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When is grasping affected by the Müller-Lyer illusion? A quantitative review

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ABSTRACT

Milner and Goodale (1995) [Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford, UK: Oxford University Press] proposed a functional division of labor between vision-for-perception and vision-for-action. Their proposal is supported by neuropsychological, brain-imaging, and psychophysical evidence. However, it has remained controversial in the prediction that actions are not affected by visual illusions. Following up on a related review on pointing (see Bruno et al., 2008 [Bruno, N., Bernardis, P., & Gentilucci, M. (2008). Visually guided pointing, the Müller-Lyer illusion, and the functional interpretation of the dorsal-ventral split: Conclusions from 33 independent studies. *Neuroscience and Biobehavioral Reviews, 32*(3), 423–437]), here we re-analyze 18 studies on grasping objects embedded in the Müller-Lyer (ML) illusion. We find that median percent effects across studies are indeed larger for perceptual than for grasping measures. However, almost all grasping effects are larger than zero and the two distributions show substantial overlap and variability. A fine-grained analysis reveals that critical roles in accounting for this variability are played by the informational basis for guiding the action, by the number of trials per condition of the experiment, and by the angle of the illusion fins. When all these factors are considered together, the data support a difference between grasping and perception only when online visual feedback is available during movement. Thus, unlike pointing, grasping studies of the Müller-Lyer (ML) illusion suggest that the perceptual and motor effects of the illusion differ only because of online, feedback-driven corrections, and do not appear to support independent spatial representations for vision-for-action and vision-for-perception.

1. Introduction

More than a decade ago, David Milner and Melvyn Goodale proposed a novel functional interpretation of the primate visual system. In their proposal, set forth in the influential book *The visual brain in action* (Milner & Goodale, 1995) and later popularized in their wonderfully accessible *Sight unseen* (Goodale & Milner, 2004), they suggested that the dorsal–ventral anatomical split after the primary visual cortex may be interpreted as the neural substrate of two independent visual modules: a vision-for-perception module (the V1–IT ventral pathway) and a vision-for-action module (the V1–PPT dorsal pathway). Although dichotomous models of the visual system were not new (Trevarthen, 1968; Ungerleider & Mishkin, 1982), the proposal substituted the earlier problematic distinction between "what" and "where" pathways with a more powerful distinction between two visual functions: recognizing and identifying objects (vision-for-perception) and guiding actions (vision-for-action). The idea has proved attractive, not only for its potential to resolve a long-standing controversy in perceptual theory (see for instance Norman, 2002) but also for its success in explaining a number of empirical facts in diverse research domains such as neuropsychology, functional imaging, and psychophysics.

Despite its success, however, the hypothesis of Milner and Goodale has remained controversial with regard to the degree of "encapsulation", or functional independence, between the two-visual functions. Milner and Goodale made the strong prediction that, under certain conditions, vision-for-action should operate on the basis of spatial representations that have different properties than, and are fully independent from, the spatial representations at the basis for our conscious experience. In support of this idea they listed several lines of evidence. In the striking phenomenon of "blindsight" (Weiskranz, 1986), for instance, patients with cortical scotomas can point to visual targets presented in blind areas of their visual field, but report that they have no experience of having seen those targets. Patients with visual form agnosia, such as the much-

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studied D.F. (Milner, 1997), cannot identify the objects they see, and yet they can reach for and grasp them in ways that are comparable to those of a healthy control. But perhaps the most important, and certainly more controversial, line of empirical findings bearing to this issue has been research on motor responses to visual illusions.

Typical visual illusions are contextual effects. For instance, in the Ebbinghaus-Titchener illusion, the same disk appears larger when surrounded by smaller disks, and smaller when surrounded by larger disks (a size-contrast effect). In an influential paper, Aglioti, DeSouza, and Goodale (1995) hypothesized that the representation of the disk's size used in the vision-for-action module should be immune from such contextual effects. The rationale for the prediction was straightforward and descended directly from the two-visual-system hypothesis. Although both pathways receive the same information from primary visual cortex, this information may be processed in different ways for the purposes of action and perception. To guide actions towards the disk, visual information must be represented within a body-relative reference frame. Within this frame, the relationship of the disk to its surroundings is not important. For instance, to guide the hand towards the disk, what is important is the position of the hand relative to the disk itself. To grasp the disk, what is important is the size of the disk in relation to the current opening of the fingers. Thus, one may find that the kinematic parameters associated with a reach-to-grasp movement are not influenced by the contextual disks, even though the context of course influences the conscious perception of the target disks. This prediction was confirmed by data on the maximum in-flight grip aperture (MGA) of the thumb and index fingers while performing a precision grip of the disks embedded in the illusion. Aglioti and collaborators reported that the MGA remained constant, and correlated to the disk true width, even though participants judged the disks to be of different sizes. This finding quickly became popular under the heading that "size-contrast illusions deceive the eye but not the hand" (the paper's own title). But it also quickly stirred a heated controversy.

For the sake of concision, we will not attempt to summarize all the positions and issues that characterized the controversy (but see Bruno, 2001; Carey, 2001; Franz, 2001; Glover, 2002; Milner & Dyde, 2003). We will limit our discussion to two main points. The first concerns the methodology of perception–action comparisons. Soon after the publication of the early Aglioti paper, methodological criticism were raised casting doubts on the validity of the reported dissociation (Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farne, 1999). The brunt of these criticism consisted in pointing out that differences between the motor and perceptual stimulus conditions in the Aglioti experiment could account for the seeming dissociation without invoking separate representations of size in vision-for-action and vision-for-perception. In response to this and similar criticisms, as well as to novel findings reporting illusion effects in some conditions but not others, the focus of the controversy has steered towards a more articulated issue concerning the conditions under which actions responses may be insensitive, or at least less responsive, to illusions than perceptual responses. This debate has helped to clarify the different ways in which one may propose a distinction between spatial representations in vision-for-action and vision-for-perception, in turn allowing for better focusing of the related experimental predictions. Both are discussed in the section below.

1.1. *Perception and action: where do we draw the line?*

We suggest that there are five different ways in which one may cast a functional division of labor between perception and action, in particular with regard to the issue of independent representations. In addition, we propose that the vast literature on motor responses on illusions in fact contains quite a wealth of information to decide which may be true. Four of the five hypotheses assume that there are two independent representations, one for perception and one for action. For this reason, we will group them into the common category of two-visual-system hypotheses (TVSH) but parse them into the "naïve TVSH", "strong TVSH", "weak TVSH", and "planning-control TVSH". In addition, we also illustrate a fifth possibility, the "motor control hypothesis", which preserves the idea of a functional division of labor but rejects the notion of independent representations.

1.1.1. *Naïve TVSH*

Adopting a simple-minded conception of perception and motor control, one may propose that *any* motor response is based on a separate representation than that underlying conscious perception. This proposal is naïve, for it neglects that behavioral responses, be they in the form of object-directed actions or of verbal reports of one's conscious experience, always ultimately entail some kind of movement. For instance, speaking is needed for a verbal report but it is obviously also a motor response. Conversely, there are silent motor behaviors that one can perform to describe one's experience, such as gesturing or pantomime. And finally, a number of experimental results have shown that certain classes of motor responses are clearly affected by illusions just as much as phenomenal reports. Thus, naïve TVSH can be dispensed with. However, we deem it important to list it here, not only because this simple-minded account is sometimes found in literatures outside the cognitive neurosciences, but also because it helps us to focus on what is the theoretically relevant question at issue. This question is often stated in this way: "Do actions resist visual illusions?" If one refers this statement to actions in general, the answer is obviously no. A more relevant question is instead: "*When* do actions resist visual illusions?" As discussed in what follows, different answers to this question in fact correspond to different ways of conceiving the hypothesized independence between the two-visual systems, and to different theoretical implications of the answer.

1.1.2. *Strong TVSH*

In its strongest but non-naïve form, the notion of independent functions for action and perception proposes that a certain class of visually driven motor responses is based on representations that are fully independent of those employed to achieve conscious percepts. The exact definition of which responses have these properties is not completely clear, but there seems to be some consensus that "low level elementary" visuomotor processing (Jacob & Jeannerod, 2003) controls movements that are rapid, automatic, programmed on the basis of visual information rather than memory, and performed in tasks that do not force object-relative codlings of spatial variables. For instance, rapid pointing or reaching towards an object may be thought to be distinguishable from deictic pointing, which calls into play a more cognitive, symbolic function. Similarly, rapid object-directed grasping may be distinguished from "pantomimed" grasping or from grasping involving a representation derived from one's memory. Thus, the strong version of the TVSH proposes that these types of actions are based on spatial representations that are context-insensitive and independent of one's phenomenology. Within the illusion literature, strong TVSH amounts to predicting what may be called *immunity* of these types of motor processes from visual illusions. Immunity implies evidence that at least some motor responses are not affected by visual illusions, that is, that quantitative assessments of these effects are consistent with random samples from a population of effect measures whose mean equals zero. Conversely, perceptual responses to comparable visual displays should show clear illusion effects.

