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Review

Visually guided pointing, the Müller-Lyer illusion, and the functional interpretation of the dorsal-ventral split: Conclusions from 33 independent studies

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Abstract

Models of the human vision propose a division of labor between vision-for-action (identified with the V1-PPT dorsal stream) and vision-for-perception (the V1-IT ventral stream). The idea has been successful in explaining a host of neuropsychological and behavioral data, but has remained controversial in predicting that visually guided actions should be immune from visual illusions. Here we evaluate this prediction by reanalyzing 33 independent studies of rapid pointing involving the Müller-Lyer or related illusions. We find that illusion effects vary widely across studies from around zero to comparable to perceptual effects. After examining several candidate factors both between and within participants, we show that almost 80% of this variability is explained well by two general concepts. The first is that the illusion has little effect when pointing is programmed from viewing the target rather than from memory. The second that the illusion effect is weakened when participants learn to selectively attend to target locations over repeated trials. These results are largely in accord with the vision-for-action vs. vision-for-perception distinction. However, they also suggest a potential involvement of learning and attentional processes during motor preparation. Whether these are specific to visuomotor mechanisms or shared with vision-for-perception remains to be established.

Keywords: Action; Perception; Perception-action dissociations; Ventral stream; Dorsal stream; Pointing; Müller-Lyer illusion

Contents

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1. Introduction

Human vision produces conscious representations of objects and events for recognition and verbalization. Vision, however, also continuously gathers information about environmental properties to guide actions. Do the cognitive (''vision-for-perception'') and pragmatic (''vision-for-action'') functions of vision use common neural mechanisms and spatial representations? According to some proposals, they do not. In these proposals (Milner and Goodale, 1995; see also Jeannerod, 1994; Jacob and Jeannerod, 2003), human vision evolved two cortical subsystems that can function independently of one another. The first of these, corresponding to the dorsal pathway from the primary visual areas to the posterior parietal cortex, uses visual information for motor control in coordination with more ancient subcortical visuomotor mechanisms. This vision-for-action subsystem is fast, can be unconscious, and privileges egocentric frames of reference useful for controlling movements in peripersonal space. The second subsystem, which corresponds to the ventral pathway from the primary visual areas to the inferotemporal cortex, provides instead a conscious and detailed representation of the world that we can describe with words. This vision-for-perception subsystem is slower, is related to visual consciousness and to memory systems, and privileges allocentric or object-relative frames of reference that are useful to compute constant object descriptions under variations of stimulus conditions.

Support for the distinction between vision-for-action and vision-for-perception has come from monkey and human work employing a variety of different techniques (for reviews see Carey, 2001; Goodale and Westwood, 2004). In particular, a prominent theoretical role has been played by behavioral experiments suggesting that visually guided actions are immune from perceptual illusions. For instance, in the Müller-Lyer illusion the same segment appears narrower when flanked by outward-pointing arrows (< >), and wider when surrounded by inward-pointing ones (> <). In the action-perception framework, this length bias is due to the spatial relations between the judged segment and the arrows, that is, to object-relative coding of spatial extensions used by vision-for-perception. However, actions such as transporting the hand from one end to the other end of the segment require egocentric (body- or effector-relative) coding of spatial features by the vision-for-action system. Accordingly, at least in some conditions hand transport may not be biased by the illusion. For instance, in a pointing task one might expect that the pointing finger would land at the same position on the segments with outward- an inward-pointing arrows.

As we shall soon see, results from numerous pointing studies are consistent with this prediction. At the same time, however, several other studies have documented substantial illusory effects on pointing. Such large contradictions in the literature pose a challenge. They suggest that understanding what lies behind these differences might bring about useful insights about the visual guidance of pointing and its implications for current interpretations of dorsal-ventral functions.

Here we review 18 papers reporting a total of 33 pointing studies using the Müller-Lyer or related illusions on independent groups of participants (plus a number of other variations within participants, see below). We chose to focus on these works for two main reasons. The first is that, despite several differences of detail, these studies looked at relatively comparable illusions and almost identical pointing movements. The second, and equally important, is that all these papers contained enough methodological detail to derive a common measure of the effect of the illusion. Armed with this measure, we discovered that almost 80% of the variability in the reported effects could be explained by a simple model, taking into account only three sources of variation: (i) the number of trials per condition of the experiment; (ii) whether programming of the action was based on visual information or on memory; (iii) the interaction of number of trials with a factor defining whether the starting position in the task favored encoding egocentric locations or relative extents.

These results support the idea that pointing is largely immune from the illusion when based on spatial representations based on vision and on coding spatial features within an egocentric frame of reference. In this, therefore, they are largely consistent with the proposal that vision-for-action generates a specific spatial representation independently from vision-for-perception. However, they suggest that illusion effects may also depend on learning to selectively attend to egocentric locations over repeated trials. If confirmed in direct experimental tests, this finding would have several implications for theories of motor responses to illusion as well as experimental practices.

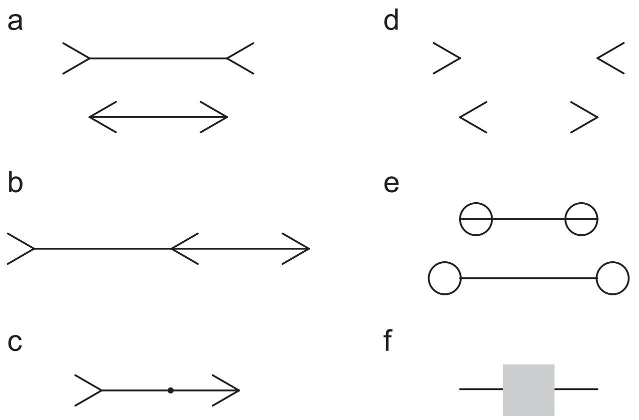

Fig. 1. Stimuli used in the studies discussed in the review: (a) the standard Müller-Lyer illusion; (b) Brentano version; (c) Judd version; (d) "no shaft" version; (e) "dumbbell" version, (f) Kanizsa's compression illusion.

