs decremental). For an example from lightness perception, see Jandó, Agostini, Galmonte, and Bruno (2003). In practice, this presents even more of a problem since the physical size of stimuli will always increase in steps, rather than continuously (e.g., Aglioti et al. 1995 used step-sizes of 1 mm, which may be too coarse for a good perceptual match). To partially account for this issue, we used smaller step sizes of .25 mm and also tested for the consistency of the perceptual matching by running the same perceptual tasks on the selected pair of matched stimuli, thereby providing additional information about the quality of the perceptual match.

Ganel, Tanzer, and Goodale (2008) took the nulling paradigm one step further in a study on the Ponzo illusion by creating opposing predictions for TVSH and IEH. Starting with perceptually-matched stimuli, reducing the size of the physically larger stimulus will make it appear perceptually smaller, such that TVSH and IEH predict opposite effects on grasping: the TVSH predicts the physically larger object to still be grasped with larger apertures (because TVSH assumes no effect of the illusion on grasping), while the IEH predicts smaller grip apertures for this object (because IEH assumes grasping to follow perception).⁴ However, a problem arises when neither hypothesis’ “strong” version is true, i.e., when there is a partial dissociation between perception and action: then, if the physical change in size is larger than the difference between the illusion effect in perception and in grasping, the results will seem to support the IEH; if it is

⁴ Ganel et al. (2008) found opposite effects on grasping and perception for the Ponzo illusion. They made use of the fact that placing objects in contrasting illusory contexts can create a situation where the physically smaller object is perceived as being bigger than the physically larger one. Nevertheless, the obtained MGAs were larger for the physically larger (but perceptually smaller) object and smaller for the physically smaller (but perceptually larger) one. Discussion whether this result for the Ponzo illusion constitutes evidence for the TVSH independent of data from the Ebbinghaus illusion, would go beyond the scope of this article. Such a discussion would need to resolve questions similar to those discussed for the Ebbinghaus illusion. This includes issues such as whether the task-demands were well matched, whether tasks should be performed in an open or closed-loop fashion, and whether the Ponzo illusion arises before or after the dorsal-ventral split (Murray, Boyaci, & Kersten, 2006).

smaller, the TVSH seems to be supported. While this allows for an upper (or lower) bound of the effect on grasping, this method suffers from the same problems mentioned above: the illusion effects are difficult to quantify due to the confounding of illusion size and physical size and the accuracy of the method is limited by the step size of the targets. In fact, the opposite effects procedure is equivalent to the nulling procedure used by Aglioti et al. (1995): whenever nulling works as proposed by the TVSH, it is possible to create an opposite effect situation, and whenever an opposite effect situation works as proposed by the TVSH, it is possible to create a nulling situation. In our study, we therefore decided to employ physically-matched conditions as well as perceptually-matched conditions to cover and compare the validity of the most widely used methods.

1.7. The present study

In the present study, we studied grasping movements using Ebbinghaus illusion displays to investigate whether or not actions are immune to visual illusions. We know of no study that has tried to account for all points of criticism and to identify the factors that may have led to the conflicting results regarding the obstacle avoidance account. This makes it difficult to interpret the studies in question (as shown in Fig. 1) which constitute key evidence in the debate about the TVSH. To solve this issue, we replicated the study by Haffenden et al. (2001) and investigated existing data inconsistencies to test the obstacle avoidance hypothesis. We also introduced some additional conditions to better generalise to grasping overall. Specifically, we aimed to assess to what extent Ebbinghaus illusion displays affect grasping and whether the possible effects can be attributed to a size contrast illusion or an obstacle avoidance strategy. Our main dependent variable was MGA. Additionally, we report the relative time to MGA, as it has been proposed that the presence of obstacles would result in a relatively earlier MGA (Smeets & Brenner, 1999; Smeets, Glover, & Brenner, 2003) and that MGA alone may not be sufficient to investigate the influence of visual illusions on grasping (Smeets & Brenner, 2006). An effect of visual illusions on MGA would then have to be explained in terms of not just size perception, but other grasping parameters as well.

This study includes a direct replication of the studies by Haffenden et al. (2001) and Franz et al. (2003), the only studies for which we identified contradictory results on effects of the Ebbinghaus illusion and obstacle avoidance on grasping. Hence, our stimuli were identical to those used by Haffenden et al. (2001) and Franz et al. (2003). We used four different conditions (see Fig. 3): the traditional Ebbinghaus conditions SN (*small context circles, annulus near target*) and LF (*large context circle, annulus far from the target*) to test the size of the illusion effect, as well as two non-traditional conditions (SF, “*small-far*” and LN, “*large-near*”), to test the proposed obstacle avoidance account. For the latter two conditions, the obstacle avoidance hypothesis and the IEH predict opposite patterns of results in grasping: the obstacle avoidance hypothesis predicts a *distance effect* (small distance → large MGA), while the IEH predicts a *context circle size effect* (small context circles → large MGA). Thus, the obstacle avoidance hypothesis predicts a larger MGA in the *large-near* and a

smaller MGA in the *small-far* condition (see Fig. 3c), while the IEH predicts the opposite pattern (Fig. 3b).

Two different procedures were used to vary the size of the central target: in one condition the physical size of the target was controlled (physically-matched), and in the other condition the perceptual size of the target was controlled (perceptually-matched). These conditions complement each other since the TVSH predicts differences in grasping in the perceptually-matched conditions but not in the physically-matched conditions, while the IEH predicts the opposite pattern.

We used three different perceptual measures: matching size perception to a graded series of stimuli (a classic perception task), ME without visual online feedback (open-loop), and ME with visual online feedback (closed-loop). We expected ME open-loop, but not the other perceptual measures to have a slope larger than one (cf. Footnote 1). Testing the variations in response functions of different perceptual tasks also provides novel information on the appropriateness of slope correction procedures as proposed by Franz (2003). Finally, by measuring the responses to “perceptually-matched” configurations in multiple perceptual measures, we also assessed the validity of the perceptual nulling procedure.

In addition to the overall size of the illusion effect, the correlation between perceptual measures and the MGA can provide information about the underlying visual representation. If grasping is guided by the same visual representation as perception, then one would predict a positive correlation between grasping and perceptual measures across participants. We tested this prediction, accounting for the fact that noisy measures predict a reduced correlation size (cf. Section 2.4).

We conducted the experiment in four different labs using exactly the same procedures and stimuli. By doing so, we obtained a precise estimate of the size of the illusion effect that combines advantages of a meta-analytical approach (large sample, multiple labs) with those of a single study (carefully controlled and comparable conditions).

We tested the following key hypotheses: (1) In the physically-matched conditions, participants grasp larger in the *large-near* condition than in the *small-far* condition (a test of the obstacle avoidance hypothesis; cf. Fig. 3). (2) In the perceptually-matched condition, participants grasp larger for the physically larger target (TVSH prediction: effect of physical size, no effect of illusory size). (3a) There is an effect of the Ebbinghaus illusion on grasping (IEH); (3b) This effect is equally strong in grasping and in perceptual measures; (3c) Across participants, the illusion effects in grasping and in perceptual measures are correlated.

2. Methods

2.1. Participants

Participants were recruited by labs from the following institutions: Università di Parma (Dipartimento di Neuroscienze – NB), University of Aberdeen (School of Psychology – CH), University of Hamburg (Department of General Psychology – KKK, VHF), University of Erlangen-Nuremberg (Department of Neurology – TS). Participants were right-handed (Edinburgh Handedness Inventory, Oldfield, 1971 – L.Q. > +47, decile R.1 or higher), had normal or corrected-to-normal eyesight, and had no history of neurological disorders. Participants' rights were protected according to the 1964 Declaration of Helsinki, and written consent was required from all participants. Ethical approval was obtained from local ethics committees.

To determine the appropriate sample size, we conducted a power analysis for an illusion display effect between two conditions as to be tested in the obstacle avoidance hypothesis (*large-near* > *small-far*; obstacle avoidance) and the IEH (*large-near* < *small-far*; illusion effect). We aggregated illusion display effects and standard deviations from previous studies (using data from a total of 6 studies and 146 participants) weighted by the number of participants to estimate Cohen's *d* (Cohen, 1988) by the formula $d = IE/SD$: $d = 1.38 \text{ mm}/1.90 \text{ mm} = .73$ (Table 1).

Since a larger distance between target and context circles might cause the target to appear smaller (Girgus, Coren, & Agdern, 1972; Roberts et al., 2005), we might expect the illusion effect in the non-traditional conditions (i.e., the difference SF–LN) to be smaller than the effect in the traditional conditions (i.e., the difference SN–LF). Considering this and some possible inter-lab variability, expecting the same effect as found in previous studies may be an overestimation. Hence, we think it is reasonable to base our calculations on an effect 70% as large as the original one of $d = .73$, as has been done in a previous power analysis for the same effect (Franz et al., 2003). Doing so would give us an effect of $d = .51$. This is close to the smallest illusion display effect observed in previous studies ($d = .50$ – Haffenden & Goodale, 1998).

We decided to aim for at least $1-\beta = 80\%$ power for each lab to ensure that data can be interpreted separately, as well as to account for possible systematic variations between labs. With an alpha-level of $\alpha = .05$, this resulted in a desired sample size of $N = 33$ for each lab. The total of $N = 132$ for all labs combined would enable us to detect an effect of $d = .28$ with $\alpha = .05$ and $\beta = .10$. To make counterbalancing easier, we tested $N = 36$ participants per lab, for a total of $N = 144$ participants. This ensured that if an illusion effect on grasping exists, we should

Table 1 – Illusion display effects on grasping found in earlier studies, as summarised by Franz and Gegenfurtner (2008).

Study	Aglioti et al. (1995)	Haffenden and Goodale (1998)	Pavani et al. (1999)	Franz et al. (2000)	Haffenden et al. (2001)	Franz et al. (2003)
Effect	1.6 mm	1.0 mm	.95 mm	1.47 mm	1.4 mm	1.55 mm
SEM	.36 mm	.47 mm	.24 mm	.38 mm	.64 mm	.26 mm
SD	1.35 mm	1.99 mm	1.00 mm	1.94 mm	2.71 mm	1.87 mm
N	14	18	18	26	18	52
<i>d</i>	1.19	.50	.95	.76	.52	.83

be able to detect it. The power analysis was conducted using the function *t*-test for difference from a constant of the program G*Power 3.1.7 (Faul, Erdfelder, Buchner, & Lang, 2009).

2.2. Stimuli

We used four different versions of the Ebbinghaus illusion. These differed in the distance between target and context circles (“near” and “far”), and size of context circles (“small” and “large”). The four resulting versions can be seen in Fig. 3. In the “near” conditions, the inner diameter of the annulus (i.e., the distance from middle point of the target circle to closest point of the context circles) was 38 mm. In the “far” conditions, the inner diameter of the annulus was 54 mm. These distances are identical to those used by Haffenden et al. (2001). In the “small” conditions, context circles were 10 mm in diameter. In the “large” conditions, context circles were 54 mm in diameter. Target discs were white plastic discs of 3 mm height and 28, 30 and 32 mm diameter. These sizes have also been used by Haffenden et al. (2001), although it should be noted that those experiments also used target discs of 31 mm diameter, which we omitted for symmetry and parsimony. This resulted in distances between the central targets and the annuli of the context circles of 3, 4 and 5 mm in the “near” conditions, 11, 12 and 13 mm in the “far” conditions. Details about measurements and distances are summarised in Table 2. Note that these values apply only for the physically-matched condition, as target sizes for the perceptually-matched condition were determined for each participant separately (see 2.4: Procedure).

2.3. Apparatus

Participants sat comfortably on a chair in front of a table. Their head was at a height of 50 cm above the table to keep the viewing distance constant and the viewing angle at about 80–90°. They were wearing PLATO liquid crystal shutter glasses (Translucent Technologies, Toronto, Ontario, Canada – Milgram, 1987) to control target visibility.