1.1.3. Weak TVSH

Another possibility is that vision-for-action and vision-for-perception subsystems may function as separate but interacting mechanisms (Goodale & Westwood, 2004). In this account, the context-sensitive internal representation that drives conscious perception always exerts some influence on the representation used to guide actions. However, in some cases this influence is reduced, such that certain classes of actions are less sensitive to contextual effects than other classes, or than conscious percepts. For instance, one may expect that rapid pointing, or rapid grasping, being largely if not completely performed on the basis of egocentric representations, may show a reduced sensitivity to contextual effects. Within the illusion literature, this weaker version of the TVSH amounts to predicting what may be called *resistance* of certain actions to illusions, meaning that these motor responses are affected by illusions to a lesser extent than perceptual responses. Weak TVSH implies evidence that measures of visually guided motor responses to illusions are random samples from a population with a non-zero mean, but that this mean is nonetheless smaller than the mean of the population of perceptual responses.

1.1.4. Planning-control TVSH

An even more specific version of the TVSH was proposed by (Glover, 2004; Glover & Dixon, 2001). As all other TVSH's, this hypothesis predicts that some action responses should be insensitive to contextual effects. In contrast to the weak TVSH, however, this model proposes a distinction between the preparatory phase (planning) and the control phase of the action. In this view, action preparation uses the same context-dependent visual representation as vision-for-perception. The control phase is instead driven by a context-independent representation, which is used within internal control loops in conjunction with visual or proprioceptive feedback, if available, or with predictive feedforward models if no feedback is available. The model assumes that the initial part of the action is based mostly on the planning representation, but as the action unfolds it becomes increasingly based on the control representation. Thus, Glover and colleagues predict a gradual decrease of the illusion effects during the unfolding of the movement, such that early movement parameters should be more affected than late movement parameters. A full evaluation of this model requires assessing such "dynamic" illusion effects during the movement. This has been done by Glover and Dixon themselves (e.g., Glover & Dixon, 2002), and by other studies with more critical outcome (e.g., Franz, Scharnowski, & Gegenfurtner, 2005; Meegan et al., 2004). For the purpose of this review, we will concentrate on a late movement parameter, the MGA (see methodological preliminaries below), for which Glover and Dixon (2001) predict that contextual effects are reduced (cf. Glover, 2004, p. 5 and p. 11). In this respect, therefore, predictions of the planning-control TVSH are identical to those of the weak TVSH, although of course, the theoretical basis of the models is quite different.

1.1.5. Motor control hypothesis

According to a final hypothesis, the difference in the use of visual information between vision-for-perception and vision-for-action may be more limited in scope, and reduced to the mere online control of the action. This account suggests that what makes motor responses less affected by context is the availability of sensory feedback during the actual movement (e.g. Post & Welch, 1996). To appreciate the difference between this proposal and the planning-control TVSH, it is useful to recall a fundamental difference between two ways of performing an action, say, a pointing response. In the first way, closed-loop (CL) pointing, visual information is continuously available both before movement onset and during the actual motion. In the second way, open-loop (OL) pointing, visual information is available before movement onset, such that the preparation of the movement can be completed from actual visual information; but once the movement begins, vision of the target is no longer available. In the motor control hypothesis, it is such visual feedback that allows motor control processes to perform online comparisons between, say, the current hand position and the target's position, and to use these to guide the movement independently of the context surrounding the target. This idea goes back to the two-phase model of actions (an early ballistic phase vs. a late feedback phase) suggested by Woodworth (1899). Note also that the motor control hypothesis is different from the planning-control TVSH, because the motor control hypothesis needs not assume that at any time a context-independent internal representation is generated. The planning-control TVSH, conversely, proposes that a context-independent representation is generated to guide the late phases of the movement, using visual or crossmodal feedback if available or internal loops based on efferent copies if not (cf. Glover & Dixon, 2002). Thus, unlike the four other different versions of the TVSH, the motor control hypothesis only needs to assume that a single representation is generated from the visual input. The division of labor between the two subsystems rests instead in the different processing of visual information during the online control phase, which necessarily uses context-insensitive, local computations driven by feedback-based error signals (for a similar interpretation of the neuropsychological evidence, see Rossetti, Pisella, & Vighetto, 2003). Within the illusion literature, the motor control hypothesis amounts to predicting that the resistance of actions to illusions should be limited to actions performed under CL conditions. Conversely, the planning-control model predicts that actions can be resistant to illusion even without visual feedback, provided that a context-independent representation can be used in internal control loops based on proprioceptive input or efferent copies.

1.2. A meta-analytic approach

Despite a large literature, there is currently no consensus regarding which of the above hypotheses is best supported by empirical data (see for instance Franz & Gegenfurtner, 2008; Goodale, 2008). However, we claim that this lack of consensus is more apparent than real. When looked at properly, the literature on motor responses on illusions in fact turns out to be strikingly consistent, and provides clear elements to decide between the theoretical alternatives outlined in the previous section. To this aim, we present a quantitative review of studies involving grasping responses on the ML illusion. The basic tools of our review are those of meta-analysis (Hunter & Schmidt, 2004; Rosenthal, 1991). Rather than focusing on the mere direction of differences between groups or conditions, as is customarily done in more standard narrative reviews, we will quantify illusion effects for each experimental condition of interest in different studies, taking care to adopt an effect measure suitable for comparison across different motor and perceptual responses (see Section 2). We will then use these effect measures to evaluate the results from different studies jointly, and to decide between different hypotheses on the nature of the division of labor within the visual system.

The backdrop for this work lies in previous meta-analytic work on rapid pointing in the ML illusion (Bruno, Bernardis, & Gentilucci, 2008). This work provided evidence for the weak version of the TVSH: Although the distribution of pointing responses was not consistent with a null effect of the illusion on pointing accuracy, the difference between the distributions of the pointing and perceptual responses was apparent, once the effect of two additional factors was taken into account. The first of these factors was related to the conditions under which pointing was programmed before motion onset. When the pointing program could be completed on the basis of online visual information, illusion effects were systematically smaller than those associated with perceptual measures. Conversely, when the program was done on the basis of the recent memory of the visual display, illusion effects became much more similar to those associated with perceptual measures. Strikingly, the availability of visual feedback during the action did not seem to have much importance in reducing the illusion effect, provided that online visual information was available during the preparatory stages of the movement (see also Goodale, Westwood, & Milner, 2004). The second factor was the number of trials performed by participants in each condition of the experiment. Given that its effect was evident for both CL and OL pointing, this factor may reflect a learning process whereby participants became increasingly adept at ignoring the contextual fins and at coding the location of the target endpoint on the illusion shaft in egocentric coordinates during the preparatory phase of the response. In this paper, we ask if these findings can be generalized to grasping responses to the same illusion.

2. Methodological preliminaries

We performed literature searches using MedLine, PsychInfo, WebOfScience, and Google. We included all studies that met the following criteria: (i) the stimuli were graspable bars placed on flat surfaces with drawn inward or outward pointing fins, such that the bar-and-fin arrangement produced the ML illusion; (ii) the motor dependent variable was the largest in-flight aperture between the index and thumb (maximum grip aperture, MGA); (iii) enough information was available (or could be obtained by contacting the authors) to derive a corrected percent measure of the illusion effect (see relevant section below).

The search yielded 16 papers or conference presentations reporting studies that met the criteria (Biegstraaten, de Grave, Brenner, & Smeets, 2007; Daprati & Gentilucci, 1997; Dewar & Carey, 2006; Franz, Fahle, Bülthoff, & Gegenfurtner, 2001; Franz, Hesse, & Kollath, this issue; Heath, Rival, & Binsted, 2004; Heath & Rival, 2005; Heath, Rival, Westwood, & Neely, 2005; Heath, Rival, & Neely, 2006; Heath, Rival, Neely, & Krigolson, 2006; Otto-de Haart, Carey, & Milne, 1999; Radoeva, Cohen, Corballis, Lukovits, & Koleva, 2005; van Doorn, van der Kamp, & Savelsbergh, 2007; Westwood, Chapman, & Roy, 2000; Westwood, Heath, & Roy, 2000; Westwood, McEachern, & Roy, 2001; see Appendix A). Given that one of these papers (Franz et al., this issue) reported three experiments using separate groups of participants, our database totaled 18 independent studies. On the other hand, most papers also performed several comparisons within their own group of participants. Thus, in addition to comparisons between independent groups of subjects in different studies, our complete dataset also included effect estimates for different conditions administered to the same groups of observers. Including these conditions as separate studies in our database brought the total number of grasping datapoints up to 32. To avoid undue complexity in the analysis, however, when examining variables that were manipulated both within and between observers by different studies, we considered all results as if they were from separate groups. From the standpoint of estimating illusion effects, this choice has no consequences (see for instance Rosenthal, 1991). From the standpoint of significance testing, this choice is conservative. When fitting a linear model, test statistics computed on groups considered as independent are always smaller, resulting in less statistical power, than the equivalent statistics computed on groups considered as dependent (see for instance Aron & Aron, 1994). Finally, we also analyzed estimates of the effects of the illusion on perception. Of the 16 references that we included in the review, 11 also included at least one experiment measuring perceptual effects (see Appendix B). This figure increased to 15 separate datapoints when including additional comparisons that were done within participants.