2. Methodological preliminaries

2.1. Criteria for inclusion in the review

We performed literature searches using Google, MedLine, and PsychInfo. We included all studies that met the following criteria: (i) the dependent variable was pointing accuracy; (ii) the stimuli were patterns involving apparent compression or expansion of a segment due to the presence of additional elements attached to it (the "Müller-Lyer family" of illusions, ML, see Fig. 1). We limited our search to single, rapid pointing movements, performed with the right hand by right handers. Studies involving cyclical pointing were not included. Because it involves a sequence of actions, cyclical pointing differs from a single, rapid pointing response in a number of ways. For instance, the sequence might be taken into account at the programming phase, such that later actions in fact influence the execution of initial ones (Gentilucci et al., 1997b). In addition, cyclical pointing typically involves repeated visual feedback each time the finger lands at the target (see for instance Lavrysen et al., 2006), a situation that is fundamentally different from what happens in a single closed-loop pointing response. Similarly, studies involving other forms of motor response (i.e., grasping or counterpointing) were also not included. While also potentially interesting, grasping responses on the Müller-Lyer illusion typically involve measuring the maximum preshape aperture between the index and the thumb, which is assumed to be an indicator of the representation of size used by the grasping visuomotor system. However, this assumption is controversial (Smeets and Brenner, 2006) and the comparability of preshape aperture to perceptual measures of size has been questioned (see for instance Franz et al., 2001). Thus, we feel that this literature is best left for a separate review. Finally, we did not include studies using other illusions such as the Ebbinghaus or the Ponzo illusion. These illusions involve illusory changes in size but require visual patterns that are not comparable to those studied here. No attempt was made to locate unpublished studies.

2.2. Studies included in the review

The search yielded 18 papers reporting studies that met the criteria (Bernardis et al., 2005; Binsted and Elliott, 1999; Bruno and Bernardis, 2003; de Grave et al., 2004, 2006; Elliott and Lee, 1995; Gentilucci et al., 1996, 1997a, 2001; Glazebrook et al., 2005; Mack et al., 1985; Meegan et al., 2004; Mendoza et al., 2005; Mon-Williams and Bull, 2000; Post and Welch 1996; Predebon, 2005; Rival et al., 2003; Welch et al., 2004). Overall, these papers reported a total of 33 studies using independent groups of participants. These assessed visually guided pointing on ML illusions in a number of different conditions, both within and between independent groups. 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 data points up to 69. 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. This choice is conservative. When fitting a linear model, such as analysis of variance, 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 and Aron, 1994).

2.3. Specific aims and data-analytic approach

Our objective was twofold. First, we sought to determine what is a typical effect of ML illusions on pointing, how variable can this be across independent studies, and how does this typical value for a motor effect compare with a typical value for a perceptual effect. To this aim, we examined the corresponding distributions of effects over the 33 independent measures mentioned in the above section, averaged across additional within-participant variables if present. Second, we sought to determine in detail what variables modulate the effect of the illusion on pointing. To achieve this second aim, we studied how effects on pointing are modulated by different variables using the 69 data points obtained after separating effects based on within participant comparisons.

2.4. Measure of illusion effect

The studies varied widely in experimental design, range of stimuli that were tested, measures of the effects of the illusion, as well as in a number of other experimental details. To provide a common measure of the effect of the illusion of pointing, for each study we derived the percent measure of the effect of the illusion

$$\%\ \text{effect} = \text{AVERAGE}\ [(\text{expanding} - \text{compressing})/\text{baseline}] \times 100,$$

where *expanding* and *compressing* refer to the amplitudes of the pointing movements for the two versions of the illusion pattern, *baseline* refers to an estimate of pointing amplitude on a segment having the same real width but no biasing elements, and *AVERAGE* signifies that the effect is averaged across participants and across physical widths (if more than one was used). Consider, for instance, the standard Müller-Lyer illusion where the expanding pattern has inward pointing arrows and the compressing pattern has outward pointing arrows (see again Fig. 1). Suppose further that a hypothetical study employs 10 and 20 cm segments between the fins. If the expanding and compressing versions of the illusion, averaged across participants, yield pointing amplitudes of 11 and 22 cm vs. 9 and 18 cm, and if the baseline responses are unbiased, then the percent effect is equal to

$$\%\ \text{effect} = \text{AVERAGE}\ [(11 - 9)/10;\ (22 - 18)/20] \times 100 = 20\%.$$

Average values for pointing amplitudes were read off published tables or estimated as accurately as possible from data reported in graphic form. In studies that did not include a baseline condition, percent effects were scaled using the mean or the median (whichever was reported or could be reconstructed) of the compressing and expanding patterns. In studies using Kanizsa's compression illusion (Bruno and Bernardis, 2003, exp. 4) and the Judd illusion (Mon-Williams and Bull, 2000, exp. 1) which involve illusion effects that can go only in one direction, the obtained value was obtained by subtracting the illusion effect from the baseline, dividing by the baseline, and then multiplying by two to make it comparable to the other illusions.