The stimulus set-up consisted of a piece of paper (A4 sized) with the context circles printed on it, laid flat on the table, such that participants viewed the targets from almost directly above (80–90°). In the physically-matched conditions, white PVC discs of 3 mm height and 28, 30 and 32 mm diameter, with a 1 mm black line drawn around the circumference, were used as target stimuli and were positioned in the middle of the context circles. These are the exact specifications of stimuli used by Haffenden and colleagues (Haffenden & Goodale,

1998; Haffenden et al., 2001–31 mm stimuli omitted), as well as Pavani and colleagues (Pavani et al., 1999–31 mm stimuli omitted, 28 mm added). In the size matching task, white circles ranging from 23 mm to 37 mm in diameter (.5 mm steps, 29 circles total) with a 1 mm line around the circumference, printed on a sheet of paper in ascending order, were used as a graded series of comparison stimuli in the size matching task. Pilot testing showed most responses to fall within this range, see Appendix B. For the perceptually-matched condition, two of 15 different discs of sizes ranging from 28 mm to 32 mm in steps of .25 mm were used.

The starting position for the participants' response hand was on the table, 20 cm from the target. For a schematic depiction of the experimental set-up, see Fig. 4. Three markers were attached to participants' right wrist, thumb, and index finger (Fig. 4a). The trajectories of the digits were recorded using appropriate motion tracking systems (see Table 3).

2.4. Procedure

There was a grasping task and three perceptual tasks: size matching, open-loop manual estimation, and closed-loop manual estimation. These tasks were presented in separate blocks. For the perceptual tasks, there were 54 trials each: 36 in the physically-matched condition (4 illusion conditions*3 target sizes*3 repetitions presented in random order) and 18 in the perceptually-matched condition. In the first perceptual task (size matching), two perceptually-matched configurations were created (SFx and LFy). They were tested the same number of times as configurations SF and LF in the physically-matched condition, which gave us an equally precise estimate of the illusion display effect. In grasping, the participants completed 90 trials (60 physically-matched: 4*3*5 + 30 perceptually-matched: 2*3*5), resulting in a total of 252 trials per participant.

The size matching task was always the first task. First, we determined for both a SF and a LF configuration which target sizes were required to create a perceptual match with a reference circle of 30.5 mm diameter (presented on a A4 sheet of paper). For both SF and LF, a 1-up, 1-down staircase procedure was conducted where participants had to indicate whether the target disc appeared to be smaller or bigger than the reference circle, using steps of .25 mm. The discs of corresponding target size were then used to create what we call the perceptually-matched SFx and LFy configuration. It is to be expected that the SFx and LFy vary between participants and that the difference between those two configurations reflects the extent to which the context influences the perceived size.

Table 2 – Sizes of and distances between the stimuli.

	Diameter of target (mm)	Number of context circles	Diameter of context circles (mm)	Inner diameter of annulus (mm)	Min. distance target – annulus (mm)
Small, near	28, 30, 32	11	10	38	5, 4, 3
Small, far	28, 30, 32	16	10	54	13, 12, 11
Large, near	28, 30, 32	5	54	38	5, 4, 3
Large, far	28, 30, 32	5	54	54	13, 12, 11

Note: Inner diameter is the diameter through the points of the context circles closest to the target. In the perceptually-matched condition, diameter of the target and minimal distance target – annulus may be different.

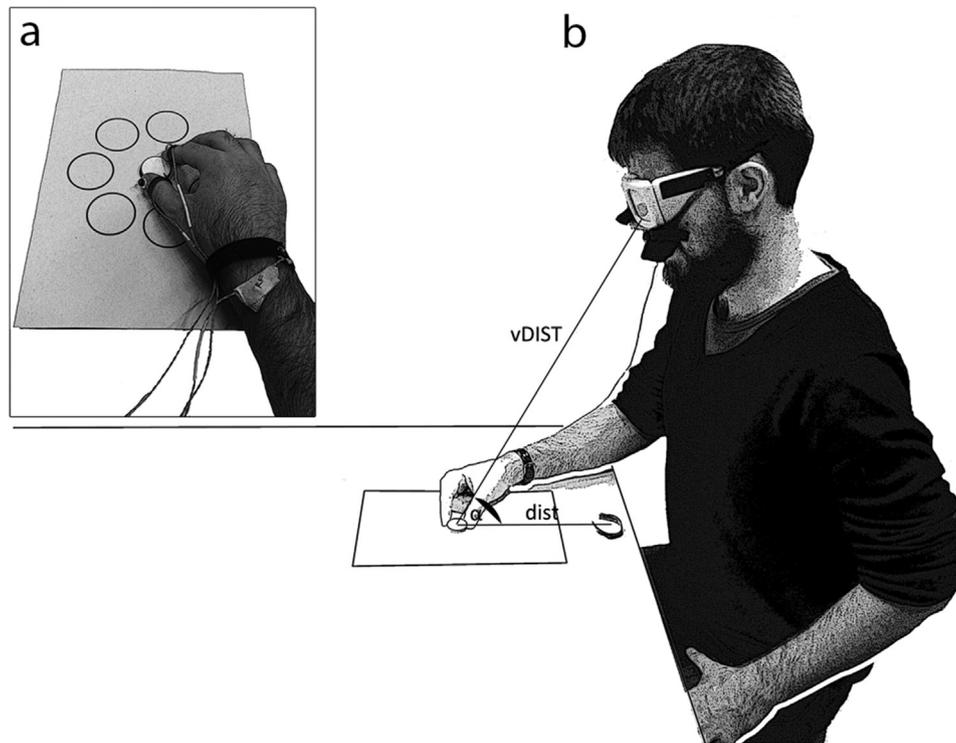


Fig. 4 – (a) Hand with three markers attached to thumb, index finger, and wrist. (b) Experimental set-up with a viewing distance ($vDIST$) of app. 50 cm, viewing angle (α) of app. 80–90°, distance ($dist$) of 20 cm between starting point and stimulus. The participant is sitting comfortably, so as not to fatigue over a large number of trials, and wearing LCD goggles with cloth blinders attached to the bottom to prevent any view below the goggles.

This means we can use this difference as a measure of the individual illusion effect. For the second component of the size-matching task, participants were presented with a target stimulus surrounded by one of the four illusion contexts (LF, LN, SF, SN), as well as an A4 sheet of paper containing a graded series of comparison circles. This was located 20 cm to the left of the target. Participants were asked to indicate verbally which comparison stimulus they perceive as equal in size to the target disc. This was done for all physically-matched (disc sizes 28, 30, 32 mm) and perceptually-matched configurations.

The *open-loop manual estimation task* started with participants resting their right hand at a starting position on the table. When they saw the stimulus, they were asked to lift their right hand and indicate the size of the target stimulus with their right thumb and index finger. They were asked to press a response button with the index finger of the left hand when they felt satisfied with their estimation. The shutter glasses closed when the right thumb or index finger had

moved 20 mm from their starting position to suppress vision. Trials that took longer than 2500 msec from opening of the shutter glasses to pressing the response button, or ended with the button pressed while the participant's thumb and index finger were still moving at more than 30 mm/sec relative to each other, were counted as errors and repeated at a random position within the same block. After this, participants were asked to grasp the target disc and lay it on the table next to the stimulus set-up. This was done to provide the same haptic feedback as in the grasping trials, as was proposed by [Haffenden and Goodale \(1998\)](#). The shutter glasses opened after the experimenter had prepared the next trial. In the *closed-loop manual estimation task*, participants were asked to indicate the size of the target stimulus in the same way as in open-loop manual estimation, except that participants had full view of their hand and of the target throughout the trial.

In the *grasping task*, participants were asked to grasp the target disc with their right hand and lay it on the table next to

Table 3 – Motion tracking systems used by each lab, including basic specifications.

Lab	System	Type	Sampling rate (Hz)	Spatial resolution (mm)
Parma (NB)	SMART System (BTS Bioengineering, Milan, Italy),	Optical (infrared)	120	.3
	Qualisys ProReflex MCU1000 (Qualisys AB, Gothenburg, Sweden)	Optical (retro-reflective)	240	.4
Aberdeen (CH)	Optotrak 3020 (Northern Digital, Waterloo, Canada)	Optical (infrared)	200	.01
Erlangen (TS)	Zebis CMS-70 (Zebris medical GmbH, Isny, Germany)	Acoustic	50	.1
Hamburg (KKK, VHF)	Optotrak Certus (Northern Digital, Waterloo, Canada)	Optical (infrared)	200	.01

the stimulus set-up. The grasping task was performed under open-loop conditions, as was proposed by Post and Welch (1996) and as has been done in most previous experiments (de Grave et al., 2005; Franz et al., 2003, 2000; Glover & Dixon, 2002; Haffenden & Goodale, 1998; Haffenden et al., 2001; Pavani et al., 1999; for a comparison of open-loop to closed-loop grasping in the Ebbinghaus illusion see: Franz et al., 2005). The shutter glasses closed when the right thumb or index finger had moved 20 mm away from the starting position. Trials ended when the participant's thumb or index finger touched the target object.

These four blocks were conducted for each participant. Before each block, participants were asked to perform 5 pseudo-random practice trials. The order of blocks was counterbalanced between participants, with size matching always being the first task, so that each of the 6 (3!) possible task orders was used six times per lab.

2.5. Data analysis

As dependent variables, we used the *diameter* of the selected circle in the graded series for the size matching task, the indicated *distance* between thumb and index finger markers for the manual estimation tasks, and the MGA for the grasping task. For each measure, we eliminated outliers that were more than 2 SD above or below the participant's mean for each condition.

For each dependent variable, a repeated measures analysis of variance (ANOVA) with the factors “target disc size” (three levels – 28 mm, 30 mm, 32 mm) and “context circle type” (four levels – “small-near”, “small-far”, “large-near”, “large-far”) was computed. We used t-tests to compare conditions separately, correcting for multiple comparisons by applying a Holm-Bonferroni correction (Holm, 1979). Wherever t-tests were used, we also calculated Bayes factors (e.g., Dienes, 2011) and denote evidence according to the thresholds proposed by Jeffreys (1961). We used the following prior distributions: in the *physically-matched* condition, the prior distribution for the effect of the illusion on grasping for H1 (prediction of the IEH) was a normal distribution with expected value and SD given by the mean and the SEM of the grasp effect predicted from the measured illusion effect in *size-matching*, taking into account the necessary slope corrections, thereby corresponding to equal effects of the illusion on perception and grasping (predictedGraspEffect = graspSlope*perceptualIllusion/perceptualSlope). The H0-prior (prediction of the TVSH) was a point-hypothesis at 0, corresponding to no illusion effect in grasping (predictedGraspEffect = 0). For the *perceptually-matched* condition, the H1-prior (prediction of the TVSH) for the effect on grasping was a normal distribution, with the expected value and the SD specified by the mean and the SEM of the predicted effect in grasping based on the physical difference alone, without any illusion effect (predictedGraspEffect = graspSlope*physicalDifference). As H0-prior (prediction of the IEH), we used a normal distribution with the expected value and the SD given by the mean and the SEM of the residual perceived differences in size between the two perceptually-matched stimuli as measured in the *size-matching* task (predictedGraspEffect = graspSlope*residualPerceptualDifference/perceptualSlope). Note that if our perceptual matching

procedure worked, mean and SEM should be close to 0. For the Fisher-z-transform of the *correlation between grasping and perceptual measures*, we used as H1-prior (prediction of IEH) a normal-distribution with the expected value and the SD corresponding to the z-transformed maximal expected correlation and its SEM as given by standard BC_a bootstrap (Efron & Tibshirani, 1993). As H0-prior (prediction of the TVSH), we used a point-hypothesis at 0, corresponding to no correlation between perceptual effects and grasp effects of the illusion. This allowed us to gather evidence in favour of the null-hypothesis in instances in which one theory predicts an effect and the other one does not. The use of Bayes factors, along with high statistical power and a setup in which both competing theories are tested as H0 as well as H1, makes it easy to argue for the null-hypothesis, should we obtain non-significant results.