2.1. Specific aims and data-analytic approach

Our objective was threefold. First, we sought to estimate typical effects of the ML illusion on grasping and on perception, as well as their variability across studies. Second, we sought to determine in detail what variables modulate the effect of the illusion on grasping and perception. Third, and final, we aimed at making a comparison between motor and perceptual measures of the illusion. Accordingly, we performed three stages of analysis.

In the first stage, we examined the distributions of effects over the 18 and 11 independent measures mentioned in the above section, averaged across additional within-participant variables if present. This assessment provides a preliminary test of the strong and weak versions of the two-visual system hypothesis. If the strong version holds, one would expect that the distribution of grasping effects is consistent with a random sample from a population with zero mean, whereas the distribution of perceptual effects is consistent with a sample from a population with non-zero mean. If the weak version holds, one would expect that both are consistent with samples from populations with non-zero means, but the perception mean should be larger than the grasping mean. For the reasons outlined in the introduction, these tests alone are not sufficient to perform a complete evaluation of the two hypotheses. In particular, it must be noted that even in the strong version the claim has often been made that grasping is immune from the illusion only when it is programmed under full visual guidance (see Goodale et al., 2004). Thus, one would expect to see illusion effects on grasping responses that do not meet these criteria, such as, for instance, grasping performed after a delay and without visual feedback during the movement. For this reason, a comprehensive test of the two-visual-system hypothesis requires that we understand what factors, besides the mere response mode, may affect the grasping and perceptual measures such that perception and grasping can be compared meaningfully.

In the second stage, we examined in detail what variables might modulate the effect of the illusion on grasping and perception. Our examination was based on theoretical considerations as well as on measures of the effects associated with different variable. In this second stage, we used the 32 and 15 datapoints obtained after separating effects based on within-participant comparisons. This second stage aimed at selecting a subset of most relevant factors to be entered in linear models that capture the most relevant sources of variability in the motor and perceptual results.

In the third stage, finally, we performed a comparison between perception and grasping after partialling out the contribution of other, potentially important, determinants of the effects. We suggest that this final comparison provides the most informative test of the two-visual system hypothesis, allowing us to make a final evaluation of the difference between the two measures, if any.

2.2. Measuring the illusion effect

Most of the 16 papers reviewed here measured the effect of the illusion on both grasping and perception by the signed difference between the expanding and the compressing version of the ML pattern. However, this method of measuring the illusion poses a number of problems when comparing across experimental conditions in different studies or different measuring methods (motor or perceptual). The reason is that different experimental conditions or measuring methods typically exhibit different psychophysical functions of the dependent measure in relation to the actual width of the stimulus.

Consider the motor measure used in the studies reviewed here, the MGA, and one of the perceptual measures that are compared to it, the "manual estimation" of size which participants provide by matching the perceived width of the stimulus by the perceived thumb–index distance of their stationary hand. In a "calibration" study (unpublished), one of us (NB) recently compared these two responses to the actual width of 3D cubes. He found that both measures were related to width by linear functions, but these functions had clearly different parameters. Manual estimations closely corresponded to actual widths, yielding linear functions with unitary slopes and minimal intercepts. MGA's, instead, yielded linear functions with slopes around only 80% of the actual width and large intercepts.[1] Franz (2003) also reported large differences between the slopes of these functions. These different psychophysical behaviors of the two measures will affect the measured difference (expanding–compressing) for reasons that have nothing to do with the illusion effect, but simply because of the different scaling of a given dependent measure to actual width. For instance, because such scaling is typically less than unitary for MGAs, this will tend to reduce the size of the difference (expanding–compressing) relative to that observed for manual estimations that tend instead to have scalings equal or greater than unity.

To address this problem, one of us (VF) has advocated correcting the signed difference (expanding–compressing) by the characteristic slope of the measure at play (see Franz et al., 2001; Franz et al., 2005). This approach has been taken by some (Dewar & Carey, 2006), but not all grasping studies involving the ML illusion. However, the resulting corrected illusion effect is still not completely satisfactory as a means of comparing across different studies and measures, particularly if one wishes to compare across different motor behaviors such as, for instance, pointing and grasping. The reason is that different studies, particularly if different motor measures are collected, may involve stimuli with different actual widths.

Consider, for instance, a hypothetical grasping study comparing the expanding and compressing versions of the illusion with actual shaft widths of 10 cm. One may find, for instance, that the expanding version yields MGA's of 10.5 cm, and the compressing version MGA's of 9.5 cm, producing an uncorrected illusion effect equal to the difference $(10.5 - 9.5) = 1$ cm (for simplicity we assume a unitary slope in this example). Now consider an hypothetical pointing study comparing expanding and

[1] These differences are typical of these two measures. For instance, the average slope associated with the MGA in the present studies turns out to be 0.62 ± 0.08, whereas that associated with perceptual measures 0.9 ± 0.16. Other studies have reported slopes of as much as about 1.85 for measures such as manual estimation (Franz, 2003; Haffenden et al., 2001). For a recent review on this topic see Franz and Gegenfurtner (2008).

compressing in a version of the illusion with actual shaft widths of 20 cm. Suppose that the expanding version yields pointing amplitudes of 20.5 cm, and the compressing version amplitudes of 19.5. The resulting uncorrected difference would be again equal to (20.5 − 19.5) = 1 cm. However, these seemingly identical differences would have different meanings, as in one case they would correspond to a 10% effect, and in the other to a smaller 5% effect.

2.2.1. A corrected percent measure

The issues examined above suggest that an appropriate measure of the illusion should take into account differences in slope and in intercept between different conditions. To this aim, we computed a corrected percent measure of the illusion effect by the formula:

$$\% = \left(\frac{\text{expanding} - \text{compressing}}{\text{slope} \times \text{true width}}\right) \times 100$$

where *expanding* and *compressing* refer to the measure associated to each of the two versions of the illusion pattern, *true width* is the actual width of the segments, and *slope* refers to the slope of the linear function describing the scaling of the employed measure to actual width. Consider, for instance, a hypothetical grasping study employing 5 and 10 cm segments between the inward or outward fins. If the expanding and compressing versions of the illusion, averaged across participants, yield MGA's equal to 5.5 and 11 cm vs. 4.5 and 9 cm, and if the baseline responses are veridical (unitary slope), then the corrected percent effect is equal to the average of the 2% illusion effects:

$$\% = \left[\frac{(5.5-4.5)/(1\times 5)\times 100 + (11-9)/(1\times 10)\times 100}{2}\right] = \left[\frac{20\% + 20\%}{2}\right] = 20\%.$$

All corrected percent measures of the illusion (either MGA's in motor experiments, or whatever perceptual measure was used) and corresponding slopes were read off published tables or estimated as accurately as possible from data reported in graphic form. In studies that did not provide sufficient information to obtain a slope for grasping, percent effects were computed using the mean slope (0.82) computed by Smeets and Brenner (1999) from a separate set of grasping studies.

2.2.2. Relation to measures in pointing studies

In the context of studies of pointing on the ML illusion, one of us (NB) has proposed to correct the signed differences (expanding–compressing) by the measure obtained in a baseline pointing task on a neutral segment with no biasing fins (Bruno and Bernardis, 2003; Bernardis, Knox, & Bruno, 2005; Bruno et al., 2008; Knox & Bruno, 2007)[2]:

$$\% = \left[\frac{(\text{expanding} - \text{compressing})}{\text{baseline}}\right] \times 100$$

Although this percent measure seems based on a different logic, it is in fact only a special case of the more general measure used in the present paper. This is so because pointing responses are typically linear functions of true width with null intercepts. Given a null intercept, the baseline is given by the product of the typical slope by the true width:

$$\text{baseline} = \text{slope} \times \text{true width}$$

Therefore both percent measures yield the same results for pointing. The more general formula used here is needed because grasping, unlike pointing, has a non-zero intercept. If one used the pointing correction in the context of grasping, the constant intercept added to the baseline measure would artificially enlarge the denominator of the fraction, reducing the resulting percent effect in comparison to perceptual measures, which instead tend to have null intercepts.