2.5. Percent effect vs. statistical effect sizes

The percent illusion effect used here should not be confused with statistical effect sizes (Cohen, 1988). Although they are often used as a common metric for comparing results in quantitative reviews, in this context statistical effect sizes would not serve us well. The reason is that they express observed differences between group means in units of the population standard deviation. This implies that differences are scaled in relation to the precision of measurements. However, when measuring dimensional effects, it is crucial that participant biases are taken into account. To this aim, it is necessary to express effects as percentages of baseline responses unaffected by the illusion, rather than precision. Consider again the example in the previous section and suppose that the estimate of the population standard deviation is 6 cm. Cohen's d for that study would be

$$d = [\text{average(expanding)} - \text{average(compressing)}]/\text{sd} = 0.5.$$

Now consider a second study again employing 10 and 20 cm segments between the arrows. Suppose however that in this study participants tend to systematically undershoot the target, such that baseline responses average 8 and 16 cm, expanding responses average 8.8 and 17.6 cm, and compressing ones 7.2 and 14.4 cm. Finally, suppose that the estimate of the population standard deviation is again 6 cm. Because the absolute difference between the group means is now smaller, Cohen's d for this study would be $d = 0.4$. However, the relative amount of compression and expansion (the illusion effect) is in fact the same as the previous study:

$$\%\ \text{effect} = \text{AVERAGE}\ [(8.8 - 7.2)/8;\ (17.6 - 14.4)/16] \times 100 = 20\%.$$

Thus, using statistical effect sizes in the present context would lead us to treat the two studies as showing a larger and a smaller effect, when in fact the dimensional effect of the Müller-Lyer illusion remained the same.

3. What is a typical effect of ML illusions?

3.1. Overall percent effect on pointing

Fig. 2 presents the distribution of the 33 mean effects in the studies we have examined. (A summary table is

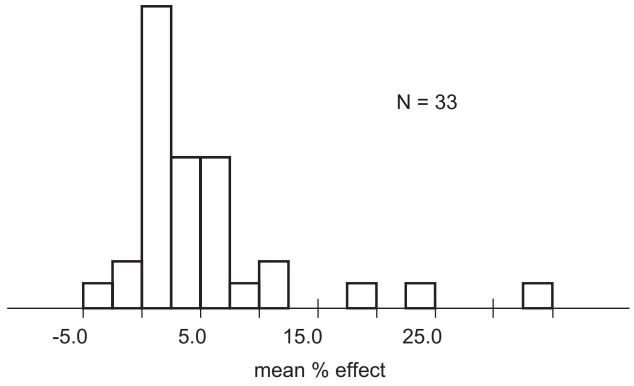

Fig. 2. Distribution of mean percent illusion effects on pointing in the 33 independent studies of the present review.

reported in the Appendix A; a full spreadsheet reporting references, experiment numbers, effect sizes, and all the variables considered in the analysis can be requested to the corresponding author.) The distribution is centered slightly above zero, with a median of 3.8% and a mean of 5.5%. The difference between mean and median is due to the right tail of the distribution, which contains three unusually large values: 33.2% and 23.8% from de Grave et al. (2006, exps. 3 and 4) and 17.5%, from Post and Welch (1996, exp. 1). Assuming a normal distribution, the mean of pointing effects is statistically different from zero, t $(32) = 4.4$, $p < 0.0001$. Repeating the test after removing the three outlier values continues to yield a significant effect, t $(29) = 5.9$, $p > 0.0001$.

3.2. Comparison with weighted effect

The 33 studies were quite homogeneous in their sample size. In fact, 30 of them used samples with $8 < N < 16$. Only one study used a very large sample size (109) and only one a relatively small one (4). In addition, there was one study with $N = 24$. This distribution suggests that our studies did not differ markedly in the precision of their sample statistics. However, to check whether the overall result was 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 percent effects was 4.9%, essentially identical to the unweighted average. Based on this comparison, we decided to perform all additional comparisons using the unweighted data.

3.3. Overall percent effect on perception

To determine how the above estimate of the overall effect on pointing compares with the effect on perception, we also evaluated measures of perceptual effects. In our corpus of 18 studies, 13 included a perceptual measure. However, two of these used non-standard methods that may be subject to bias. Specifically, Rival et al. (2003; exp. 1) asked participants to report whether a comparison shaft was the same as the reference shaft in the illusion, but the range of their comparison shafts went only from 6% below to 6% above the reference. Thus, their procedure could not measure effects larger than 12%, even in the unlikely event that all participants always chose the smallest comparison when seeing the compressing reference and the largest one when seeing the expanding reference. Meegan et al. (2004; exp. 1) used a range of comparison stimuli that went from 15% below to 15% above the reference. This range is also not optimal to measure a percent effect of about 25–30%, because actual participants are not likely to always choose the smallest and larger comparisons. In addition, this experiment used a variant of the matching method which makes the estimation of the effect problematic. They allowed participants three response choices for each comparison shafts: larger than, smaller than, or the same as the reference. This choice leaves open the possibility that participants used different response criteria when switching from a discriminative to an equality judgment. For these reasons, we chose not to consider these two results. The 11 remaining papers used either variants of the methods of adjustment, such as drawing the perceived extent or setting the length of a variable shaft, or used verbal estimations of length. In these 11 papers (see Appendix B), the average percent effect of the illusion was 22.4%. The median effect was 22.8%.

3.4. Comparing overall effects

A direct comparison of the distributions of percent effects on pointing and on perception is provided by the box-plots in Fig. 3. The two distributions are clearly different in their central tendency. Additionally, they differ markedly in shape. Whereas the distribution of perceptual effects is approximately symmetrical with an interquartile range between 18% and 28%, the distribution of pointing effects has most values between 0% and 10% but also a few large outliers, yielding a marked skew. Assuming homogeneous variances, a direct comparison of the two means yields a statistically significant difference, t $(14) = 5.9$, $p < 0.0001$.