To compare the illusion display effects between dependent variables, we needed to calculate a corrected illusion effect for each variable (Franz, 2003) to adjust the illusion effect for different slopes between size and the outcome measure. To make illusion effects comparable to other studies, we used the formula employed among others by Bruno and Franz (2009) for illusion effects as a percentage of the actual size:

$$i_{\text{corr}} = i_{\text{raw}}/s*100/t,$$

with i_{corr} = corrected illusion effect, i_{raw} = mean raw illusion effect, i.e., mean difference between responses of two conditions, s = slope, t = target size. Standard errors were calculated using a Taylor-approximation (Franz et al., 2009):

$$SE_{i_{\text{corr}}} = i_{\text{raw}}/s*\sqrt{\sigma_s^2/s^2 + \sigma_i^2/i_{\text{raw}}^2 - 2\sigma_{is}/(i_{\text{raw}}*s)*100/t},$$

where $SE_{i_{\text{corr}}}$ stands for standard error of corrected illusion effect, with i_{raw} = mean illusion effect, s = mean slope, σ_s = slope S.E.M., σ_i = illusion S.E.M., and σ_{is} = illusion effect-slope covariance. For details on this formula, see Franz et al. (2005) and Franz (2007). This procedure requires the slopes to be significantly different from 0, which we can reasonably expect them to be.

Illusion effects were calculated as the difference between two conditions. The three effects that are of the most interest to us were the traditional illusion effect (*small-near vs large-far*), the distance-matched illusion effects (*small-far vs large-far* and *small-near vs large-near*), and the critical test condition for the obstacle avoidance effect (*large-near vs small-far*).

To test the across-subject correlations between the illusion effect on MGA and on perceptual measures, correlations were computed between each perceptual measure and grasping. These correlations were then compared to the upper bound of the correlation predicted by the IEH and to 0 (as predicted by TVSH) by submitting the Fisher-z-transformed correlations to t-tests and calculating Bayes factors in the same fashion as described above.

For the expected correlation between effects of the illusion on perception and grasping, we can employ a formula from classical test theory. We are interested in correlating two latent variables (the “true” illusions in grasping and perception). This is analogous to the question in classical test theory of how well a “true” test value and a “true” value of an external criterion will correlate (external validity). In classical test

theory, an upper bound for the measured correlation of a test-score with an external criterion is given by:

$$r_{T,Tc} = r_{tc} / \sqrt{r_{tt} * r_{cc}},$$

with $r_{T,Tc}$ = the “true” correlation between latent variables. In classical test theory, these are the “true” test value and the “true” value of an external criterion. In our case, these are the “true” illusions in grasping and perception. r_{tc} = the measured validity of the test (classical test theory: measured correlation between test score and external criterion; here: measured correlation between grasp illusion and perceptual illusion), r_{tt} = the reliability of the test (here: reliability of grasp illusion), r_{cc} = the reliability of the criterion (here: reliability of perceptual illusion). If the grasp illusion were perfectly based on the perceptual illusion $r_{T,Tc}$ would be 1. Solving the equation for r_{tc} , gives:

$$r_{tc} = r_{T,Tc} * \sqrt{r_{tt} * r_{cc}} = \sqrt{r_{tt} * r_{cc}}.$$

This is the maximal correlation we can expect between the measured illusions in grasping and perceptual tasks, given their reliabilities. Because this prediction is based on strong assumptions, we call it the maximal expected correlation. This is the correlation that a strong version of the IEH would predict. The strong version of the TVSH would predict a correlation of 0. We also conducted a power analysis based on data from a previous experiment (Franz et al., 2003) that gave us split-half reliabilities of .22 and .47 for grasping and size adjustment, respectively, resulting in a maximal expected correlation of .32. With $\alpha = .05$ and $N = 144$, we would have 98% power to detect this effect.

Our hypotheses, in statistically testable terms, were as follows: in the physically-matched condition, we tested for a significant main effect of the factor *illusion condition* on MGA and all three perceptual measures. (1) Furthermore, we examined whether the conditions *large-near* produce a larger MGA than the conditions *small-far* (obstacle avoidance). (2) In the perceptually-matched condition, we examined whether we would find a difference between SFx and LFy in MGA, and ME. (3a) We also tested whether the corrected illusion effects in grasping differed significantly from 0 and (3b) from the corrected illusion effects in any of the three perceptual measures, as well as (3c) whether there is a correlation between illusion effects in grasping and perceptual measures.

For all of these comparisons, paired-sample t-tests were employed, as well as a Bayesian equivalent, i.e., Bayes factors for the null-hypothesis versus an alternative hypothesis. We report Bayes factors and *p*-values as exact values when above .001, and use a significance level of $\alpha = .05$ for all analyses. 95% confidence intervals are reported where applicable; means are reported including the appropriate standard error as $M \pm SEM$.

3. Implementation of preregistered protocol

The introduction and methods section of the present study were reviewed and accepted in-principle as a registered report in September 2014 and were not modified after that (allowing

for minor language adjustments). We collected all data after in-principle acceptance and finished data collection in May 2015.

3.1. Data collection: deviations from preregistered protocol

During testing, the SMART system in Parma had technical difficulties and had to be replaced with a Qualisys system (Table 3). Because of this, the editor agreed to extend the time frame for submission from 10 to 12 months. There were also a few minor inconsistencies in the experimental procedures between labs: (a) In the ME-tasks in Erlangen, participants did not record their ME by pressing a button (as in the other labs), but by keeping their fingers still and indicating verbally to the experimenter that they were showing the perceived size. This meant that the pre-registered time limit of 2500 msec was sometimes exceeded. Both procedures are common practice. (b) Three participants had a slightly smaller handedness score than pre-specified (but were still classified as right-handed, $LQ > 24$ instead of $LQ > 47$). Otherwise, we fully adhered to the registered protocol.

3.2. Post-hoc design critique: would a dual-illusion display be a better test of TVSH predictions?

After we submitted our data in phase 2 of this registered report, a reviewer worried that presenting observers with only one Ebbinghaus figure at a time may not be a fair test of the TVSH. The original studies of Aglioti et al. (1995) and Haffenden and Goodale (1998) used a dual-illusion display, showing two Ebbinghaus figures side-by-side, as is often used in textbooks to demonstrate the illusion. In contrast, our design used only one Ebbinghaus figure at a time, thereby employing a single-illusion display that has typically been used in perceptual research (e.g., Coren & Enns, 1993; Coren & Girgus, 1972; Girgus et al., 1972). We chose a single illusion design at phase 1 because it represents, in our opinion, the optimal choice for testing our hypotheses. All studies (independent of whether they use single- or dual-illusion displays) have to ensure that the task demands are as similar as possible in all conditions. However, when a dual-illusion display is used, the magnitude of the illusion depends on whether the targets in the two Ebbinghaus figures are compared to each other (direct-comparison condition) or whether they are successively and separately compared to a neutral disc (separate comparison). Specifically, in a direct comparison the effect is app. 50% larger than the sum of the effects in two separate comparisons (Foster & Franz, 2014; Franz et al., 2000). This raises an obvious problem: in the perceptual task, participants can compare two discs, whereas in the grasping task, they typically grasp only one target. In other words, when using a dual-illusion display there is a fundamental mismatch of task demands between the perception and action conditions, leading to an underestimation of the action effect relative to the perceptual effect. This has been known for some time (Franz et al., 2000; Pavani et al., 1999). In consequence, it is common practice to use single-illusion displays in research on the TVSH, also by proponents of the TVSH (e.g., Haffenden et al., 2001; for related work see Dewar & Carey, 2006; Foster & Franz, 2014; Foster, Kleinholdermann, Leifheit, & Franz, 2012; for further discussion of the issue of task demand mismatches in perception and action, see Bruno, 2016; Schenk et al., 2011).

4. Results

4.1. Frequentist analyses, Bayesian analyses, and open data

Results of traditional frequentist tests are reported as usual and accompanied (where appropriate) by corresponding Bayes-factors. For the logic of Bayes factors, see Section 2.5 and Dienes (2011). In essence, the Bayes factor indicates the relative likelihoods of two competing hypotheses, which we stated for all our tests in Section 2.5, thus giving us a continuous measure of how strongly either hypothesis is favoured. The evidence for the H1 always equals $1/(\text{evidence for H0})$. Bayes factors may be interpreted following the guidelines proposed by Jeffreys (1961), such that we can speak of strong evidence for H0 for Bayes factors smaller than $1/10$, substantial evidence for H0 for Bayes factors between $1/10$ and $1/3$, inconclusive results for Bayes factors between $1/3$ and 3 , substantial evidence for H1 for Bayes factors between 3 and 10 , and strong evidence for H1 for Bayes factors above 10 .

We first report the results of the pre-registered analyses. Then, in Section 4.7, we report results of post-hoc analyses that were not pre-registered. In some cases it seemed easier for the reader that we also include post-hoc analyses before Section 4.7. These are clearly marked as not pre-registered analyses.

All data, analyses and materials for this study can be downloaded via Mendeley Data at <http://dx.doi.org/10.17632/4676n2pdf.3>. After results were submitted in the stage 2 registered report, the study was reviewed by the same anonymous reviewers as in stage 1. Below, we report minor changes and issues related the design of the study that surfaced after in-principle acceptance.

4.2. Participants

We invited $N = 160$ participants to the laboratory, 16 of which were not included in the data analysis: 9 due to technical errors (recording did not produce analysable data or could not be finished), 3 due to experimenter errors (the experimenter followed the wrong protocol), 4 because they were not unambiguously right-handed (negative LQ or left-handed by self-report; two of these were not tested further but had been given an ID, two were tested because their handedness inventories were evaluated after testing). Thus, we obtained and included the data from $N = 144$ right-handed participants, $N = 36$ in each lab. The order of blocks was counterbalanced between these participants.

4.3. Overall data

Mean responses for all tasks and conditions are depicted in Fig. 5. We will discuss the physically-matched condition and the perceptually-matched condition successively. In both conditions, participants completed the tasks: grasping, classic perception (size matching), closed-loop ME, and open-loop ME as outlined in Section 2.4. For brevity, we will sometimes talk about perceptual tasks in general, which comprises classic perception as well as ME (because the TVSH assumes this to be a perceptual task).

4.4. Physically-matched conditions

The physically-matched conditions consisted of three objects (discs of 28, 30, 32 mm diameter), presented within four context circle types (LF, LN, SF, SN; Table 2). We submitted the results of each task to a 3 (target size) $\times 4$ (context circle type) ANOVA. Results show that both factors affected all tasks (Table 4). In some tasks, there was also a significant interaction between target size and context circle type. Since such small modulations of the context circle type effect are not unusual (Franz et al., 2000) and do not change the overall pattern of results (Fig. 5), these interactions will not be discussed further. Importantly, we found a main effect of context circle type in grasping, meaning that the MGA in grasping was affected by the illusion configuration. This is to be expected if we assume that grasping follows the perceived size (IEH), but needs to be explained by some other mechanism like obstacle avoidance (Haffenden & Goodale, 2000; Haffenden et al., 2001) if we assume that grasping is immune to illusions (TVSH).

To investigate these effects in more detail, we calculated contrasts between specific illusion configurations in each task. Most relevant are the contrasts SN–LF (the traditional Ebbinghaus illusion contrast), as well as SF–LF and SN–LN (the distance-adjusted conditions which should ameliorate obstacle avoidance effects). If the effect of the illusion configuration on MGA is indeed caused by obstacle avoidance, then the TVSH predicts no difference in the adjusted contrasts, while the IEH predicts a difference. Results from our study are depicted in Fig. 6a.

The strongest test of obstacle avoidance is comparing the configurations LN and SF. Here, the IEH and the obstacle avoidance hypothesis make opposite predictions (Fig. 3). We found a larger MGA for the SF condition than for the LN condition [$t(143) = 2.68, p = .008$; Fig. 7], which is consistent with the IEH but not with obstacle avoidance.

Next, we compared the size of the illusion effects between measures. For this, we calculated slope-corrected illusion effects (Fig. 6c) and compared grasping to the perceptual measures (Table 5).