2.2.3. Relation to statistical effect sizes

The percent illusion effect used here should not be confused with statistical effect sizes (Cohen, 1988). For a detailed motivation of the use of percent effects rather than Cohen's d as a measure of the illusion, see Bruno et al. (2008).

3. What is a typical effect of the ML illusion on grasping and perception?

3.1. Overall percent effect on grasping

The distribution of the 18 independent effects in the examined studies ranged from 0% to 14.3% and was reasonably symmetrical, with a median of 6.5% and a mean of 6.1%. Given this range of values it appears unlikely that these sample medians were drawn from a distribution centered at zero. Assuming that they were, from the *t* distribution with 17 degrees of freedom we estimate the probability of obtaining a value of 6.1% or larger as $p < 0.0001$.

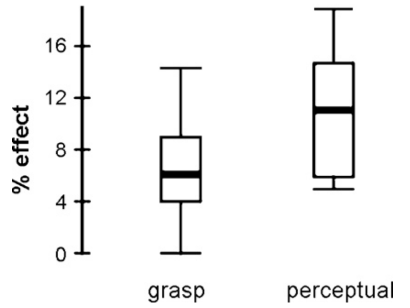

Fig. 1. Box plots comparing distributions of median percent effects on grasping and perception. Thick lines: medians. Boxes: data between the 1st and 3rd quartile. Whiskers: minimum and maximum values.

3.2. Comparison with weighted effect

The 18 studies were quite homogeneous in their sample size. In fact, all of them used samples with $8 < N < 26$, as is typical for grasping studies. Only one study used a somewhat larger sample size, 40 (Franz et al., this issue; exp. 3). These sample sizes suggest that the studies examined here did not differ markedly in the precision of their sample statistics. However, to check whether the overall results were changed by the precision of estimates, we computed the weighted average of sample effects using the inverses of the sample sizes as weights. Confirming our impression, the weighted average of the effects was 6.8%, essentially identical to the unweighted average. Based on this comparison, we performed all additional comparisons using the unweighted data.

3.3. Overall percent effect on perception

To determine how the overall effect on grasping compares with the effect on perception, we also evaluated measures of perceptual effects. In our corpus of 16 papers, 11 included at least one perceptual measure. The percent effects for these 11 measures are listed in Appendix B. They ranged from 5% to 18.8% with an average equal to 10.7% and a median equal to 11.2%.

3.4. Comparing effects on grasping and perception

A direct comparison of the distributions of percent effects on grasping and perception is provided by the box-plots in Fig. 1. Although they show a substantial degree of overlap, the two distributions are clearly different in their central tendency. The sign of the difference is consistent with the prediction that perceptual measures should produce larger illusory effects. Assuming that the two samples were drawn from the same population, such that the expected value for their sample difference between means would be zero, from the t distribution with 31 degrees of freedom we estimate the probability of observing at least the current difference as $p < 0.01$.

3.4.1. Preliminary conclusion

From our first assessment of 18 independent grasping and 11 independent perceptual results, we conclude that a typical effect of the illusion on grasping is smaller than its effect on perception. Nonetheless, the overall effect of ML illusions on grasping is

[2] Other pointing works (for instance, de Grave, Brenner, & Smeets, 2004) have used a slightly different approach, correcting by the average of the expanding and compressing measures. This is similar to correcting by the baseline, as the unbiased measure is typically in between the expanding and compressing measures.

Table 1
Grasp illusion effects by duration of preview period.

Preview	*N* (studies)	Mean	Median	S.E.
1–2s	23	7.9	7.9	1.1
3–5s	2	1.8	1.8	0.4
Ad libitum	7	6.8	7.6	1.3

Table 2
Grasp illusion effects by nature of go signal.

Go signal	*N* (studies)	Mean	Median	S.E.
External	27	7.4	6.8	1.0
Self-generated	5	7.0	8.3	1.9

also obviously different from zero. Thus, and in analogy with the earlier pointing results (Bruno et al., 2008) our analysis does not support the prediction of the strong TVSH. Grasping (as measured by the MGA) is not immune to the ML illusion. Given the difference between the motor and the perceptual data, the reviewed studies may be consistent with the weak TVSH and the planning-control TVSH, or with the motor control hypothesis.

4. What drives effects on grasping?

We evaluated 9 candidate factors by comparing mean and median illusory effects across levels. Candidates were selected on the basis of theoretical, methodological, and practical considerations, as stated in detail in the three sections below. We grouped the candidate factors into three general categories: The first 4 factors correspond to different aspects of the processes related to guiding the action. Factors 5–7 are related to properties of the employed stimuli. Factors 8 and 9, finally, are related to features of the experimental methodology. To provide a quick reference to all our findings in this part of the review, within each category factors are discussed within subsections that are numbered 1–9. The same numbers are then used for summary tables reporting the discussed effects. As stated in the Methodological Preliminaries section above, we performed this more fine-grained analysis after including both within- and between-participant manipulations. An overview of the dataset used in this analysis is presented in Appendix A.

4.1. Factors related to action guidance

1. Preview period. In all reviewed studies, participants could inspect the ML display before the initiation of each trial. However, the duration of this preview period varied across studies. In some cases it was relatively long (up to 5 s). In others, it was short. In still other cases, the preview period was not fixed but it instead lasted until the participant decided to start. Given that a long preview period may contribute to a better coding of the object structure, leading to more accurate grasps even if the stimulus was no longer visible during the action, we compared effects after grouping the available studies into three categories: short preview (1–2 s), long preview (3–5 s), or ad libitum preview (duration depends on when participant decides to start). Summary statistics of effects for these three categories are presented in Table 1. Interestingly, effects associated with long previews are much smaller than those associated with short previews. This may indicate that participants benefited from inspecting the display before the trial. In addition, we note that typical effects in studies employing ad libitum preview periods were as big as those in studies using short periods. Possibly, when left free to start when they wish to, participants start after briefly glancing at the stimulus[3]—thereby effectively reducing the preview period to 1–2 s. We note, however, that the number of studies employing long previews is very small. This suggests caution in drawing conclusions from the difference. For this reason, we conclude that there is not enough evidence for an effect of longer previews, although this factor may be worth a direct experimental test in further work.

2. Nature of go signal. In the large majority of the studies examined here, participants began the action after they heard a specific go signal, such as a tone or verbal instruction. In some studies, however, participants were left free to start when they felt they were ready to perform the grasp. This second method implies that participants could choose to benefit from a longer preview period and complete the preparation of the action while the stimulus remained available for inspection. For these reasons, it seems reasonable to predict that a self-generated go signal may improve accuracy. Table 2 compares effects after dividing the studies according to the type of go signal. As predicted, a self-generated go signal tends to yield a somewhat smaller effect than an external go signal. However, the mean difference is small in comparison with the size of the standard errors, and it becomes almost zero when considering median effects. We conclude that the nature of the go signal does not, *per se*, influence the effect of the illusion on grasping.

3. Visibility of stimulus or hand during movement. If the stimulus remains visible during the movement, participants can use afferent feedback to fine-tune the grasp in flight. For instance, they can combine visual information about hand and finger positions with information about the position of the grasping target, and use this to optimize the grasping movement. In addition, even if the hand is not visible during the movement, they could monitor proprioceptive information about the hand and finger positions and cross-modally compare this with visual information about the target. Thus, an obvious prediction is that illusion effects on the grasping MGA should be smaller when the stimulus remains visible during the movement. Similarly one might expect that illusion effects are smaller when the hand remains visible during the movement. Visual feedback about the hand could be used in conjunction with visual feedback about the target, as argued above. Alternatively, it is also possible that seeing the hand during the movement remains advantageous even if the stimulus is no longer visible. In this case, one could still compare visual information about the hand with the recent memory of the target position and size. Therefore, we would expect that illusion effects on the grasping MGA should be smaller when the hand remains visible during the movement. Although visibility of stimulus and hand could, therefore, excert independent effects on the illusion effects, it turned out that visibilities of the stimulus and the hand are strongly correlated in the present dataset. In fact, in all studies visibility was controlled by the use of shutter goggles, which became opaque either at the go signal or at movement onset (depending on the method used) thereby preventing to obtain further visual information about hand and stimulus alike. Thus, at least in this dataset, the issue of the visibility of hand and stimulus reduces to that of visually open-loop (OL) vs. closed-loop (CL) guidance (see for instance Rosenbaum, 1991). We will return to this issue in the next subsection, where we suggest two alternative ways of combining the information provided by the examination of factors 1–3. In this subsection, we show in Table 3 the relevant summary statistics for visibility of hand and stimulus, which unsurprisingly confirm the predictions.