3.5. Preliminary conclusions

We conclude that a typical effect of the illusion on pointing is markedly smaller than its effect on perception—as predicted by the vision-for-action and vision-for-perception distinction. Nonetheless, the overall effect of ML illusions on pointing is statistically different from zero and varies across studies from values close to zero to values comparable to those found in perceptual measures. Such variability suggests that other factors beside the mere response mode (motor, or "perceptual" as inferred from verbal or matching responses) can modulate the effect. To identify these factors, we analyzed the pointing experiments further.

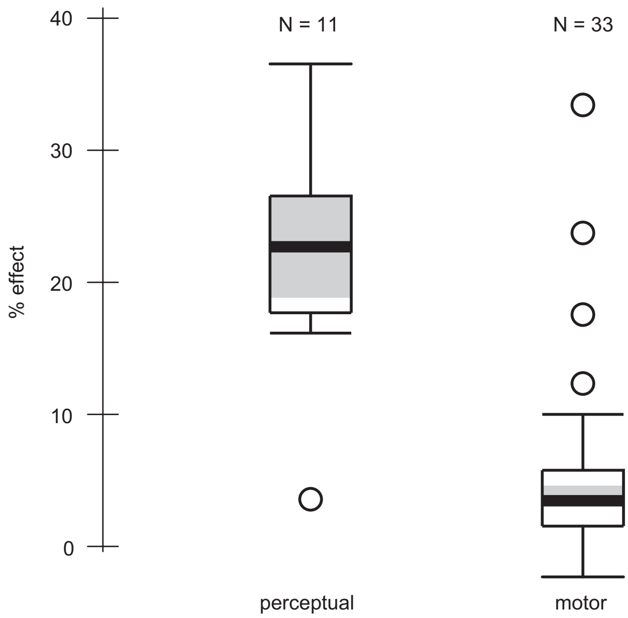

Fig. 3. Comparing the distributions of percent illusion effects in perceptual and visuomotor tasks. Thick lines are group medians. Upper and lower sides of boxes indicate the central 50% of the distributions. Whiskers indicate maximum and minimum values. Circles represent outliers. Grey areas are approximate 95% confidence intervals around the group medians.

4. What factors modulate the effect on pointing?

We evaluated 13 candidate factors by comparing median illusory effects across studies. Candidates were selected on the basis of theoretical and methodological considerations, as stated in detail in the relevant sections below. To provide a quick reference to all our findings in this part of the review, sections are numbered 1–13 and the same numbers are used for summary tables reporting the discussed median effects. As shown in these tables, the first 7 factors seem to play little role in modulating the illusory effect on pointing. The last 6 seem instead to have an impact.

4.1. Participants' age

Some of the reviewed studies included tests of children between 7 and 11 years. However, pointing (Gentilucci et al., 2001; Rival et al., 2003, 2004) and blind-walking (Giovannini et al., 2006) studies have provided evidence that vision-for-action in children may comparable to adults' as early as 7 years of age. For this reason, it is unlikely that participants' age contributes to the variability of results. Confirming this impression, median effects in children and adults were quite similar (see Table 1).

Table 1
Median effects by participant age

Children	Adult
3.7	2.6

4.2. Type of illusion

Given that illusions in the ML family differ somewhat, we compared effects associated with different members (see Table 2). Effects associated with the standard Müller-Lyer and with the Judd version were identical and relatively small. Effects associated with the dumbbell version and with Kanizsa's compression illusion were negative or essentially zero. Given that negative or zero effects were observed also with the other types of illusions, however, and given the small number of studies involved (2 and 1, respectively), we doubt that this difference reflects a peculiarity of these versions of the illusion relative to the other, more common patterns. The effect associated with the Brentano version is instead large (13.8%). We note, however, that this large value is entirely due to the two large effects from de Grave et al. (2006; exp. 3 and 4). When these were excluded from the computation, the median effect reduced to 1.7%. This suggests that the difference is not due to a peculiarity of the Brentano version of the illusion, but to other features of those two experiments.

Table 2
Median effects by type of illusion

Brentano	Dumbbell	Judd	Kanizsa	Müller-Lyer
13.8 (1.7)	−2	3.3	0.1	3.3

4.3. Measuring device

Methods used to measure pointing amplitudes varied considerably in the precision of measurements as well in their presumed sensitivity to experimenter effects. In some studies, actors pointed using a pencil to leave a mark on paper or waited with the finger in the final position. In both these cases a ruler was used by the experimenter to measure pointing amplitude. In other studies, amplitudes were measured using touch monitors or motion tracking devices. Table 3 presents median effects associated with the methods used to measure pointing accuracy. There are little substantial differences, with a somewhat larger figure associated with the use of touch monitors. This is again due to the fact that the two largest effects (see previous section) used this method.

Table 3
Median effects by measuring device

Touch screen	Mot. tracking	Pencil/ruler	Finger/ruler
5	3.1	3.6	4.1

4.4. Plane of stimulus presentation

Some studies presented illusions on a horizontal surface. This mode of presentation affords comfortable pointing in a position similar to that used for writing. Other studies presented illusions on a frontal-parallel surface. This mode of presentation is somewhat more tiring over repeated arm raises (see also Fig. 3). Table 4 presents median effects associated with the planes used to present stimuli. The difference between the two methods is small and cannot account for the large variability in the overall effects.