Results show that all but one t-test indicate similar corrected illusion effects for grasping and the different perceptual measures (all $p > .15$). Only one t-test is significant (grasping vs closed-loop ME, SF–LF: $p = .044$; Table 5, row 3). However, this difference is not significant after applying the Bonferroni-Holm correction.⁵ Such an alpha-correction is needed if we wish to interpret the fact that only one out of nine t-tests is significant as evidence that there is an effect. Instead, it seems that the closed-loop ME simply showed an unusually large illusion effect, as is also suggested by the fact that the same contrast is also significantly different when classic perception is compared to closed-loop ME [$t(143) = 2.62, p = .010$, see also Table A.1 in the Appendix; this

⁵ In general, the Bonferroni-Holm correction is less conservative than the classic Bonferroni correction (Holm, 1979). In our case, however, both lead to the same result: in Bonferroni-Holm, the divisor of the alpha level is initially the same as in the Bonferroni correction. This divisor then decreases by one each time a significant result is found at the current alpha level. Thus, the corrections are equivalent in our case of only one significant result.

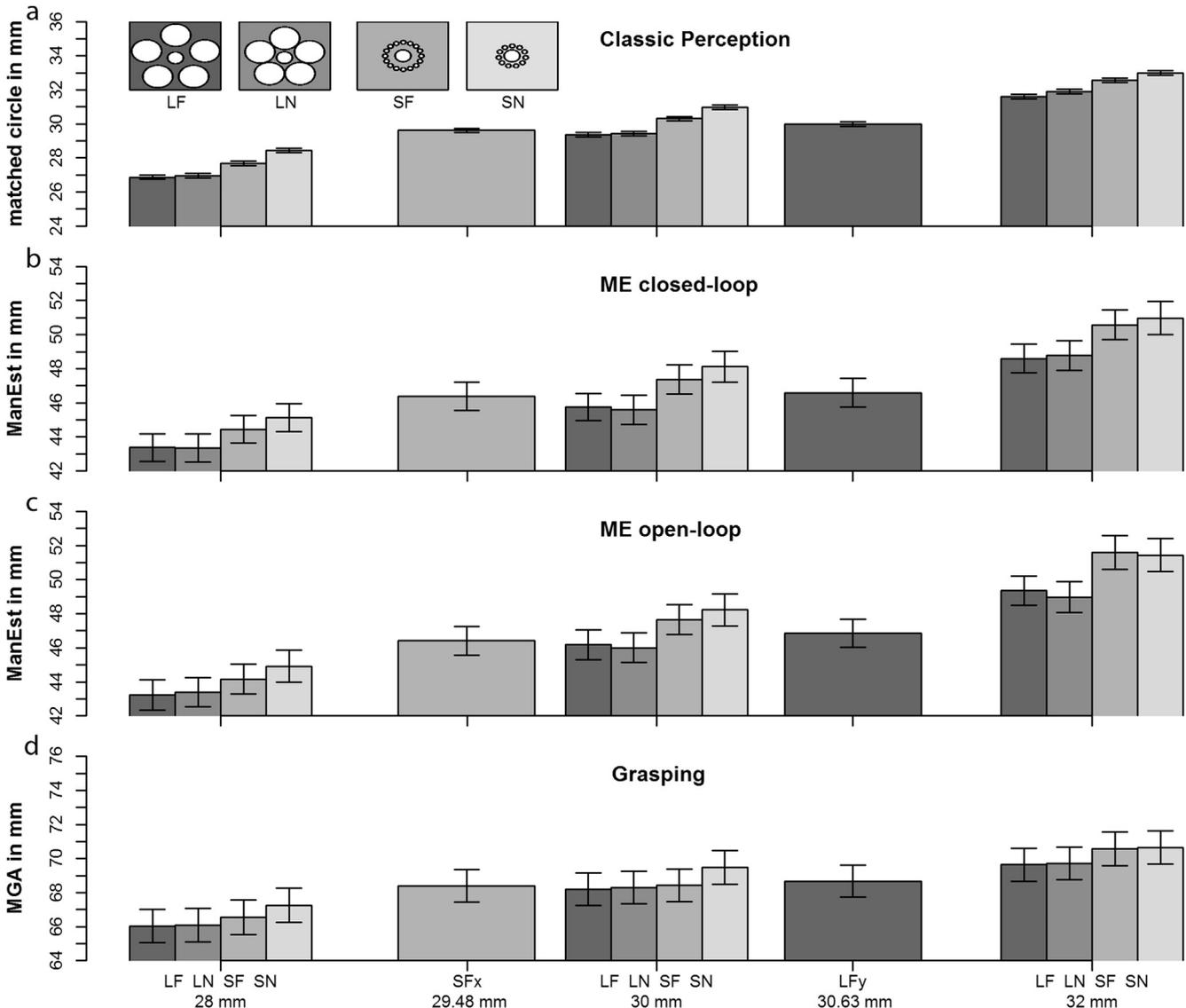


Fig. 5 – Mean responses for each object size and context circle type. **a:** Classic perception task, **b:** closed-loop ME, **c:** open-loop ME, **d:** grasping. The relative width of the bars corresponds to the number of trials in each configuration. Error bars indicate between-subjects SEM. These SEM contain between-subjects variance and can therefore not be used to interpret differences between conditions (because conditions were varied within-subjects). See the following figures for error bars that allow such interpretations (cf. Franz & Loftus, 2012; Loftus & Masson, 1994).

analysis was not pre-registered]. This interpretation is also consistent with the Bayesian analysis because all Bayes factors strongly support the H1 (illusion effects in grasping are comparable to illusion effects in other measures; Table 5).

Finally, we tested whether there is a correlation between illusion effects in grasping and perception. According to the IEH, participants with a relatively large perceptual illusion should also have a large illusion effect in grasping. The TVSH on the other hand predicts no correlation. The main problem when testing for such a correlation is that grasping and ME are relatively noisy measures, such that *a-priori* the correlation must be small, even if grasping and perception were based on perfectly identical size representations and noise is only generated when creating the actual response. Small correlations require very large sample sizes to be detected reliably (e.g., a correlation of $r = .20$ would require $N = 314$ participants

to achieve 95% power). To estimate a lower limit for a meaningful sample size, we used a formula from classic test theory to calculate the maximal theoretically possible correlation given the reliabilities of the measures (Section 2.4). Our sample is large enough to at least detect the maximum possible correlation with sufficient power, while the usual smaller sample sizes would not be able to detect even this upper limit of the correlation with sufficient power.

Table 7 shows the reliabilities and correlations between all illusion contrasts. As expected, the reliabilities are relatively small for grasping and ME, because these measures are affected by noise generated during hand and finger movement. Classic perception is not affected by such movement noise and therefore has considerably larger reliabilities. Given the small reliabilities of grasping and ME, the correlations are also small. Out of 9 correlations, 5 were significantly

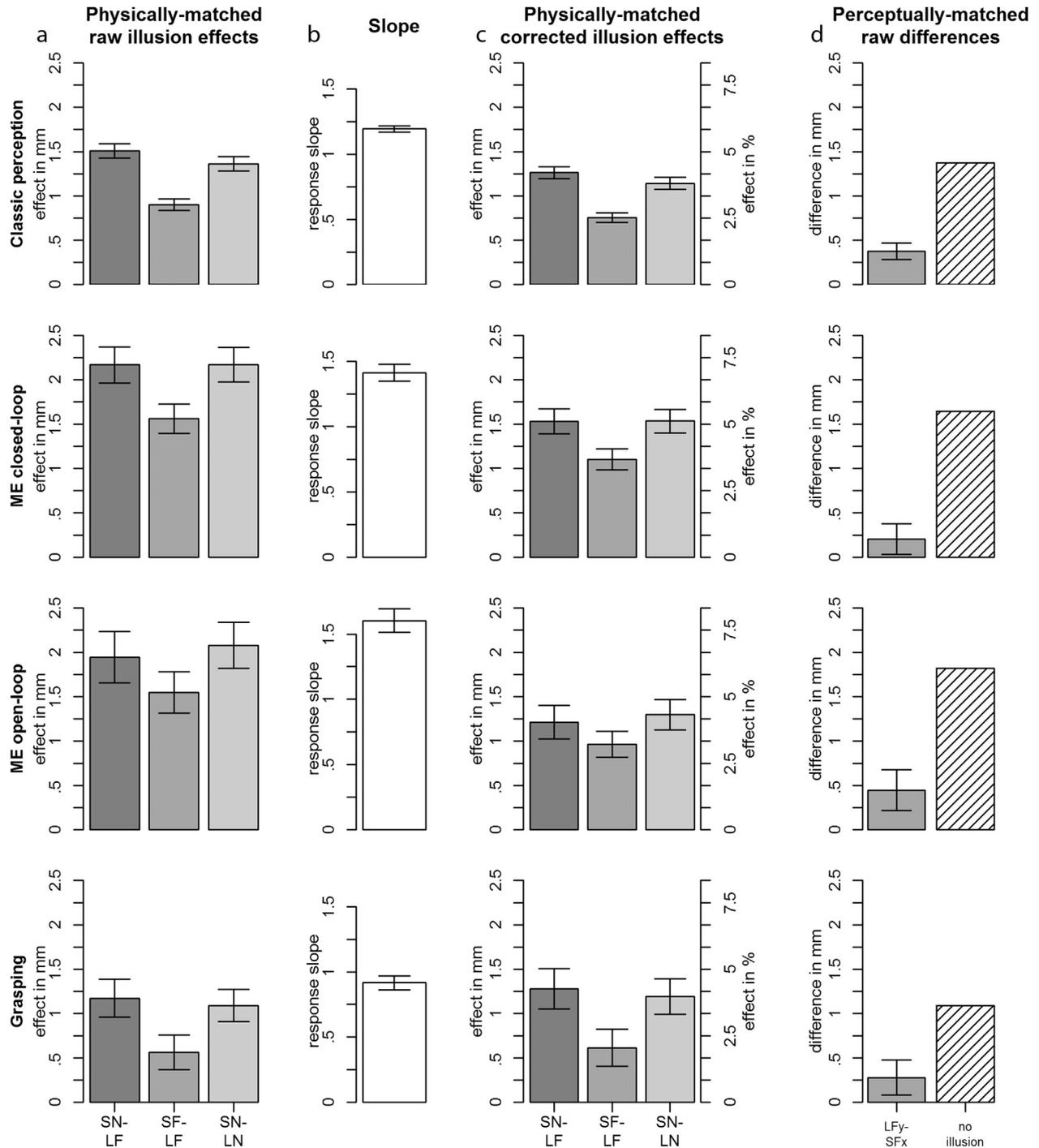


Fig. 6 – Mean illusion effects in the physically-matched conditions and differences between the perceptually-matched conditions. **a:** Raw illusion effects for the traditional contrast (SN–LF) and the adjusted contrasts (SF–LF and LN–SN). **b:** Slopes of the response functions. **c:** Corrected illusion effects (calculated by dividing each raw illusion effect by the corresponding slope). Results show similar corrected illusion effects in all tasks. This is consistent with the IEH but not with the TVSH. **d:** Differences between the perceptually-matched conditions (LFy–SFx). If a response followed perceived size (as determined by our nulling procedure and as predicted by the IEH), the difference should be zero. If a response followed physical size (as predicted by the TVSH), the difference should be equal to the hatched bars (this prediction is calculated by multiplying the physical difference between LFy and SFx by the slope of each response). Results show similar small effects in all tasks (indicating that nulling did not work perfectly). These small effects clearly differed from the no-illusion predictions, indicating that all tasks (including grasping) follow perceived size and not physical size. Error bars depict the within-subjects SEM. Because these SEM are for within-subject differences, they do not contain between-subjects variance and are therefore consistent with the results of a t-test against zero (cf. Franz & Loftus, 2012).

Table 4 – ANOVA results for all tasks in the physically-matched condition.

Task	Main effect				Interaction	
	Context circle type		Object size		Context circle type x object size	
	<i>F</i> (3, 429)	<i>p</i>	<i>F</i> (2, 286)	<i>p</i>	<i>F</i> (6, 858)	<i>p</i>
Grasping	17.10	<.001**	217.71	<.001**	1.36	.227 n.s.
Perception	218.52	<.001**	2304.89	<.001**	4.87	<.001**
ME CL	76.99	<.001**	401.86	<.001**	1.81	.094 n.s.
ME OL	36.84	<.001**	259.47	<.001**	2.53	.019*

Note: n.s. indicates non-significant, * indicates $p < .05$, ** indicates $p < .001$. Statistically significant p -values are given in italics.

different from zero, indicating a relationship between grasping and the perceptual measures. This is a pattern we would expect given a small effect size and, accordingly, relatively low statistical power: if we assume the factual correlation to be $r = .2$, with $N = 144$ we achieved a power of 68% for each test of a correlation against 0. This would be a small effect size according to Cohen (1988) and similar to most correlations we found.