4. Delay. There is evidence that spatial representations for motor control are relatively short lived, lasting for 1–2 s at most (Hay & Redon, 2006; Hu & Goodale, 2000). This suggests that introducing a 2 s delay (or longer) before the beginning of an open-loop motor

[3] This hypothesis is informally supported by observation of participants in one study performed by one of us (Franz et al., this issue).

Table 3
Grasp illusion effects by visibility of stimulus/hand.

Stimulus/hand	*N* (studies)	Mean	Median	S.E.
Not visible	14	11	9.8	1.1
Visible	18	4.4	3.4	0.7

Table 4a
Grasp illusion effects by delay.

Condition	*N* (studies)	Mean	Median	S.E.
CL	18	4.4	3.4	0.7
OLmove	7	9.4	9.2	1.1
OLsignal	3	12.7	13.8	1.7
OLdelay	4	12.6	11.9	2.9

response should recruit other forms of spatial memory, possibly under the control of vision-for-perception. Accordingly, one would predict that MGA's are more strongly affected by the ML illusion when grasping takes place after a delay. To evaluate this prediction here, we divided the dataset according to a four-way classification: closed-loop (CL: stimulus and hand always visible, delay issue not applicable), open-loop-move (OLmove: vision is removed at movement onset, therefore there is effectively no delay), open-loop-signal (OLsignal: vision is removed at the presentation of an external go signal, such that the effective delay is the participant's reaction time), open-loop-delay (OLdelay: vision is removed, there is a waiting period, then an external go signal is provided and the action begins; the delay is therefore the length of the waiting period – in the current studies 2–5 s – plus the reaction time).

Relevant summary statistics are presented in Table 4a, which reveals an informative pattern. In the CL measures, median effects are small (about 3%), but they become larger in the OLmove measures (about 9%), and substantial in the OLsignal and OLdelay measures (about 12–14%). Interestingly, there is little difference between the OLsignal and the OLdelay condition, suggesting that a delay as short as the participant's reaction time (presumably, no more than 500 ms) is sufficient to produce as large an increase in the illusion effect as more substantial waiting periods. The above considerations suggest that the OLsignal and OLdelay conditions can be grouped into a single category. The resulting statistics, presented in Table 4b, reflect both the CL–OL distinction and the role of the go signal. Thus we suggest that this summary provides the most compact characterization of factors related to the guidance of the action.

4.2. Factors related to properties of the stimuli

5. Plane of stimulus presentation. The studies examined here also differed in important ways in some properties of the employed stimuli. The first is whether the ML stimulus were presented on a horizontal surface, such that they were more or less parallel to the transverse plane (dividing the upright participant's body into top and bottom), or on a vertical surface such that the stimulus was perpendicular to the transverse plane. The former mode of presentation affords comfortable grasping with the arm in a position similar to that used for writing. The latter mode of presentation is somewhat more tiring over repeated arm raises, and it may be speculated that this causes less natural or more "awkward" grasps. The possibility that awkward grasping may be less automatic and for this more under the control of vision-for-perception has been recently invoked as one of the possible sources of variation in motor effects of illusions (see Goodale, 2008). Table 5 presents the relevant summary statistics, which is not in accord with this prediction. We conclude that fatigue over repeated arm raises does not, *per se*, account for variations in illusion effects.

6. Stimulus orientation. A second obvious characteristic of the stimuli that changed in the present dataset was the orientation of the stimulus in relation to the participant's body. In some cases, this was parallel to the sagittal plane (dividing the body into left and right), such that the grasping position was natural. This happened for instance when the stimulus was on a table top and the illusion shaft could be grasped with the index finger on the distal and the thumb on the proximal end, or when it was mounted on a vertical support, such that the shaft was grasped with the index on the top end and the thumb on the lower end. Both these grasping positions involve no rotation of the wrist, given that the hand is placed in the correct position by raising or lowering the forearm through the elbow. In other cases, some table top stimuli were perpendicular to the sagittal plane, such that grasping the shaft required bringing the elbow towards the trunk and rotating the wrist to bring the thumb forward and the index backward. As can be readily verified by attempting a grasp in this way, this manner of presentation affords a somewhat less comfortable movement. Table 6 presents the relevant summary statistics, which are consistent with this prediction although the difference is small.

7. Angle of fins. In addition to the stimulus-related differences discussed in subsections 5 and 6, some of the studies reviewed here used slightly different versions of the ML illusion. In particular, they used context fins that formed slightly different angles relative to the graspable shaft. It is well established that fin angle modulates the strength of the dimensional effect in the ML illusion, as measured by standard psychophysical procedures (Pressey, Di Lollo, & Tait, 1977; Pressey & Martin, 1990), with fin-to-shaft angles around 30–40° being more efficacious than larger or smaller angles. To evaluate whether this factor may also affect a grasping measure, we divided our studies into two groups, fin angles less than 45° and angles greater than or equal to 45°. Table 7 presents the summary statistics, which suggest that fin angle may indeed be an important factor. Again, a word of caution is needed in drawing this conclusion due to the small number of studies that used larger angles (3 against 29 using smaller angles).

Table 4b
A summary characterization of factors related to action guidance.

Condition	*N* (studies)	Mean	Median	S.E.
CL	18	4.4	3.4	0.7
OLmove	7	9.4	9.2	1.1
OLsignal/delay	7	12.7	13.8	1.7

Table 5
Grasp illusion effects by plane of stimulus presentation.

Stimulus plane	*N* (studies)	Mean	Median	S.E.
Parallel	27	7.4	6.9	1.0
Perpendicular	5	6.8	6.8	1.7

Table 6
Grasp illusion effects by stimulus orientation.

Stimulus orientation	*N* (studies)	Mean	Median	S.E.
Parallel	15	7.8	6.9	1.3
Perpendicular	17	6.8	6.1	1.1

Table 7
Grasp illusion effects by fins angle.

Fin angle	*N* (studies)	*M*	*M*	S.E.
30–37	29	7.9	8.0	0.9
45–53	3	1.2	1.4	0.6

Table 8
Grasp illusion effects by device for measuring MGA.

Measuring device	*N* (studies)	Mean	Median	S.E.
Passive	3	4.8	5.6	1.4
Active	27	7.4	6.9	1.0
"Goniometer"	2	10	10	1.7

Table 9
Grasp illusion effects as a function of trials/condition.

Parameter	Coefficient	S.E. of coefficient
Intercept	11.7	2.03
Slope	−0.1	0.05

4.3. Factors related to experimental methods

8. Device for measuring the MGA. The studies examined here used somewhat different methods to monitor the finger aperture during the grasps. In particular, one study (Radoeva et al., 2005, 2 datapoints) used a sort of custom-made goniometer consisting of thin bars mounted on the fingers and connecting to a joint at the wrist where a potentiometer recorded the aperture between the bars. Because this method constrains the movement of the fingers in a significant way, it has been argued that grasping movements made under these conditions may be more controlled than automatic, thus relying more on perceptual information (see for instance Goodale, 2008, p. 19). Two studies used motion tracking equipment with passive markers applied on the participant's finger (Daprati & Gentilucci, 1997; Otto-de Haart et al., 1999; 3 datapoints). The remaining studies (totaling 27 datapoints) employed active markers. While both techniques are widely used, it is not clear if they imply differences in the degree to which they interfere with a completely natural movement. For instance, it may be speculated that cables connected to active markers and taped on the fingers and wrist cause participants to move more carefully and slowly than they normally would. Alternatively, one could argue that passive markers, consisting of half-spheres mounted on the fingernails, could also interfere especially if they are large in comparison to the fingertips. For all these reasons, we considered it worthwhile to evaluate potential differences in illusion effects. The relevant summary statistics, presented in Table 8, confirm that the recording device may have contributed to the variation in the observed illusion effects. We note, however, that the number of studies using passive markers or the goniometer method remain rather small in comparison to those using active markers. For this reason, it remains difficult to determine whether the differences are indeed caused by the measuring method or by other features of the studies. This may be an issue that will need to be addressed in a direct experimental comparison in further work.