4.5. Direction of movement

For reasons similar to those given in the previous section, illusion effects may vary somewhat along different directions of movement. Table 5 presents median effects associated with the three possible directions of movement: right or left, up or down, and towards or away from the body (see again Fig. 3). The effects are similar except for vertical movement that yield a much larger effect. Only the two outlier studies from de Grave et al. (2006) included conditions with vertical movements. However, these studies also included conditions with horizontal movements and found comparably large effects. Therefore, we can rule out that such unusually large effects are due to vertical movements per se.

4.6. Range of shaft lengths

Although most studies varied the length of the shafts in the illusion, some used one length only. Lack of variation in the length of the stimulus may reduce the effect of the illusion over repeated trials, especially if visual feedback about the accuracy of each pointing movement is available. To check this possibility, we compared median percent effects in studies that used only one length with those in studies that varied length. As shown in Table 6, in contrast with the expectation the median effect was slightly larger, not smaller, for studies using only one length. However, the difference was small and cannot account for the variability in the overall effects.

4.7. Spatial uncertainty of the target location

In some of the studies, stimulus positions were arranged such that the target endpoint for the pointing movement was always the same. For reasons similar to those provided above, this feature may have reduced the effect of the illusion over repeated trials. To check this possibility, we compared median effects in studies that kept target position constant with those in studies that varied target position. As shown in Table 7, the median effect was indeed slightly smaller for the group that kept target position constant. Again, however, the difference is clearly too small to account for the large variability in the overall effects.

4.8. Hemifield of stimulus presentation

Neuropsychological and behavioral evidence suggests that the left hemisphere may play a special role in visuomotor transformations (Gonzalez et al., 2006; Perenin and Vighetto, 1988; Radoeva et al., 2005; Serrien et al., 2006). Of the present 33 studies, only 3 employed insured presentation in a specific hemifield. Nonetheless, as shown in Table 8a, it is of interest that median effects suggest greater immunity from the illusion in the right hemifield. Specifically, the illusion is substantial in the left hemifield, negligible in the right, and intermediate when presentation involves both hemifields or when hemifield is not controlled. Interestingly, all three studies compared left and right hemifields within participants in the same experiment. As shown in the table, despite large overall values all three found larger effects in the left hemifield (see Table 8b). Although the number of such studies does not warrant definitive conclusions so far, we suggest that the lateralization issue merits further scrutiny.

Table 4
Median effects by plane of presentation

Horizontal	Frontal-parallel	Unknown
2.4	4.8	3

Table 5
Median effects by movement direction

Up/down	Right/left	Forward/backward	Unknown
25.9	2.7	4	3

Table 6
Median effects by range of shaft lengths

1	>1
3.1	4.3

Table 7
Median effects by target location

Constant	Variable
3.3	4.3

Table 8a
Median effects by hemifield of presentation

Both	Left	Right	Uncontrolled
4.4	9	0.3	4

4.9. Delay

Grasping and pointing studies provide evidence that spatial representations for motor control are relatively short lived, lasting for 1–2 s at most (Hu and Goodale, 2000; Hay and Redon, 2006). This suggests that introducing a 2 s delay (or longer) before the beginning of an open-loop motor response should recruit other forms of spatial memory, possibly under the control of vision-for-perception. As shown in Table 9, this prediction is confirmed. In studies with long delays, the median effect is more than 4 times larger than in studies with short delays. The median effect is extremely large in studies leaving participants free to start when they wanted after stimulus presentation, and therefore did not allow experimental control of delay times. This is again due to the contribution of the two experiments by de Grave et al. (2006), which fall in this category. When those datapoints are excluded, then the median effect becomes intermediate between the short and the long delay results (4.4%).

4.10. Conditions at the programming phase

As pointed out by an anonymous reviewer, a crucial role in modulating the illusion effect may be played by the stimulus conditions at the programming phase of the pointing responses. Consider a long delay introduced between the end of the stimulus presentation and a go signal. Under these conditions, it is reasonable that whatever processing had been going on during stimulus presentation is now obsolete, and that programming must be based on memory rather than the representation derived while viewing the stimulus. However, the distinction between memory-based and vision-based programming may provide a more useful, and predictive, conceptual tool to account for the variability of illusion effects on pointing than the mere measurement of delay. The reason is that, while trials with long delays invariably also imply memory-driven programming, trials with short or zero delays sometimes involve vision-driven programming but sometime they can also involve memory-driven programming, depending on subtle differences in experimental procedures. Consider three studies of grasping on the Müller-Lyer illusion (Westwood et al., 2000, 2001; Westwood and Goodale, 2003). These studies reported a small effect of the illusion on grasping even when vision was removed in synchrony with an auditory go signal. Because trials of this type were randomly interleaved with full vision trials, participants were unlikely to program the grasp as soon as the stimulus appeared. Thus, although the delay was effectively zero in these conditions, the programming of the grasp may have had to resort to the recent memory of the display rather than on actual visual information. Similar considerations apply to many of the present pointing studies. Consider, for instance, the methodology of de Grave et al. (2006) and Bernardis et al. (2005). In both of these studies, participants responded immediately to stimuli that were briefly flashed in random directions relative to a fixation mark. Thus, there was no delay between the removal of the stimulus and the potential initiation of the action. However, because the presentation was very brief and in an unexpected location, it is unlikely that participants fully programmed the action while still seeing the display. At least in part, they may have had to resort to a recent memory of the display. This was not necessarily the case, however, for all studies of pointing without vision. Consider the studies of de Grave et al. (2004) and Bruno and Bernardis (2003), which used very similar general methods but presented displays on touch monitors as long as the index finger was lifted from the starting position. Under these conditions, there was no external go signal and vision of the display was allowed as long as participants decided to move. Under the plausible assumption that one does not decide to start moving before programming has been completed, we argue that this type of methodology allowed for vision-based programming even if vision of the display was removed as soon as the action begins. Based on this reasoning, we considered experimental procedures carefully for all results included in the review and classified each as involving memory-driven or vision-driven programming. Median effects are reported in Table 10. Consistent with the suggestion of the referee, median effects from studies involving memory-driven programming are more than 5 times larger than methods involving vision-driven programming.