In our pre-registered Bayesian analysis, we contrasted the hypothesis that there is no correlation (H_0) with the hypothesis that the correlation is equal to the theoretical upper bound (i.e., the maximal expected correlation; H_1). This gives a somewhat mixed result, with 5 Bayes factors supporting the H_0 , 2 supporting the H_1 , and 2 being inconclusive (BF_n in Table 7). However, after pre-registration, we learned that this analysis is problematic and will discuss a more appropriate analysis in Section 4.7.2.

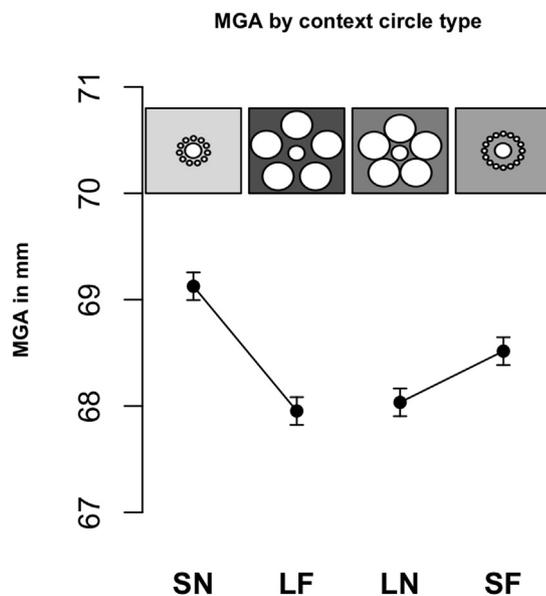


Fig. 7 – Mean grasping responses for the physically-matched conditions. Results for SN and LF replicate the literature, LN and SF are the adjusted configurations testing the obstacle-avoidance hypothesis. Results follow the predictions of the IEH (Fig. 3b) but not the predictions of the TVSH (Fig. 3c). Error bars indicate within-SEM for the pooled difference between context circle types and can therefore be used to interpret differences between conditions (Franz & Loftus, 2012; Loftus & Masson, 1994).

To summarise, we found illusion effects on grasping in all relevant contrasts, including contrasts where the distance of context elements was matched, so that the obstacle avoidance hypothesis as suggested by Haffenden et al. (2001) cannot explain these effects. The illusion effects are of similar size as in the perceptual tasks (classic perception, closed-loop ME, and open-loop ME) and most effects correlate significantly between grasping and the perceptual tasks.

4.5. Perceptually-matched conditions

For the perceptually-matched condition, we used two staircase procedures to determine a pair of target discs for each participant such that the one presented within the SF configuration and the one within the LF configuration would be perceived as equal in size. We called these discs SFx and LFy, respectively. Since the IEH assumes that grasping follows perception, it is now the IEH that predicts a null-difference in grasping between SFx and LFy (H_0), while the TVSH assumes that grasping follows physical size and that therefore the two discs should be grasped with different MGAs (H_1).

The LFy disc had an average diameter of 30.63 mm (± 0.06 mm) and the SFx of 29.48 mm (± 0.08 mm), such that the LFy disc was on average 3.91% larger than the SFx disc (Fig. 5). As specified in Section 2.4, the two discs were included in all perceptual tasks to confirm whether they were in fact perceived as being equally large. In the grasping task, these discs were used to detect influences of physical size on MGA that cannot be explained by perceived size. We found a difference in perceived size in the classic perception task [$t(143) = 3.99$, $p < .001$], indicating that the physically larger LFy was also perceived to be slightly larger (Fig. 6d). The same was true in all other tasks, although these differences were not significantly different from zero [open-loop ME: $t(143) = 1.95$, $p = .053$; closed-loop ME $t(143) = 1.18$, $p = .242$; grasping: $t(143) = 1.42$, $p = .158$]. Importantly, the MGA in grasping did not differ between LFy and SFx.

Using the same slope correction as in the physically-matched conditions (Figs. 6d and 8), we found the difference between LFy and SFx in MGA to be $1.01\% \pm .71\%$ of the mean object size, which may be interpreted as the effect of physical size on grasping that is not explained by perceived size as measured by our staircase. Note that the observed difference is in the same direction as in the perceptual tasks. Thus, the remaining perceptual difference may still explain some of the difference in MGA, which makes

Table 5 – Comparisons between corrected illusion effects in grasping and in the perceptual tasks.

Comparison	SN-LF			SF-LF			SN-LN		
	t(143)	p	BF	t(143)	p	BF	t(143)	p	BF
Grasping versus 0	5.63	<.001**	-	2.95	.004*	–	5.96	<.001**	–
Perception versus grasping	–0.07	.942	>1000	0.65	.515	51.7	–0.24	.813	>1000
		n.s.			n.s.			n.s.	
ME CL versus grasping	0.94	.347	>1000	2.03	.044*	8.4	1.42	.157	>1000
		n.s.						n.s.	
ME OL versus grasping	–0.22	.823	>1000	1.38	.169	22.1	0.40	.689	>1000
		n.s.			n.s.			n.s.	

Note: The contrasts SN–LF (traditional Ebbinghaus contrast), SF–LF and SN–LN (adjusted contrasts with controlled context circle distance) are tested for a difference against 0 in grasping (top row) and for a difference between each task and grasping (rows 2 to 4). We used slope-corrected illusion effects for the comparisons between tasks. Bayes factors compare the hypotheses of illusion in grasping = 0 (H0) versus illusion in grasping = illusion in perceptual task (H1). CL and OL are used to abbreviate closed-loop and open-loop, respectively. n.s. indicates non-significant, * indicates $p < .05$, ** indicates $p < .001$. Statistically significant p-values, as well as Bayes factors smaller than 1/3 or larger than 3, are given in italics.

this a slight overestimate for the effect of physical size. Importantly, not only did the difference in MGA not differ significantly from 0, the corrected residual difference was also almost exactly the same as the LFy–SFx differences found in the classic perceptual task ($1.05\% \pm .26\%$) and in ME (open-loop: $.93\% \pm .47\%$, closed-loop: $.48\% \pm .41\%$).

These results are supported by Bayes factors: we compared the hypothesis that MGA follows perceived size (H0) to the hypothesis that MGA follows physical size (H1). As perceived size, we used the results of our classic perceptual task as well as the results of closed-loop ME and open-loop ME. All Bayes factors decisively supported the H0 (grasping vs classic perception task BF: 1/554, grasping vs open-loop ME BF: 1/490, grasping vs closed-loop ME BF: 1/421), indicating that grasping followed perceived size.

To summarise, the results in the perceptually-matched conditions suggest that grasping follows perception and not physical size. This is consistent with our results in the physically-matched conditions.

4.6. Additional analyses

Our large sample size allowed us to run further pre-registered analyses that were more exploratory in nature and concerned general properties of our measures. Firstly, we analysed response slopes (Section 4.6.1), which are the basis for the corrected illusion effects. Secondly, we assessed grasping kinematics, testing the predictions of another theory of obstacle avoidance in grasping the Ebbinghaus illusion (Section 4.6.2).

Table 6 – Grasp parameters in the physically-matched condition by illusion condition and object size.

Context circle type	MGA in mm	MT in msec	MGA time in msec	Relative MGA time in %
LF	67.97 ± .95	958 ± 45	691 ± 34	75.50 ± 1.09
LN	68.03 ± .95	951 ± 44	692 ± 34	75.83 ± 1.07
SF	68.53 ± .98	956 ± 46	686 ± 33	75.34 ± 1.09
SN	69.12 ± .97	975 ± 47	690 ± 34	74.67 ± 1.15
Object size in mm				
28	66.48 ± .98	961 ± 46	690 ± 33	75.62 ± 1.11
30	68.60 ± .95	953 ± 45	688 ± 34	75.53 ± 1.06
32	70.16 ± .96	967 ± 46	690 ± 34	74.82 ± 1.09

Note: Between-subject standard errors are given for each cell.

4.6.1. Response slopes in different tasks

Our correction method takes into account the slopes of the response-functions. Based on previous studies, we had anticipated that grasping would show a response slope slightly smaller than 1 (e.g., Smeets & Brenner, 1999, report .82), while closed-loop ME (e.g., Dewar & Carey, 2006) and classic perception (e.g., Franz et al., 2000) should show a slope close to 1, and open-loop ME a slope larger than 1 (e.g., Haffenden & Goodale, 1998; Haffenden et al., 2001). In our data (Fig. 6b), we found slopes of $.92 \pm .05$ for grasping and $1.19 \pm .02$ for classic perception, which are both very similar to previous results (Franz et al., 2000; Smeets & Brenner, 1999). For closed-loop ME we observed a slope of $1.41 \pm .06$ and for open-loop ME a slope of $1.60 \pm .09$. Contrary to our expectations, the two ME slopes are numerically quite similar, although statistically they differ significantly [$t(143) = 2.36, p = .020$]. This is due to a larger than expected slope in closed-loop ME, while open-loop ME behaved roughly as we expected. Therefore, further research is needed to elucidate the reason for the relatively small slope in closed-loop ME in studies like Dewar and Carey (2006). See also Foster et al. (2012) for a further discussion of that study.

4.6.2. Grasping kinematics

In each grasping trial, we computed the time between the start of the movement and the occurrence of the MGA (MGA time), as well as between the start of the movement and touching the target disc (movement time, MT). MGA was reached on average at 75.35% of the total movement duration. This is consistent with classic studies on grasping (e.g., Jeannerod, 1984 reported the typical time of MGA to be between 74% and 81% in his participants, in one case earlier).

Analysing the grasping kinematics allowed us to test an idea put forward by Smeets et al. (2003). Based on their grasping model (Smeets & Brenner, 1999), they suggested that grasping kinematics can be used to detect more general obstacle avoidance mechanisms than those proposed by Haffenden et al. (2001). The main idea was that the cause of an increase of MGA might either be different contact points on the object (caused by a physical or illusory change of object size) or a different approach of the objects (possibly caused by obstacle avoidance mechanisms). While both effects could increase the MGA in similar ways, their influence on the relative timing of the MGA would be in opposite directions,

Table 7 – Full correlation table between illusion effects, all measures.