9. Number of trials. Finally, an important methodological difference between the included studies is related to the number of trials that were combined to obtain an average measure of the MGA. It has been repeatedly reported that the perceptual effect of the ML illusion weakens over repeated presentation of the display (Judd, 1902; Köhler & Fishback, 1950; Lewis, 1908; Predebon, 2006). In a recent report Heath, Rival, Neely (2006) suggested that a similar decrease over repeated responses can occur for grasping on the ML illusion, and Gonzalez, Ganel, Whitwell, Morrissey, and Goodale (2008) suggested that awkward (less practiced) grasps are affected by the illusion initially but become increasingly less sensitive to illusions with practice. In their earlier review, Bruno et al. (2008) found that illusion effects on pointing were affected by number of trials, and reported a clear interaction between trial number and the direction of approach of the hand to the illusion pattern. They interpreted this effect as due to increasingly efficient egocentric coding of the target endpoint, as if participants could learn to better ignore the contextual fins after more trials. They also showed that this learning effect required less trials when the direction of approach already favored egocentric encoding of position, as was the case when the target was approached from an outside position and along a trajectory orthogonal to the illusion shaft, in comparison to when the direction of approach made it harder to ignore the fins as is the case when pointing was performed from one to the other endpoint and with a trajectory along the illusion shaft. While direction of approach is not relevant in the current grasping studies, it is nonetheless interesting to test the generality of this earlier finding in the current dataset. To this aim, we plotted effects as a function of the number of trials per condition. Consistent with the earlier findings, this plot showed a trend towards smaller effects with larger number of trials (a reduction of approximately 1% every 10 additional trials, see Table 9). After a log transformation of the percent effects to reduce a slight non-linearity in the plot, the linear effect of trial number accounted for about 18% of the total variability in the grasping effects.

4.4. Modeling the effect of the ML illusion on grasping

Having examined nine potential factors, on theoretical as well as statistical grounds, we conclude that a large portion of the variability analyzed here may be explained by three factors: the conditions for action guidance (see Table 4), the angle of fins (Table 7), and the number of trials per condition in the experiment (Table 9). To construct a descriptive model of the effect of the ML illusion on grasping, we subjected the percent effects to analysis of covariance (ANCOVA) using number of trials as the quantitative covariate and the other two factors as categorical predictors. Given the nature of the data, we used sequential sum of squares to account for the effect of trial number before computing *F* values associated with the other factors, and performed a log transformation of the dependent variable before entering it into the analysis. The quantitative covariate was entered in the analysis first, followed by angle and by the guidance conditions.[4] Overall, this three-predictor model captured 64% of the total variability. The strongest predictor was the summary factor related to action guidance, accounting for 33% of the variance, $F(2, 27) = 12.2$, $p < 0.0002$; followed by trials per condition, 18%, $F(1, 27) = 13.7$, $p < 0.001$; and fin angle, 13%, $F(1, 27) = 9.6$, $p < 0.005$. A graphical depiction of this fitted model is presented in Fig. 2.

We conclude that the differences of illusion effects on grasping in different studies can be captured remarkably well by only three factors. In addition, individual analyses also provided some grounds for possible contributions of the stimulus orientation and of the measuring device. Because the size of the differences or the lack of sufficient observations suggest caution, we preferred to leave these potential predictors out of our core model. We note, however, at least in the present dataset, adding them would increase the percentage of variance accounted for to 79%. As already stated when discussing these additional candidate factors individually, it may be worthwhile to examine their contributions directly in specific experiments.

[4] Using sequential sum-of-squares, the chosen order for entering predictors can alter the pattern of significance as well as the variance explained by each factor. It should be stressed, however, that the ordering does not change the total percentage of variability explained by the model, which therefore remains an overall measure of its descriptive power.

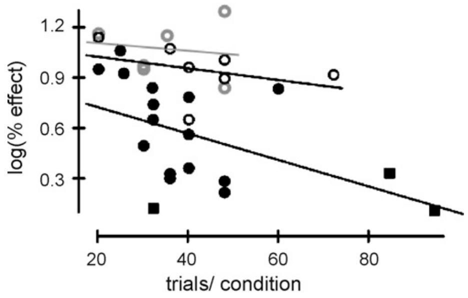

Fig. 2. Depiction of the linear model describing the variability of the grasping results. Black symbols: CL condition. Black circles: OLmove. Grey circles: OLsignal/delay. Squares: fin angles larger than or equal to 45°. Overall, this model captured almost 64% of the total variability in the grasping results.

Table 10
Perceptual effects by plane of stimulus presentation.

Stimulus plane	*N* (studies)	Mean	Median	S.E.
Parallel	10	8.5	7.6	1.0
Perpendicular	5	15.3	16.7	1.9

5. What drives effects on perception?

To determine which factors modulate the effect on perception, we took the same approach we adopted for grasping. We evaluated five candidate factors derived from methodological and practical considerations. For each, we computed summary statistics as presented below. Again, factors are numbered in the same way as the corresponding tables. A full summary of the dataset used in this second analysis is presented in Appendix B.

10. Plane of stimulus presentation. As for grasping, perceptual measures were based on illusions that could be presented parallel or perpendicular to the transverse plane of the participant's body. In the grasping data, this variation had no obvious effect. As shown in Table 10, however, the perceptual data indicate that when the plane of presentation was perpendicular participants tended to report stronger illusions. We cannot think of any theoretical or methodological rationale for this difference, which appears to be heavily influenced by the large illusion effects reported by Radoeva et al. (2005) which used a perpendicular plane but also a non-standard apparatus for recording both the MGA and the perceptual measure (see subsection 8 above).

11. Stimulus orientation. The summary statistics in Table 11 indicate that stimulus orientation may also have contributed to modulating the perceptual effects. This conclusion is tempered, however, by comparing the size of the standard errors with that of the difference between the two conditions. Given this variability, the evidence remains ambiguous concerning a perceptual effect of orientation.

12. Method for measuring perceptual effects. Most of the studies reviewed here assessed the conscious perceptual representation of shaft length in the illusion by a "manual estimation" method (Haffenden & Goodale, 1998; Haffenden, Schiff, & Goodale, 2001). In this method, participants are instructed to keep their hand near the body and to report, by opening the thumb and index fingers, their phenomenal impression of the actual shaft length. As such, manual estimation may be considered a variation of the classic method of adjustments. Instead of adjusting the length of a reference shaft to match the perceived length in the illusion, participants adjust the length of an imaginary line connecting their fingers. In some studies this is done while preventing participants from seeing their hand, making this a cross-modal match. In all the studies reviewed here, however, manual estimations were done while seeing the hand such that this issue can be neglected. Given that manual estimation is not a standard psychophysical method, some researchers have raised concerns about its comparability to other, more standard methods (see for instance Franz, 2003; Franz & Gegenfurtner, 2008). To investigate this issue, we compared in Table 12 summary statistics for manual estimation with those of the three results based on more standard psychophysical methods, such as the method of adjustments or matching methods, and with the single result that used a drawing method to assess perception. The manual estimation results appear comparable to those of more standard methods, especially when comparing the average difference with the size of the standard errors or when considering the medians. This result is consistent with the results of Franz (2003) and is due to the fact that our percent measure corrects for the larger slope of manual estimation. The effect associated with the drawing method is instead conspicuously smaller but again the finding is hard to interpret given that it is derived from a single experiment.

13. Angle of fins. By reasons similar to those given for grasping, one would expect that perceptual effects might vary as a function of the angle formed by the illusion fins relative to the shaft. Table 13 demonstrates that, as for the grasping data, larger angles are indeed associated with smaller illusion effects.

14.Number of trials. Finally, for the reasons already discussed for grasping, we expected that perceptual effects should vary as a function of the number of trials per experimental condition in the study. To evaluate this prediction, we plotted the 15 perceptual results as a function of trial number and fitted a linear regression model. As shown in Table 14, the parameters of the model closely matched those derived from the grasping results, involving a reduction of approximately 1% every 10 additional trials, although this estimate was slighly less precise due to the increase in the standard error of the slope in the smaller dataset.

5.1. Modeling the effect of the ML illusion on perception

The above analyses provide evidence for a potential effect of trial number on the perceptual illusion, as well as for additional effects

Table 11
Perceptual effects by stimulus orientation.

Stimulus orientation	*N* (studies)	Mean	Median	S.E.
Parallel	5	8.8	8.3	1.4
Perpendicular	10	11.7	12.1	1.7

Table 12
Perceptual effects by measurement method.

Measurement	*N* (studies)	Mean	Median	S.E.
Drawing	1	5.9	5.9	
Manual estimation	11	11.4	11.2	1.6
Standard	3	9.8	11.4	2.4

Table 13
Perceptual effects by fin angle.

Fin angle	*N* (studies)	Mean	Median	S.E.
30–37	11	12.5	12.7	1.4
45–53	4	5.9	5.5	0.7

Table 14
Perceptual effects as a function of trials/condition.