Table 8b
Within-participant comparisons of left vs. right

Ref.	Exp.	Hemifield	% Effect
1	3	Right	5
1	3	Left	9
5	3	Right	33
5	3	Left	36
8	1	Right	1.3
8	1	Left	3.3

Table 9
Median effects by delay before initiating movement

<2 s	2–5 s	Uncontrolled
1.9	8.3	20.5 (4.4)

Table 10
Median effects by condition at programming

Vision-driven	Memory-driven
1.95	10

Table 11
Median effects by type of visual feedback

		Hand		
		Invisible	Visible	
Stimulus	Invisible	7	13	7.7
	Visible	3.7 4.9	1.8 2.2	1.9

4.11. *Visual feedback during the online control stage*

In a well known study, Gentilucci et al. (1996) showed that the effect of the Müller-Lyer illusion on pointing may be modulated by the availability of visual feedback during the action. More specifically, Gentilucci et al. (1996) suggested that if both hand and stimulus are continuously visible during the action, the effect is minimized. Conversely, if both the hand and the target are invisible the effect tends to be enhanced. In the studies examined here, both modes of pointing are represented, as well as the two intermediate cases where the hand was visible but the stimulus was not, or vice versa. Table 11 summarizes the median effects associated with these four kinds of visual feedback. As the table shows, the visibility of the stimulus seems to have a strong impact on the illusion effect, reducing it from a median value of almost 8% to less than 2%. The visibility of the hand seems to go in the same direction but produces a smaller reduction (from about 5% to slightly more than 2%). When both hand and stimulus are visible, the data yield the smallest median effect (1.8%). Surprisingly, however, the largest effect is not associated with the invisibility of the both hand and stimulus (7%), but with invisible stimuli while the hand is still visible (13%).

4.12. *Starting position and direction of approach*

Several authors have argued that a critical factor in neutralizing illusion effects on motor responses is the exclusion of object-relative frames of reference for coding spatial features (Vishton et al., 1999; Bruno, 2001; Wraga et al., 2000; Bruno and Bernardis, 2003; Schenk, 2006; Smeets et al., 2002). For instance, Bruno and Bernardis (2003) compared pointing and counterpointing on the dumbbell illusion. In pointing, participants moved their finger from one to the other endpoint of the illusion shaft. In counterpointing, they moved the finger parallel to the shaft from one endpoint to an empty area of the screen, attempting to reproduce the apparent length of the shaft. Pointing showed no effect of the illusion, but counterpointing showed an effect as large as perceptual effects. Presumably, the pointing task could be performed based exclusively on an egocentric representation of the target endpoint. In the counterpointing task, instead, the aim point for the action had to be derived from an object-relative representation of shaft length. In another study, de Grave et al. (2004) argued that when pointing is started from a position outside the illusion, such that the direction of approach is not parallel to the shaft, the action system tends to construct a unique representation of egocentric position and therefore this mode of response should weaken the effect of the illusion. Conversely, when pointing is started on one shaft endpoint and proceed parallel to the shaft, the system also tends to code shaft length relative to the arrows. Thus, one might expect a larger effect of the illusion in this latter case. Table 7 compares the median effects associated with variations of these two pointing procedures in our reviewed studies (see also Fig. 4). In accord with the above expectations, starting from outside the illusion shows a smaller median effect (1.2%) than pointing along the shaft (4.5%) (Table 12).

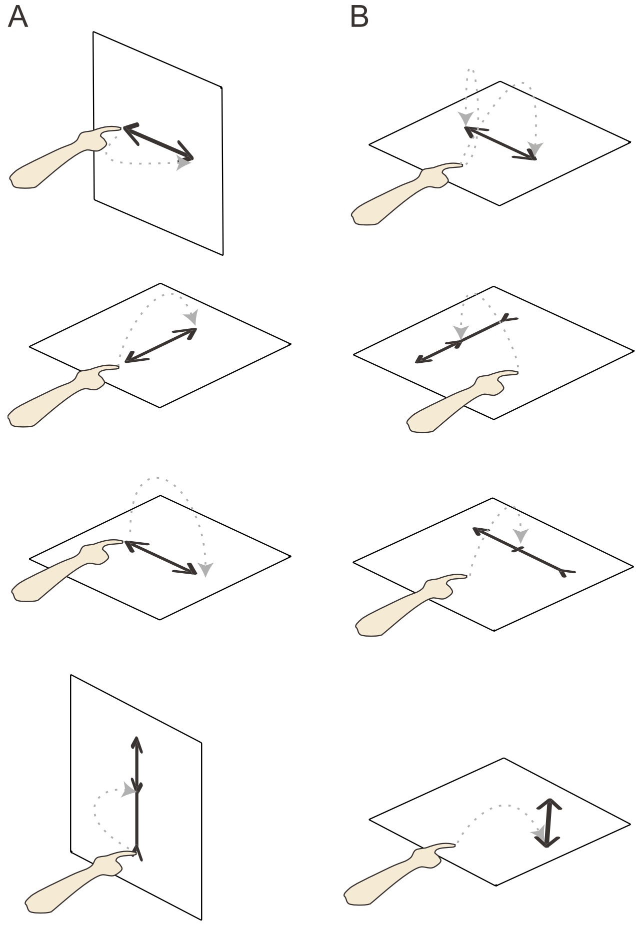

Fig. 4. Starting positions relative to the illusion were either outside the pattern (B), such that the direction of approach was orthogonal to the shaft, or near one endpoint of the shaft (A), such that approach to the target was along the shaft. Planes of presentation and directions of movement are representative of those in the reviewed studies.