SN–LF	Grasping	Classic perception	ME closed-loop	ME open-loop
Grasping	Rel. = .31	$r = .18$ $p = .031^*$ MEC = .62 $BF_n = 1/41$ $BF_u = 3.0$	$r = .30$ $p < .001^{**}$ MEC = .51 $BF_n = 103$ $BF_u = 355$	$r = .11$ $p = .170$ MEC = .52 $BF_n = 1/112$ $BF_u = 1/1.2$
Classic perception		Rel. = .71	$r = .20$ $p = .014^*$ MEC = .69 $BF_n < 1/1000$ $BF_u = 5.0$	$r = .34$ $p < .001^{**}$ MEC = .68 $BF_n = 1.7$ $BF_u > 1000$
ME closed-loop			Rel. = .39	$r = .27$ $p = .001^*$ MEC = .57 $BF_n = 1/1.6$ $BF_u = 66$
ME open-loop				Rel. = .40
SF–LF				
Grasping	Rel. = .32	$r = .18$ $p = .027^*$ MEC = .61 $BF_n = 1/64$ $BF_u = 3.4$	$r = .19$ $p = .026^*$ MEC = .43 $BF_n = 1.5$ $BF_u = 5.6$	$r = .15$ $p = .073$ MEC = .41 $BF_n = 1/1.2$ $BF_u = 2.4$
Classic perception		Rel. = .62	$r = .32$ $p < .001^{**}$ MEC = .54 $BF_n = 282$ $BF_u = 671$	$r = .23$ $p = .006^*$ MEC = .51 $BF_n = 6.9$ $BF_u = 18$
ME closed-loop			Rel. = .23	$r = .25$ $p = .002^*$ MEC = .36 $BF_n = 42$ $BF_u = 61$
ME open-loop				Rel. = .21
SN–LN				
Grasping	Rel. = .27	$r = -.04$ $p = .640$ MEC = .58 $BF_n < 1/1000$ $BF_u = 1/8.7$	$r = .26$ $p = .002^*$ MEC = .48 $BF_n = 16$ $BF_u = 66$	$r = .06$ $p = .490$ MEC = .44 $BF_n = 1/78$ $BF_u = 1/2.4$
Classic perception		Rel. = .65	$r = .13$ $p = .120$ MEC = .64 $BF_n < 1/1000$ $BF_u = 1/1.2$	$r = .39$ $p < .001^{**}$ MEC = .58 $BF_n > 1000$ $BF_u > 1000$
ME closed-loop			Rel. = .37	$r = .27$ $p = .001^*$ MEC = .48 $BF_n = 30$ $BF_u = 82$
ME open-loop				Rel. = .30

Note: MEC stands for “maximal expected correlation”, as described in Section 2.5. Rel. stands for ‘reliability’, r denote a correlation. P-values are given for a t-test of each correlation against 0; Bayes factor BF_n compares the hypotheses $correlation = 0$ (H0) versus $correlation = MEC$ (H1); Bayes factor BF_u is a non-preregistered analysis that compares the hypotheses $correlation = 0$ (H0) versus $correlation$ is positive (i.e., between zero and MEC, H1). n.s. indicates non-significant, * indicates $p < .05$, ** indicates $p < .001$. Statistically significant p-values, as well as Bayes factors smaller than 1/3 or larger than 3, are given in italics.

such that obstacle avoidance mechanisms would lead to an earlier MGA, while a larger object would result in a later MGA. Such opposite effects on the timing of MGA might serve as evidence for obstacle avoidance mechanisms, although the expected difference is small (Smeets & Brenner, 1999; Smeets

et al., 2003) and it is unclear whether these obstacle avoidance mechanisms would be comparable to those proposed by Haffenden et al. (2001). In their study, Smeets et al. (2003) did not find any such effects and argued that the expected effects are too small to be detected with the sample size and power of

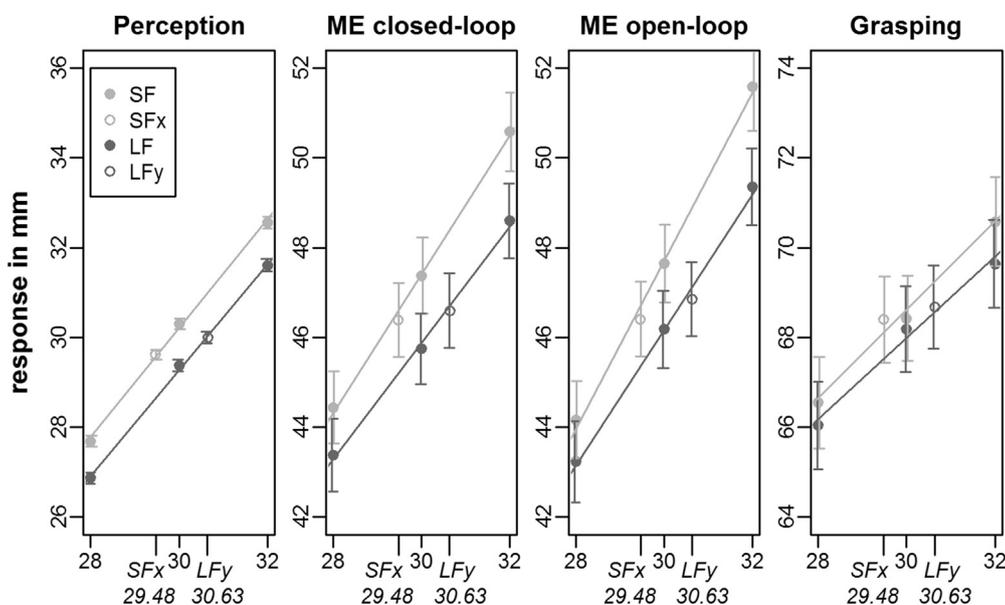


Fig. 8 – Mean responses to configurations LF and SF for physically-matched and perceptually-matched conditions. The x-axis indicates object size in mm. SFx and LFy are the data from the perceptually-matched condition (depicted at the means of the corresponding matched sizes, i.e., at 29.48 mm and 30.63 mm, respectively). The responses in the perceptually-matched condition are fully consistent with the responses in the physically-matched conditions. This indicates that there is no qualitative difference between perceptually-matched and physically-matched conditions. The regression lines were obtained from the physically-matched condition. Error bars indicate between-subjects SEM.

their study (p. 319). Given our very large sample size, we were in a better position to test this idea.

We tested whether an increase of MGA due to a change of physical size had opposite effects on MGA time than an increase due to the illusion configuration. A 3 (object size)*4 (context circle type) ANOVA with relative MGA time as the dependent variable revealed main effects of both factors: object size [$F(2, 286) = 3.57, p = .029$] and context circle type [$F(3, 429) = 2.87, p = .036$]. However, the interaction was not significant [$F(6, 858) = 1.80, p = .096$], thereby indicating that we did not find the predicted opposite effects. Instead, we found that no matter if MGA increased as a result of an increase in object size or because of a change of the illusion configuration, the MGA always occurred slightly earlier (Table 6). This is surprising, given that previous research has generally found larger MGAs to occur later (Jeannerod, 1984; Smeets & Brenner, 1999), but the finding remains that actual size and illusory size did not impact the timing of the MGA differently.

In short, we found no evidence for general obstacle-avoidance mechanisms as suggested by the grasping model of Smeets and Brenner (1999). This is consistent with our overall conclusions that the effects of Ebbinghaus illusion displays on grasping cannot be explained by obstacle avoidance (Haffenden & Goodale, 2000; Haffenden et al., 2001). However, our study was not designed to test Smeets and Brenner's model (1999). Therefore, our results do not constitute evidence against it. Also, even if grasping perfectly followed the perceptual effect of the Ebbinghaus illusion, this does not necessarily contradict the Smeets and Brenner (1999) model, as it is possible that the Ebbinghaus illusion affects

grasp position (the central variable in this model) in a similar way as object size (the central variable in more traditional accounts of grasping), such that the model could still be consistent with our results and conclusions.

4.7. Post-hoc analyses

4.7.1. Comparing raw illusion effects

As has been laid out in Sections 1.2 and 2.5, we consider it necessary to correct for the slope of the response function before we compare illusion effects obtained from different tasks. However, it may be interesting to also analyse the data without these corrections, especially since some researchers are sceptical of this procedure (Goodale, 2014; Westwood & Goodale, 2011). Therefore, we also compared raw illusion effects for grasping and all perceptual tasks (cf. Table A.2 in the Appendix).

In the physically-matched conditions, we found that for all relevant illusion contrasts (SN–LF, SF–LF and SN–LN), there was no significant difference between the illusion effects in grasping and classic perception (all $p > .08$), while all comparisons of illusion effects in grasping and ME were significant (all $p < .03$). This is fully consistent with the literature, as among studies that did not apply slope-correction, those that compared grasping to ME (e.g., Haffenden & Goodale, 1998) found significant differences between the measures, while those that compared grasping to classic perception tasks (Franz et al., 2001; Pavani et al., 1999) did not.

Interestingly, all ME versus classic perception comparisons (SN–LF, SF–LF and SN–LN) also yielded significant differences

(all $p < .002$), except for one [open-loop ME – classic perception, SN–LF: $t(143) = 1.62, p = .108$]. Almost all of these apparent differences between classic perception and ME disappear when slope-correction is applied (see [Tables A.1 and A.2 in the Appendix](#)). This emphasises the importance of the correction, as even tasks that are unambiguously considered to be perceptual by the TVSH do not produce coherent results without correction (for a similar argument, see [Hesse, Franz, & Schenk, 2016](#)).

In the *perceptually-matched conditions*, we found no differences between the LFy–SFx contrasts [grasping – open-loop ME: $t(143) = .61, p = .540$; grasping – closed-loop ME: $t(143) = .31, p = .760$; grasping – classic perception: $t(143) = .52, p = .606$] or between LFy–SFx and 0. This is confirmed by the Bayes factor for the comparison of H0: LFy–SFx = 0 versus H1: LFy–SFx = physical difference (uncorrected), which also decisively supported the H0 (BF = 1/1988). These results are fully consistent with the results we found with slope correction (which is not surprising, as the perceptually-matched conditions would not require a slope correction if the perceptual match was perfect).

4.7.2. A better Bayesian analysis for the correlations between measures

For the correlations between dependent measures (Section 4.4), we had pre-registered a Bayesian analysis that used a normal-distribution centred at the maximal expected correlation as the H1-prior. However, in the meantime we learned that in a situation where one expects the effect to be larger than 0 but smaller than an upper bound, it is more appropriate to specify a uniform distribution from 0 to the upper bound as the H1 ([Dienes, 2008](#), chap. 4). Because the maximal expected correlation constitutes an upper bound (e.g., [Nunnally, 1967](#); [Vul, Harris, Winkelman, & Pashler, 2009](#)), we recalculated the Bayesian analysis using a uniform distribution between 0 and the maximal expected correlation as prior, thereby contrasting the hypothesis that there is no correlation (H0) with the hypothesis that the correlation is between 0 and the maximal expected correlation (H1). For the most interesting correlations between grasping and the perceptual measures we found support for the H1 in 5 cases, support for the H0 in only one case and inconclusive data in 3 cases, (see BFu in [Table 7](#)). This is consistent with the frequentist analyses (see p -values in [Table 7](#) and Section 4.4). Both results suggest that the correlations between grasping and the perceptual measures are statistically reliable, as predicted by the IEH.

5. Discussion

We tested whether there is an effect of the Ebbinghaus illusion on grasping using a paradigm that accounted for the alternative explanation of obstacle avoidance. We took great care to consider all methodological criticism raised in previous studies. To this end, we replicated and extended two studies that had previously reported inconsistent results on grasping the Ebbinghaus illusion, and specifically on obstacle avoidance ([Franz et al., 2003](#); [Haffenden et al., 2001](#)). Also, we created a symmetric situation with regard to the problem of “proving the null-hypothesis”: in addition to calculating Bayes factors, we employed both a standard physically-matched

design where we manipulated the perceptual context of the target discs (IEH predicts a difference in grasping between physically-matched but perceptually different discs), and a perceptually-matched design similar to that used by [Agioti et al. \(1995\)](#), (TVSH predicts a difference in grasping between perceptually-matched but physically different discs). The experiment was run in four labs ([Table 3](#)) to achieve more statistical power and to strengthen the generalisability of our results. Together, these factors allow us to draw strong conclusions from our results.

The main reason why we focussed on the Ebbinghaus illusion are the many possible confounds and non-obvious methodological issues described in previous sections. While some work on other illusions has reported dissociations between grasping and perception (e.g., [Ganel et al., 2008](#); [Stöttinger et al., 2012](#)), the Ebbinghaus illusion is by far the most studied paradigm. In consequence, the discussion has advanced to a point where potential confounds related to this paradigm have been identified and can thus be avoided. To the best of current knowledge, we conducted a confound-free test of whether or not grasping is affected by visual illusions in a similar way as perception.

5.1. Physically-matched conditions: grasping and perception are affected by the illusion

Our results clearly show that there is an illusion effect on grasping. In all labs, having discs surrounded by small context circles (thus appearing larger in size) consistently caused a larger MGA than having the same discs surrounded by large context circles (thus appearing smaller in size).