Parameter	Coefficient	S.E. of coefficient
Intercept	14.4	2.64
Slope	−0.1	0.06

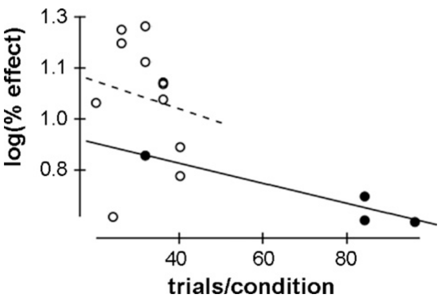

Fig. 3. Depiction of the linear model describing the variability of the perceptual results. (○) Fin angles less than 45°. (●) Greater than or equal to 45°. Overall, this model captured 71% of the total variability in the perception results.

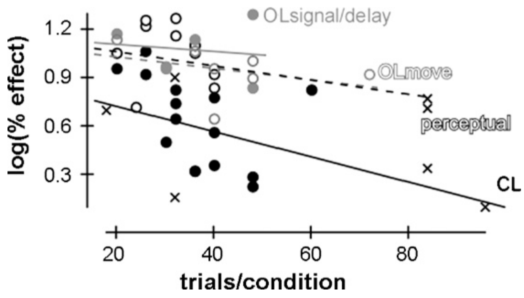

Fig. 4. Comparing perception and grasping while controlling for factors that affect both. (○ and ●) Different types of grasping or perceptual measures. X's: Fin angles greater or equal than 45°.

of the stimulus plane, stimulus orientation, and fin angle. To test these, we again proceeded as for the grasping data. We subjected the perceptual results to an analysis of covariance (ANCOVA) with trial number as numerical covariate, measuring methods, stimulus plane, stimulus orientation, and fin angle as categorical predictors. To account for the effect of the numerical covariate before assessing those of the categorical predictors, we used sequential sums of squares and entered the variables in the following order: trials, methods, plane, orientation, and fin angle. The results indicated that the stimulus orientation mattered little, $F(1, 10) < 1$, accounting for essentially no variability. Fin angle turned out to be the most important predictor, $F(1,10) = 12.5$, $p < 0.005$, accounting for 30% of the variability, followed by the stimulus plane, $F(1,10) = 11.7$, $p < 0.007$, 28%, and by the number of trials, $F(1,10) = 6.9$, $p < 0.03$, accounting for 17% of the variability. Overall, this model accounted for 76% of the total variation. These results suggest that at least two factors that affected the grasping results, trial number and fin angle, also had an effect on the perceptual results. A graphical depiction of the effect of these two factors is presented in Fig. 3.

6. Perception and action: a direct comparison

Our detailed analysis of the factors that modulate illusion effects in perception and grasping indicate that at least two factors affect both: the number of trials and the fin angle. This in turn suggests a way of performing a comparison between perception and action while controlling the effects of these two additional factors. To do this we performed a third ANCOVA on both the perception and grasping data, using again trial number as the quantitative covariate, along with two categorical predictors: type of measure (perceptual, OLsignal/delay grasp, OLmove grasp, or CL grasp), and fin angle (<45° or ≥45°). Given that we wanted to compare the different measures after accounting for differences due to number of trials and fin angle, we again used sequential sum of squares and entered trials first and angle second.

The results of this test revealed a significant effect of trial number, $F(1,41) = 19.3$, $p < 0.0001$, as well as of angle, $F(1, 41) = 6$, $p < 0.02$. Most importantly, however, they demonstrated a clear effect of the type of measure, $F(3, 41) = 16.5$, $p < 0.0001$. The pattern of these differences can be visualized in Fig. 4. This figure revealed smaller effects in the CL grasping measures than in perception and in the OLsignal/delay measures. Critically, however, it failed to reveal unequivocal differences between the OLmove grasping measures and either the perception or OLsignal/delay measures. As can be seen from the graph, grasping in OLmove conditions tended to yield smaller effects than grasping in OLsignal/delay conditions, but not than perception. In fact, the perceptual measures and the OLmove measures were almost identical when plotted in this way. This visual impression was further confirmed by a series of pairwise Scheffé post-hoc test, which yielded significant differences between CL grasping and all other measures, $p < 0.005$, but no significant differences between the OLmove condition and either perception, $p > 0.83$, or the OLsignal/delay condition, $p > 0.85$.

7. Discussion

Our detailed analysis of the factors that modulate illusion effects on perception and grasping supports two main conclusions. First, grasping is *always* affected by the illusion to some extent. Even with full visual feedback throughout the action (CL), there is a measurable effect on the maximum in-flight aperture between the finger and thumb during the grasp. This effect becomes larger when online feedback is removed while still allowing that the grasping program is formulated on the basis of available visual information (OLmove), and slightly larger still with no online feedback while performing the action and no online vision while programming the action (OLsignal/delay). This pattern of results confirms our preliminary conclusion against a strong TVSH (see Section 3). In no condition does grasping appear to be immune from the ML illusion. Second, effects are modulated by the conditions that control how observers use visual information to guide the grasp. As predicted by the weak TVSH, truly visually guided grasps (either in CL or OLmove conditions) are less affected by the illusion than memory-guided grasps. However, as predicted by the motor control hypothesis, only in CL conditions there is clear evidence that grasping yields smaller effects than perception. In all other motor conditions (including OLmove), illusion effects cannot be distinguished from the perceptual ones. Furthermore, both grasping and perception are modulated by at least two other factors: a factor related to a learning mechanisms, captured by the number of trials per experimental condition in the study, and a second factor related to a low-level stimulus property, the angle formed by the illusion fins. Comparing the perceptual and motor measures while controlling for these confirms the substantial similarity between the open-loop motor measures and the perceptual measures. Thus, this pattern of results suggests that visual feedback is critically important, which in turn speaks against the weak TVSH. This pattern of results is also not consistent with the planning-control TVSH, which predicts visuomotor resistance to the illusion in both the OLmove and the OLsignal conditions (Glover & Dixon, 2002). We conclude that the outcome of our meta-analysis is consistent with what we have called the motor control hypothesis.

In many respects, the present findings are consistent with those of the earlier meta-analysis on pointing (Bruno et al., 2008). However, they also differ from the pointing results in two crucial details. Consider similarities first. As in the pointing dataset, we found that the effects were modulated by the number of trials performed by participants, both in closed-loop and in open-loop conditions. This suggests that this effect is real and general, and it is important

Table 15
Comparison with dataset in Bruno et al. (2008).

	This meta-analysis		Bruno et al. (2008)	
	N (studies)	Mean	*N* (studies)	Mean
CL	18	4.4	31	2.1
OLmove	7	9.4	12	1.0
OLsignal/delay	7	12.6	25	14.6
Perception	15	10.7	10	24.3

to control it when comparing different effects either in perceptual or motor measures. In addition, as in pointing we found clear evidence for a difference between the perceptual measures and the action measures in CL conditions. Finally, also as in pointing we found evidence for a substantial similarity between the perceptual measures and the action measures when the action was delayed. But now turn to the differences. Consider Table 15, which summarizes average percent-corrected effects in the CL, OLmove, OLsignal/delay, and perceptual measures in the present data and in the pointing data of Bruno et al. (2008). As shown in the table, the two data sets yielded fairly similar effects in the CL and OLsignal/delay motor measures. However, they showed a clear difference in the OLmove condition, where the pointing results were small whereas in the current grasping dataset they were definitely larger than the CL measures and, at least in the current dataset, smaller but in fact statistically indistinguishable from the OLsignal/delay data. This difference between the two datasets may be interpreted to signify a different role of online feedback in pointing and grasping, at least as captured by the corresponding measures (displacement amplitude vs. MGA). This in turn may be thought to reflect the involvement of different cortico-cortical networks for the control of hand transport and manipulation. It is of some interest here that, based on anatomical and physiological evidence, Rizzolatti and Gallese (2006) recently suggested that only the dorso-dorsal stream within posterior parietal cortex corresponds to the characteristics of Milner and Goodale's TVSH. And, interestingly, the dorso-dorsal VIP-F4 network has been implicated in the visual control of reaching (see for instance Rizzolatti & Matelli, 2003).