Table 12
Median effects by starting position

Endpoint	Outside
4.5	1.2

4.13. *Number of trials per experimental condition*

The perceptual effect of the Müller-Lyer illusion weakens over repeated presentation of the illusion display (Eysenk and Slater, 1958; Judd, 1902; Köhler and Fishback, 1950; Lewis, 1908; Porac, 1994; Predebon, 1998, 2006; Schiano and Jordan, 1990). In a recent report Heath et al. (2006) suggested that a similar decrease over repeated responses can occur for grasping on the Müller-Lyer illusion, and Gonzalez et al. (2006) suggested that awkward (less practiced) grasps are affected by the illusion initially but become increasingly less sensitive to illusions with practice. To test the possibility that this occurred for pointing in the studies reviewed here, we plotted median effect sizes against the number of trials per experimental condition of 67 of the present studies (for 2 additional cases the number of trials could not be retrieved from the paper). This plot showed that the likelihood of observing very large effects tended to decrease with the number of trials, although this effect was not clearly visualizable due to some nonlinearity and heteroskedasticity of the relation. Fitting a linear regression yielded a slope equal to -0.03%, consistent with a small decrease of the effect with more trials, but explaining only 4.2% of the variance. After excluding negative values and applying a log transformation to correct the nonlinearity, a second linear fit explained 9.2% of the variance yielding a slope equal to $-0.004\,\log(\%)$, $p<0.02$.

5. Modeling the effect of ML illusions on pointing

The above analyses provide evidence for a possible modulating effect of six factors: hemifield of stimulus presentation, delay after initiating the movement, conditions at the programming phase of the action, nature of visual feedback during the online control of the action, starting position and consequent direction of approach to the illusion, and number of trials per condition of the experiment. As a preliminary step towards modeling, we noted three things. First, none of these factors appears to have a strong enough effect to completely account for the large variability in the pointing data. This suggests that a successful description of the effects of the Müller-Lyer illusion on pointing might require considering more than one factor. Second, although interesting the hemifield effect is based on a very small number of studies. For this reason and to simplify the analysis we decided to exclude this factor from our modeling attempt. Third, the relative contributions of delay, conditions at programming, and online feedback are confounded in complex ways. For instance, studies using long delays will typically also imply memory driven programming and necessarily imply removal of feedback during the action. This suggests that a joint consideration of these three factors is in order to understand which is relevant. In light of this and of the previous consideration, we started our modeling attempt with an exploration of potential interactions between variables. This exploration clarified two important features of the dataset that are detailed below.

5.1. *Delay, programming conditions, and feedback conditions*

To explore the relations between delay, conditions at the programming phase, and type of visual feedback during the online control phase, we constructed three new tables. Table 13 presents median illusion effects as a function of conditions at the programming phase and delay. The table suggests that conditions at programming account for a large change in the effect, whereas long delays imply only a relatively small increase relative to short delays. Table 14 presents median effects as a function of feedback during the control phase and delay. We note that at longer delays essentially all studies removed vision of both hand and stimulus during the control phase. The only exception was a condition in a study (Meegan et al., 2004; exp. 2; see value with asterisk in the table) that used a long delay followed by a trial where both hand and stimulus were visible. Thus, by all practical means the distinction between long delays and short delays appears to coincide with that between no visual feedback vs. some visual feedback (from seeing the stimulus, the hand, or both). Table 15, finally, presents median effects as a function of feedback and conditions at programming. We note that the distinction

Table 13
Median effects by delay and conditions at programming

		Programming	
		Vision-driven	Memory-driven
Delay(s)	<2	1.7	7.7
	2–5	2.5	9.5

Table 14
Median effects by delay and online feedback

		Stimulus visible		Stimulus invisible	
		Hand visible	Hand invisible	Hand visible	Hand invisible
Delay(s)	<2	1.5	2.8	4.2	2.8
	2–5	2.5*	None	None	9.4

Table 15
Median effects by feedback and conditions at programming

			Hand	
			Invisible	Visible
Stimulus	Invisible	Memory-driven	9.4	24.2
		Vision-driven	4.35	0.0
	Visible	Vision-driven	3.7	1.8

between memory-driven and vision-driven programming is nested within the different types of feedback. In fact, about half of the studies that removed visual feedback about the stimulus also used a procedure involving memory-based programming, whereas no study that allowed feedback about the stimulus did. Once the nesting is made explicit, the data show there is a large difference between memory-based and vision-based programming conditions within comparable feedback conditions, but only a relatively small difference between stimulus feedback and absence of stimulus feedback within comparable programming conditions.