Importantly, the effect on MGA persisted not only for the SN–LF comparison, where an effect has been frequently reported (for reviews, see [Franz & Gegenfurtner, 2008](#); [Schenk et al., 2011](#); [Schenk & McIntosh, 2010](#)), but also for comparisons in which the context–element distance was equal for small and large context circles, the SF–LF and SN–LN comparisons ([Fig. 6](#) and [Table 5](#)). Hence, our study yielded results similar to those reported by [Franz et al. \(2003\)](#), but is in contrast to the findings reported by [Haffenden et al. \(2001\)](#). Since the distance between the context circles and target discs is equal, these illusion effects can only be explained by the difference in context circle size, thus matching the predictions of the IEH, but not those of the obstacle avoidance hypothesis. The key assumption of the obstacle avoidance hypothesis is that participants fit their fingers between target and context elements in the far conditions and grasp around the entire stimulus display in the near conditions ([Fig. 2](#)). Thus, finding a difference in MGA between configurations using the same context circle distance (SF and LF, SN and LN) as we did is incompatible with the obstacle avoidance hypothesis. An even stronger demonstration that obstacle avoidance cannot explain these illusion effects is obtained by comparing the SF and LN conditions ([Fig. 7](#)). The perceived size of the disc in SF is larger than in LN, which should result in a larger MGA in the SF condition according to the IEH, while the obstacle avoidance account would predict the opposite, a larger MGA in the LN condition ([Fig. 3](#)).

We also found, consistent with the IEH, that illusion effects in perception and in grasping tend to correlate ([Table 7](#)). The correlations are small, and only 5 of the 9 tested correlations are significantly different from zero. However, this is to be expected

when correlating two measures with relatively low reliability. To reliably detect such correlations requires very large sample sizes, even larger than the already unusually large sample size employed in our study. Therefore, we interpret these results as consistent with the notion that participants who displayed a large perceptual illusion effect also tended to display a larger illusion effect in grasping. This would be predicted if a common size representation underlies both tasks. A similar result was recently found for perceptual illusions and saccades (Dassonville & Reed, 2015). In addition to MGA, saccades are another prominent action measure that has been frequently used to argue for a functional subdivision between vision-for-action and vision-for-perception (but see Bruno, Knox, & de Grave, 2010; de Brouwer, Smeets, Gutteling, Toni, & Medendorp, 2015).

5.2. *Perceptually-matched conditions: physical size does not trump perceived size*

In the physically-matched condition, the strong version of the TVSH predicts no illusion effect on grasping (H0), while the IEH predicts an illusion effect (H1). Arguing for the H0 is often seen as problematic (Westwood & Goodale, 2011), especially since some effect of perception on grasping has been demonstrated in many paradigms (Bruno & Franz, 2009; McIntosh & Lashley, 2008) and may be compatible with a weaker version of the TVSH (Goodale, 2008). Therefore, we added the perceptually-matched condition: here, the TVSH predicts a difference in grasping for physically different but perceptually matched discs (H1), while the IEH predicts no difference (H0).

Consistent with the IEH, we did not find a difference (Figs. 6d and 8). As our power-analysis and the Bayes factors reveal, our sample is large enough to interpret these null results as evidence that participants did not scale their grip to the physical size of the discs but to the perceived size, thereby indicating an illusion effect on grasping. Because the distance between context circles and target discs was equal in the perceptually-matched condition, these illusion effects cannot be explained by the obstacle avoidance hypothesis.

Our results also indicate that the matching procedure did not work perfectly, but this is unproblematic for our argument for two reasons: firstly, the deviation from 0 in the classic perceptual task was small. We argue that with a step size of .25 mm, and controlling for the illusion's superadditivity (see Foster & Franz, 2014), our match was close to optimal. As explained in Section 1.6, we did not expect to be able to achieve a perfect match. Secondly, the physically larger object was also perceived to be slightly larger in the classic perceptual task. This means that the physical difference between the two targets was larger than necessary to achieve perceptual equivalence. Consequently, we should have found an even larger difference in grasping than we would have had we been able to create a perfect match. Thus, if anything, the perceptually-matched condition was over-sensitive to detecting a dissociation. The fact that this dissociation was not found suggests that the illusion effect on grasping is sufficiently pronounced to eliminate the physical difference of the target objects. In summary, the results in the perceptually-matched condition are consistent with the results of the physically-matched conditions: both indicate that the Ebbinghaus illusion affects grasping.

5.3. *Is there no effect of obstacle avoidance at all?*

For a reader with a background in motor control, it might seem implausible to argue that obstacle avoidance has no effect on grasping. In fact, it is well known that distractors can affect movements (e.g., Tipper, Lortie, & Baylis, 1992). However, what we tested and argue against is only one very specific obstacle avoidance hypothesis, namely the notion that the context circles produce distinct grasping behaviour identical to the perceptual illusion in the “classic” illusion display (SN-LF) as used by Aglioti et al. (1995) and many studies after that. This specific obstacle-avoidance hypothesis assumes that in the far condition participants aim to fit their grasping fingers between target and context whereas in the near condition the fingers do not fit in this space and therefore grasp larger. Haffenden and Goodale (2000) and Haffenden et al. (2001) proposed this obstacle avoidance mechanism in order to reconcile the existence of an effect of the Ebbinghaus illusion on grasping in the traditional display with their notion that grasping is immune to the illusion. They argued that the observed illusion effects on grasping in those studies were methodological artefacts due to imperfect stimuli. They suggested that if better stimuli were used – such as stimuli with equated distance of the context elements – the Ebbinghaus illusion would not affect grasping. We tested this claim and can safely refute it.

Note that for our claim it is not necessary that the context elements have no obstacle-like effects on grasping at all. For example, de Grave et al. (2005) found (small) effects of rotating Ebbinghaus displays on grasping parameters other than MGA. What we do claim is that the context elements do not affect MGA in a way that mimics the perceptual illusion effect. Even with our very large sample, we did not find an obstacle avoidance effect on MGA. Thus, it seems unlikely that we have missed an effect large enough to be reliably detected by studies with much smaller samples. Any obstacle effects of the context circles on the MGA, if they exist, would be too small by far to explain the illusion effects that were found in grasping.

6. Conclusion

In summary, we can draw the following conclusions: there is no doubt that there is an effect of the Ebbinghaus illusion on grasping. This effect correlates with the illusion effect on classic perceptual measures as well as on manual estimation. Crucially, this effect cannot be explained as an artefact of obstacle avoidance. A dissociation between vision-for-perception and vision-for-action when grasping the Ebbinghaus illusion, as suggested by the TVSH, is not supported.

Acknowledgements

We thank Brian Roberts and Mike Harris for responding to our questions regarding their paper; Zoltan Dienes for advice on Bayes factors; Denise Fischer, Melanie Römer, Ioana Stanciu, Aleksandra Romanczuk, Stefano Uccelli, Nuria Martos Sánchez, and Rosa María Beño Ruiz de la Sierra for help collecting data; Eva Viviani for managing data collection in

Parma. We thank Maurizio Gentilucci for letting us use his lab, and the Centro Intradipartimentale Mente e Cervello (CIMeC), University of Trento, and especially Francesco Pavani for lending us his motion tracking equipment. We thank Rachel Foster for proofreading. KKK was supported by a Ph.D. scholarship as part of a grant to VHF within the International Graduate Research Training Group on Cross-Modal Interaction in Natural and Artificial Cognitive Systems (CINACS; DFG IKG-1247) and TS by a grant (DFG – SCHE 735/3-1); both from the German Research Council.

Appendix A. Supplementary results tables

Table A.1 – Corrected illusion effects tested against each other, all measures.

Comparison		SN–LF		SF–LF		SN–LN	
		t(143)	<i>p</i>	t(143)	<i>p</i>	t(143)	<i>p</i>
Grasping	versus perception	-.07	.942 n.s.	.65	.515 n.s.	-.24	.813 n.s.
	versus ME CL	.94	.347 n.s.	2.03	.044*	1.42	.157 n.s.
	versus ME OL	-.22	.823 n.s.	1.38	.169 n.s.	.40	.689 n.s.
Perception	versus ME CL	1.71	.089 n.s.	2.62	.010*	2.61	.010*
	versus ME OL	-.24	.810 n.s.	1.35	.179 n.s.	.85	.398 n.s.
ME CL	versus ME OL	1.34	.181 n.s.	.73	.469 n.s.	1.09	.276 n.s.

Note: n.s. indicates non-significant, * indicates $p < .05$, ** indicates $p < .001$. Statistically significant p -values are given in italics.

Table A.2 – Uncorrected illusion effects tested against each other, all measures.

Comparison		SN–LF		SF–LF		SN–LN	
		t(143)	<i>p</i>	t(143)	<i>p</i>	t(143)	<i>p</i>
Grasping	versus perception	1.55	.123 n.s.	1.76	.081 n.s.	1.35	.180 n.s.
	versus ME CL	3.92	<.001**	4.27	<.001**	4.66	<.001**
	versus ME OL	2.26	.025*	3.57	<.001**	3.18	.002*
Perception	versus ME CL	3.26	.001**	4.15	<.001**	3.98	<.001**
	versus ME OL	1.61	.108 n.s.	2.85	.005*	2.97	.003*
ME CL	versus ME OL	.71	.476 n.s.	.05	.959 n.s.	.31	.756 n.s.

Note: n.s. indicates non-significant, * indicates $p < .05$, ** indicates $p < .001$. Statistically significant p -values are given in italics.

Appendix B. Pilot data

We tested 4 participants (mean age 33.5 years) on a simple perceptual judgement task to examine two issues: First, we considered including a “large-very far” (LVF) condition as an extra test of obstacle avoidance and wanted to gauge the perceptual illusion effect with different target-annulus distances. This condition was discarded during the review

process (and will not be reported in detail here). Second, we wished to examine how large the illusion effects and variation between responses would be, so that we would be able to create a graded series of comparison stimuli that would not result in floor or ceiling effects.

In this task, 8 different Ebbinghaus illusion displays were displayed to the participants: SN, SF, LN, LF as described in Section 1.6, and 4 versions of LVF, each with a different annulus diameter (67, 82, 96 and 110 mm). Target circles were 28, 30, and 32 mm in diameter. Each of the resulting 24 conditions was presented 6 times to each participant, resulting in a total of 144 trials per participant. The task was to determine which one of 8 comparison circles was equal in size to the

target circle and to press the corresponding number on the numpad of a standard German QWERTZ-keyboard. The comparison circles were displayed on the left side of the screen, sorted by size, ascending, in steps of 1.136 mm (4 pixels). The sizes were pseudo-randomised, but always chosen such that the smallest comparison circle was at least 8 pixels (2.272 mm) smaller, and the largest comparison circle at least 8 pixels larger than the target. The specifications and mean illusion effects of interest can be found in Table B1.

Table B1 – Conditions and corresponding mean illusion effects in our perceptual pilot data.

Condition	Number of context circles	Diameter of context circles (in mm)	Inner diameter of annulus (in mm)	Mean illusion effect \pm SD (in mm)
SN	11	10	38	1.42 \pm .255
SF	16	10	54	.71 \pm .586
LN	5	54	38	-1.18 \pm .626
LF	5	54	54	-1.23 \pm .673

The observed illusion effects are in the expected range, with 97.1% of the responses being within 12 pixels (3.41 mm) of the actual size. The remaining 2.9% of all responses were within 16 pixels (4.54 mm) of the actual size. Based on these results, we felt confident that our comparison stimuli ranging from 5 mm smaller than the smallest target to 5 mm larger than the largest target would produce no floor or ceiling effects.