We note, finally, that the largest difference between the two datasets is in the size of the perceptual effects. Within the pointing literature, most perceptual effects are large, almost twice as big even than the average effect in the delayed conditions. In the current grasping dataset, these perceptual effects appear greatly reduced. Such large reduction in the perceptual results is not really surprising, if one considers that in the current experiments participants viewed ML stimuli that were very different from those that were viewed, in most studies, by participants in the earlier pointing dataset. Because of the need to use graspable targets, participants viewed three-dimensional parallelepipeds, which were placed on a surface to form the ML configuration in conjunction with drawings representing the fins. Involving 3D and 2D parts, as well as various occlusion and lighting cues to their segregation, such an arrangement is unlikely to create a strong perceptual grouping of the fins with the shaft. Thus, given that the contextual cues were not grouped strongly with the target object, it is not surprising that the influence of context was reduced. One may then ask why the motor measures were not also reduced. At this stage, however, answers to such questions would necessarily be speculative and for this reason we will not pursue them here.

8. Conclusions

The proposal that vision-for-perception and vision-for-action operate on independent and distinguishable internal representations remains one of the most controversial aspects of Milner & Goodale's functional interpretation of the primate visual system. The controversy has focused on the interpretation of motor and perceptual responses to visual illusions in healthy participants, a literature that is often regarded as wildly contradictory. We believe that a meta-analytical approach to this literature is now beginning to show that, contrary to common belief, this literature is consistent and can be described well by a very limited set of principles. Our purpose in this paper was to make a second contribution in this direction after that of Bruno et al. (2008). We have shown that several of the explanatory principles that were successfully applied in the earlier work on pointing can indeed be applied to grasping as well, despite the differences in the measured parameters and in the employed stimuli. At the same time, however, our analysis also revealed important differences in the sensitivity to contextual effects of these two motor responses, in particular with reference to the role of online feedback. These differences may be interpreted as evidence that the preparatory phase of a grasp, unlike that of pointing, operates on the same spatial representation as perception. Unlike pointing, therefore, grasping responses to the ML illusion do not appear to support independent and distinguishable internal representation in vision-for-perception and vision-for-action as predicted by Milner and Goodale's model.

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Appendix A. Overview of grasping data

Study	Exp	*N*	Trial/condition	Visual guidance	Fin-angle	Preview	Go-signal	Stim/hand	Stim-plane	Stim-orient	Method	Percent-effect
Biegstraaten et al. (2007)	1	12	60	CL	30	adlib	self	vis	para	para	act	6.75
Daprati and Gentilucci (1997)	1	8	84	CL	45	5	ext	vis	para	para	pas	2.18
Dewar and Carey (2006)	1	15	32	CL	53	3	ext	vis	perp	para	act	1.42
Franz et al. (2001)	1	16	72	OLmove	30	adlib	self	nvis	para	para	act	8.36
Franz et al. (this issue)	1	16	48	CL	35	1	ext	vis	para	para	act	1.96
Franz et al. (this issue)	1	16	48	OLdelay 5s	35	1	ext	nvis	para	para	act	19.7
Franz et al. (this issue)	2	8	48	OLmove	35	1	ext	nvis	para	para	act	10.16
Franz et al. (this issue)	2	8	48	OLdelay 5s	35	1	ext	nvis	para	para	act	6.91
Franz et al. (this issue)	3	40	36	CL	35	1	ext	vis	para	para	act	2.13
Franz et al. (this issue)	3	40	36	OLmove	35	1	ext	nvis	para	para	act	11.83
Franz et al. (this issue)	3	40	36	OLsignal	35	1	ext	nvis	para	para	act	13.85

Appendix A (*Continued*)

Study	Exp	*N*	Trial/condition	Visual guidance	Fin-angle	Preview	Go-signal	Stim/hand	Stim-plane	Stim-orient	Method	Percent-effect
Heath et al. (2004)	1	15	40	CL	30	2	ext	vis	para	perp	act	3.67
Heath et al. (2004)	1	15	40	OLmove	30	2	ext	nvis	para	perp	act	4.5
Heath et al. (2005)	1	21	40	CL	30	2	ext	vis	para	perp	act	2.32
Heath et al. (2005)	1	21	40	OLmove	30	2	ext	nvis	para	perp	act	9.17
Heath, Rival, Neely (2006)	1	14	48	CL	30	2	ext	vis	para	perp	act	1.67
Heath, Rival, Neely (2006)	1	14	48	OLmove	30	2	ext	nvis	para	perp	act	7.97
Heath, Rival, Neely et al. (2006)	1	15	32	CL	30	2	ext	vis	para	perp	act	4.49
Heath and Rival (2005)	1	18	40	CL	30	2	ext	vis	para	perp	act	6.1
Otto-de Haart et al. (1999)	1b	14	32	CL	37	adlib	ext	vis	perp	para	pas	5.58
Otto-de Haart et al. (1999)	1m	14	32	CL	37	adlib	ext	vis	perp	para	pas	6.78
Radoeva et al. (2005)	1l	26	26	CL	30	adlib	self	vis	perp	para	gon	8.33
Radoeva et al. (2005)	1r	26	26	CL	30	adlib	self	vis	perp	para	gon	11.67
van Doorn et al. (2007)	1	8	96	CL	45	adlib	self	vis	para	perp	act	0.01
Westwood, Chapman et al. (2000)	1	6	36	CL	30	2	ext	vis	para	perp	act	2.09
Westwood, Heath et al. (2000)	1	9	30	CL	35	2	ext	vis	para	perp	act	3.15
Westwood, Heath et al. (2000)	1	9	30	OLsignal	35	2	ext	nvis	para	perp	act	9.45
Westwood, Heath et al. (2000)	1	9	30	OLdelay 3s	35	2	ext	nvis	para	perp	act	9.09
Westwood et al. (2001)	1	10	20	CL	35	2	ext	vis	para	perp	act	9.09
Westwood et al. (2001)	1	10	20	OLmove	35	2	ext	nvis	para	perp	act	13.8
Westwood et al. (2001)	1	10	20	OLsignal	35	2	ext	nvis	para	perp	act	14.81
Westwood et al. (2001)	1	10	20	OLdelay 2s	35	2	ext	nvis	para	perp	act	14.81

Note. Column "fin-angle": all values are in degree; Column "preview": all values are in seconds, adlib: ad libitum; Column "go-signal": self: self-generated, ext: external; Column "stim/hand": stimulus and hand visible/not visible during movement; Column "stimulus-plane": perp/para: perpendicular/parallel to transverse plane of body (dividing body into top and botton); Column "stimulus-orientation": perp/para: perpendicular/parallel to sagittal plane of body (dividing body into left and right); Column "method": pas: passive markers, act: active markers, gon: goniometer. Heath, Rival, Neely (2006): only the "blocked" conditions; Heath, Rival, Neely et al. (2006): only the "veridical" condition; Otto-de Haart et al. (1999): 1b/1m: binocular/monocular condition; Radoeva et al. (2005): Only data from control group, 1l/1r: data for left/right hand and visual field; Westwood et al. (2001): Slopes estimated from CL condition.

Appendix B. Overview of perceptual data

Study	Exp	*N*	Trials/condition	Fin-angle	Stim-plane	Stim-orient	Method	Percent-effect
Daprati and Gentilucci (1997)	1	8	84	45	para	para	drawing	5.93
Daprati and Gentilucci (1997)	1	8	84	45	para	para	man-est	5.08
Dewar and Carey (2006)	1	15	32	53	perp	para	man-est	7.84
Franz et al. (2001)	1	16	24	30	para	para	adjust	5.18
Franz et al. (this issue)	1	16	36	35	para	para	adjust	11.4
Franz et al. (this issue)	1	12	36	35	para	para	match	12.78
Heath et al. (2004)	1	15	40	30	para	perp	man-est	8.33
Heath and Rival (2005)	1	18	40	30	para	perp	man-est	6.83
Otto-de Haart et al. (1999)	1b	14	32	37	perp	para	man-est	14.69
Otto-de Haart et al. (1999)	1m	14	32	37	perp	para	man-est	18.88
Radoeva et al. (2005)	1l	26	26	30	perp	para	man-est	16.67
Radoeva et al. (2005)	1r	26	26	30	perp	para	man-est	18.33
van Doorn et al. (2007)	1	8	18	45	para	perp	man-est	5
Westwood, Chapman et al. (2000)	1	6	36	30	para	perp	man-est	12.65
Westwood et al. (2001)	1	10	20	35	para	perp	man-est	11.23

Note. Column "fin-angle": all values are in degree; Column "stimulus-plane": perp/para: perpendicular/parallel to transverse plane of body (dividing body into top and botton); Column "stimulusorientation": perp/para: perpendicular/parallel to sagittal plane of body (dividing body into left and right); Column "method": adjust: adjustment method, man-est: manual estimation, match: matching to a graded series. Heath et al. (2004) and Heath and Rival (2005): values are from "stable grip aperture"; Otto-de Haart et al. (1999): 1b/1m: binocular/monocular condition; Radoeva et al. (2005): Only data from control group, 1l/1r: data for left/right hand and visual field.

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