REFERENCES

- Aglioti, S., DeSouza, J. F. X., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, 5(6), 679–685.
- de Brouwer, A. J., Smeets, J. B. J., Gutteling, T. P., Toni, I., & Medendorp, W. P. (2015). The Müller-Lyer illusion affects visuomotor updating in the dorsal visual stream. *Neuropsychologia*, 77, 119–127. <http://dx.doi.org/10.1016/j.neuropsychologia.2015.08.012>.
- Bruno, N. (2016). Visual illusions in action. In A. Shapiro, & D. Todorovic (Eds.), *The Oxford Compendium of visual illusions*. Oxford, UK: Oxford University Press.
- Bruno, N., & Franz, V. H. (2009). When is grasping affected by the Müller-Lyer illusion? A quantitative review. *Neuropsychologia*, 47, 1421–1433.
- Bruno, N., Knox, P. C., & de Grave, D. D. J. (2010). A meta-analysis of the effect of the Müller-Lyer illusion on saccadic eye movements: no general support for a dissociation of perception and oculomotor action. *Vision Research*, 50(24), 2671–2682. <http://dx.doi.org/10.1016/j.visres.2010.09.016>.
- Carey, D. P. (2001). Do action systems resist visual illusions? *Trends in Cognitive Sciences*, 5(3), 109–113.
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). New York, NY: Psychology Press.
- Coren, S., & Enns, J. T. (1993). Size contrast as a function of conceptual similarity between test and inducers. *Perception & Psychophysics*, 54(5), 579–588.
- Coren, S., & Girgus, J. S. (1972). A comparison of five methods of illusion measurement. *Behavior Research Methods & Instrumentation*, 4(5), 240–244. <http://dx.doi.org/10.3758/BF03210006>.
- Dassonville, P., & Reed, S. A. (2015). The Two-Wrongs model explains perception-action dissociations for illusions driven by distortions of the egocentric reference frame. *Frontiers in Human Neuroscience*, 9(March), 1–16. <http://dx.doi.org/10.3389/fnhum.2015.00140>.
- Dewar, M. T., & Carey, D. P. (2006). Visuomotor “immunity” to perceptual illusion: a mismatch of attentional demands cannot explain the perception-action dissociation. *Neuropsychologia*, 44(8), 1501–1508. <http://dx.doi.org/10.1016/j.neuropsychologia.2005.11.010>.
- Dienes, Z. (2008). *Understanding psychology as a science. An introduction to scientific and statistical inference*. New York: Palgrave Macmillan.
- Dienes, Z. (2011). Bayesian versus Orthodox statistics: which side are you on? *Perspectives on Psychological Science*, 6(3), 274–290.
- Efron, B., & Tibshirani, R. J. (1993). *An introduction to the bootstrap*. New York: Chapman & Hall.
- Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: tests for correlation and regression analyses. *Behavior Research Methods*, 41, 1149–1160.
- Foster, R. M., & Franz, V. H. (2014). Superadditivity of the Ebbinghaus and Müller-Lyer illusions depends on the method of comparison used. *Perception*, 43(8), 783–795. <http://dx.doi.org/10.1068/p7802>.
- Foster, R. M., Kleinholdermann, U., Leifheit, S., & Franz, V. H. (2012). Does bimanual grasping of the Müller-Lyer illusion provide evidence for a functional segregation of dorsal and ventral streams? *Neuropsychologia*, 50, 3392–3402.
- Franz, V. H. (2003). Manual size estimation: a neuropsychological measure of perception? *Experimental Brain Research*, 151, 471–477.
- Franz, V. H. (2007). Ratios: A short guide to confidence limits and proper use. Retrieved from <http://arxiv.org/pdf/0710.2024v1.pdf>.
- Franz, V. H., Bühlhoff, H. H., & Fahle, M. (2003). Grasp effects of the Ebbinghaus illusion: obstacle avoidance is not the explanation. *Experimental Brain Research*, 149, 470–477.
- Franz, V. H., Fahle, M., Bühlhoff, H. H., & Gegenfurtner, K. R. (2001). Effects of visual illusions on grasping. *Journal of Experimental Psychology: Human Perception and Performance*, 27(5), 1124–1144.
- Franz, V. H., & Gegenfurtner, K. R. (2008). Grasping visual illusions: consistent data and no dissociation. *Cognitive Neuropsychology*, 25, 920–950.
- Franz, V. H., Gegenfurtner, K. R., Bühlhoff, H. H., & Fahle, M. (2000). Grasping visual illusions: no evidence for a dissociation between perception and action. *Psychological Science*, 11(1), 20–25.
- Franz, V. H., Hesse, C., & Kollath, S. (2009). Visual illusions, delayed grasping, and memory: no shift from dorsal to ventral control. *Neuropsychologia*, 47, 1518–1531.
- Franz, V. H., & Loftus, G. R. (2012). Standard errors and confidence intervals in within-subjects designs: generalizing Loftus and Masson (1994) and avoiding the biases of alternative accounts. *Psychonomic Bulletin & Review*, 19, 395–404.
- Franz, V. H., Scharnowski, F., & Gegenfurtner, K. R. (2005). Illusion effects on grasping are temporally constant not dynamic. *Journal of Experimental Psychology: Human Perception and Performance*, 31(6), 1359–1378.
- Ganel, T., Tanzer, M., & Goodale, M. A. (2008). A double dissociation between action and perception in the context of visual illusions: opposite effects of real and illusory size. *Psychological Science*, 19(3), 221–225.
- Girgus, J. S., Coren, S., & Agdern, M. (1972). The interrelationship between the Ebbinghaus and Delboeuf illusions. *Journal of Experimental Psychology*, 95(2), 453–455.
- Glover, S., & Dixon, P. (2002). Dynamic effects of the Ebbinghaus illusion in grasping: support for a planning/control model of action. *Perception & Psychophysics*, 64(2), 266–278.
- Gonzalez, C. L. R., Ganel, T., & Goodale, M. A. (2006). Hemispheric specialization for the visual control of action is independent of handedness. *Journal of Neurophysiology*, 95, 3496–3501.
- Gonzalez, C. L. R., Ganel, T., Whitwell, R. L., Morrissey, B., & Goodale, M. A. (2008). Practice makes perfect, but only with the right hand: sensitivity to perceptual illusions with awkward grasps decreases with practice in the right but not the left hand. *Neuropsychologia*, 46, 624–631.
- Goodale, M. A. (2008). Action without perception in human vision. *Cognitive Neuropsychology*, 25(7–8), 891–919.
- Goodale, M. A. (2014). How (and why) the visual control of action differs from visual perception. *Proceedings of the Royal Society B*, 281, 20140337. <http://dx.doi.org/10.1098/rspb.2014.0337>.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20–25.
- Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, 349, 154–156.
- de Grave, D. D. J., Biegstraaten, M., Smeets, J. B. J., & Brenner, E. (2005). Effects of the Ebbinghaus figure on grasping are not only due to misjudged size. *Experimental Brain Research*, 163, 58–64.
- Haffenden, A. M., & Goodale, M. A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience*, 10(1), 122–136.

- Haffenden, A. M., & Goodale, M. A. (2000). Independent effects of pictorial displays on perception and action. *Vision Research*, 40, 1597–1607.
- Haffenden, A. M., Schiff, K. C., & Goodale, M. A. (2001). The dissociation between perception and action in the Ebbinghaus illusion: nonillusory effects of pictorial cues on grasp. *Current Biology*, 11, 177–181.
- Hesse, C., Franz, V. H., & Schenk, T. (2016). Pointing and anti-pointing in Müller-Lyer figures: why illusion effects need to be scaled. *Journal of Experimental Psychology: Human Perception and Performance*, 42(1), 90–102.
- Himmelbach, M., Boehme, R., & Karnath, H.-O. (2012). 20 years later: a second look on DF's motor behaviour. *Neuropsychologia*, 50, 139–144.
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6(2), 65–70.
- Jandó, G., Agostini, T., Galmonte, A., & Bruno, N. (2003). Measuring surface achromatic color: toward a common measure for increments and decrements. *Behavior Research Methods, Instruments & Computers*, 35(1), 70–81.
- Jeannerod, M. (1984). The timing of natural prehension movements. *Journal of Motor Behavior*, 16(3), 235–254.
- Jeffreys, H. (1961). Theory of probability. In N. F. Mott, E. C. Bullard, & D. H. Wilkinson (Eds.), *The international series of monographs on physics* (3rd ed.). Oxford: Oxford University Press.
- Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review*, 1, 476–490.
- McIntosh, R. D., & Lashley, G. (2008). Matching boxes: familiar size influences action programming. *Neuropsychologia*, 46, 2441–2444.
- Milgram, P. (1987). A spectacle-mounted liquid-crystal tachistoscope. *Behavior Research Methods, Instruments & Computers*, 19(5), 449–456.
- Milner, A. D., Dijkerman, H. C., Pisella, L., McIntosh, R. D., Tilikete, C., Vighetto, A., et al. (2001). Grasping the past: delay can improve visuomotor performance. *Current Biology*, 11, 1896–1901.
- Milner, A. D., Ganel, T., & Goodale, M. A. (2012). Does grasping in patient D.F. depend on vision? *Trends in Cognitive Sciences*, 16(5), 256–257.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action* (1st ed.). Oxford: Oxford University Press Inc.
- Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action* (2nd ed.). Oxford: Oxford University Press Inc.
- Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, 46, 774–785.
- Murray, S. O., Boyaci, H., & Kersten, D. (2006). The representation of perceived angular size in human primary visual cortex. *Nature Neuroscience*, 9(3), 429–434.
- Nunnally, J. C. (1967). *Psychometric theory*. New York, NY: McGraw-Hill.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.
- Pavani, F., Boscagli, I., Benvenuti, F., Rabuffetti, M., & Farnè, A. (1999). Are perception and illusion affected differently by the Titchener circles illusion? *Experimental Brain Research*, 127, 95–101.
- Post, R. B., & Welch, R. B. (1996). Is there dissociation of perceptual and motor responses to figural illusions? *Perception*, 25(5), 569–581.
- Ramachandran, V. S., & Blakeslee, S. (1999). *Phantoms in the Brain: Probing the mysteries of the human mind*. New York, NY: William Morrow.
- Roberts, B., Harris, M. G., & Yates, T. A. (2005). The roles of inducer size and distance in the Ebbinghaus illusion (Titchener circles). *Perception*, 34, 847–856.
- Schenk, T. (2006). An allocentric rather than perceptual deficit in patient D.F. *Nature Neuroscience*, 9(11), 1369–1370.
- Schenk, T. (2010). Visuomotor robustness is based on integration not segregation. *Vision Research*, 50, 2627–2632.
- Schenk, T. (2012). No dissociation between perception and action in patient DF when haptic feedback is withdrawn. *The Journal of Neuroscience*, 32(6), 2013–2017.
- Schenk, T., Franz, V. H., & Bruno, N. (2011). Vision-for-perception and vision-for-action: which model is compatible with the available psychophysical and neuropsychological data? *Vision Research*, 51, 812–818.
- Schenk, T., & McIntosh, R. D. (2010). Do we have independent visual streams for perception and action? *Cognitive Neuroscience*, 1(1), 52–62.
- Smeets, J. B. J., & Brenner, E. (1999). A new view on grasping. *Motor Control*, 3(3), 237–271.
- Smeets, J. B. J., & Brenner, E. (2006). 10 Years of illusions. *Journal of Experimental Psychology: Human Perception and Performance*, 32(6), 1501–1504.
- Smeets, J. B. J., Glover, S., & Brenner, E. (2003). Modeling the time-dependent effect of the Ebbinghaus illusion on grasping. *Spatial Vision*, 16(3–4), 311–324.
- Stevens, S. S. (1959). Cross-modality validation of subjective scales for loudness, vibration, and electric shock. *Journal of Experimental Psychology*, 57(4), 201–209.
- Stöttinger, E., Pfusterschmied, J., Wagner, H., Danckert, J., Anderson, B., & Perner, J. (2012). Getting a grip on illusions: replicating Stöttinger et al. [Exp Brain Res (2010) 202:79–88] results with 3-D objects. *Experimental Brain Research*, 216(1), 155–157. <http://dx.doi.org/10.1007/s00221-011-2912-8>.
- Tipper, S. P., Lortie, C., & Baylis, G. C. (1992). Selective reaching: evidence for action-centered attention. *Journal of Experimental Psychology: Human Perception and Performance*, 18(4), 891–905.
- Vul, E., Harris, C., Winkielman, P., & Pashler, H. (2009). Puzzlingly high correlations in fMRI studies of emotion, personality, and social cognition. *Psychological Science*, 4(3), 274–290. <http://dx.doi.org/10.1111/j.1745-6924.2009.01132.x>.
- Weiskrantz, L. (1990). Outlooks for blindsight: explicit methodologies for implicit processes. *Proceedings of the Royal Society B*, 239, 247–278.
- Westwood, D. A., & Goodale, M. A. (2011). Converging evidence for diverging pathways: neuropsychology and psychophysics tell the same story. *Vision Research*, 51, 804–811.
- Whitwell, R. L., Milner, A. D., Cavina-Pratesi, C., Byrne, C. M., & Goodale, M. A. (2014). DF's visual brain in action: the role of tactile cues. *Neuropsychologia*, 55, 41–50. <http://dx.doi.org/10.1016/j.neuropsychologia.2013.11.019>.