5.2. Trial number, starting positions, and programming conditions

The exploration of potential interactions revealed a second, unexpected feature in the structure of the data. When plotting percent effects as a function of trials per condition, coloring the data points according to starting position demonstrated a clear interaction. This interaction can be visualized, again after applying a log transformation to the illusion effects, by comparing the open (blue online) to the filled (red online) data points in Fig. 5. As the figure shows, for both starting positions effects tend to decrease with larger trial numbers but this effect occurs faster when the starting position favors encoding egocentric location (starting from outside the illusion such that movement is approximately orthogonal to the shaft) than when it favors encoding of relative extent (starting from one endpoints of the shaft such that movement is along the shaft itself). In the same graph we can also visualize the difference between memory-based programming (plotted as open (blue online) and filled (red online) stars) and vision based programming (open (blue online) and filled (red online) circles).

5.3. Linear model

To construct a descriptive model of the effect of the ML-family illusions on pointing, we subjected the log-transformed percent effect to an analysis of covariance (ANCOVA) using number of trials as the quantitative covariate and four categorical factors: type of visual feedback, conditions at programming (defined as a factor

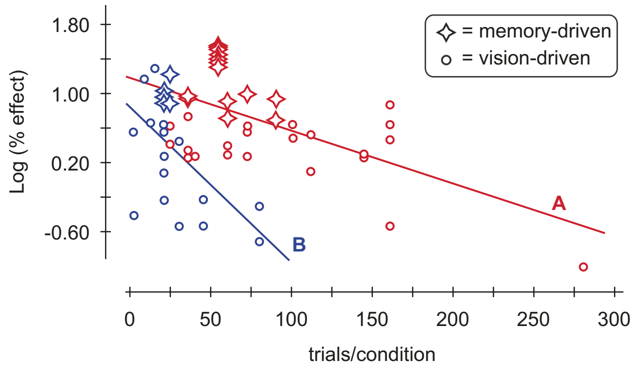

Fig. 5. (Colour online) Log-transformed percent effects as a function of: (i) trials per condition of the experiment, (ii) starting position (filled (red online) = shaft endpoint, see A in Fig. 4; open (blue online) = outside the illusion, see B), (iii) conditions at the programming phase (✧ = memory driven; o = vision driven). The model described a substantial part of the variability very well. Including additional predictors provided only negligible improvements.

nested within type of feedback), delay, and starting position. In addition, given the considerations above, we also included the interaction between starting position and number of trials. 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. Overall, this six-predictor model captured 79.7% of the total variability, with all predictors reaching statistical significance except starting position, $F(1, 49) = 2.1$, $p > 0.38$. Given that starting position was not significant, we tried omitting it from the model. This resulted in a negligible reduction of the proportion of variance accounted for (from 79.7% to 79.3%), with conditions at programming and feedback accounting for approximately equal proportions, eta-squared = 28% and 24%, and delay providing only a marginal additional contribution, eta-squared = 4%. Given the nesting of conditions at programming within feedback, and given the marginal contribution of delay, we tried omitting feedback and delay as well. We found out that again this resulted in a negligible reduction of the overall proportion of variance accounted for (from 79.3% to 78.9%) while preserving the significance of all three remaining predictors: trial number, $F\ (1,53) = 23.1$, $p<0.0001$, eta-squared = 9%; conditions at programming nested within feedback, $F\ (4,\ 53) = 32.5$, $p<0.0001$, eta-squared = 52%, and the interaction between trials and starting position, $F\ (1,1) = 43.3$, $p<0.0001$, eta-squared = 21%. To evaluate the extent to which the relative contributions of the two categorical predictors depended on being entered in the analysis in the second or third positions, we also run this analysis again, this time entering trials first, the interaction second, and conditions at programming third. Inverting the order of the two categorical predictors did not change the pattern of statistical significance, but it did change the descriptive power of the model in a substantial way. Specifically, the proportion of variance accounted by the interaction increased to about 30%, the proportion accounted by conditions at programming decreased to about 20%, but this also reduced the total proportion of variance accounted for from about 79% to only 60%. Thus, we conclude that the effect of ML-family illusions on pointing can be described best by accounting for the effect of number of trials first, and then partitioning the remaining variability first into a large component due to conditions at programming and then into a smaller, but still substantial component due to the interaction of trials with the starting position.

6. General conclusions

Theories positing separate vision-for-perception and vision-for-action subsystems make the counterintuitive prediction that actions should resist visual illusions. Whether this prediction is supported by data has been highly controversial (see Bruno, 2001; Carey, 2001; Franz, 2001; Pavani et al., 1999; Glover, 2002, Milner and Dyde, 2003; Smeets and Brenner, 2006).

In the first part of the present review, we have examined 33 independent estimates of the effect of ML-family illusion on rapid pointing. Most of these estimates are indeed fairly small, and definitely smaller than most estimates derived from perceptual tasks. However, many of them are also substantially higher than zero, and some are as large as typical perceptual effects. This finding suggests that rapid pointing can be essentially unaffected by ML-family illusions under certain conditions, but it can also be affected in a substantial way in other conditions. Thus, the hypothesized immunity to illusions does not appear to be a mere matter of response mode (motor tasks as opposed to procedures designed to tap into conscious perception). Rather, it seems that there are other factors that can modulate the effect of the illusion on pointing responses.

In the second part of this review, we have looked in detail at potential factors and interactions of factors. The results of this detailed examination suggest that percent effects can be shown to vary as a function of a number of factors. However, when the relationships between these factors are examined in detail, all the variability in this apparently controversial literature can be explained well by only two general ideas. The first is that the illusion has little effect when pointing is programmed while viewing the target, but can have a substantial effect when pointing is programmed from a memory representation of the target. The second that the illusion effect is weakened when conditions favor egocentric encoding of target locations. Such encoding is favored when pointing starts far from the shaft endpoint and approaches the illusion more or less orthogonally to the shaft. In addition, such encoding can be favored by practice in two interesting ways. Specifically, it seems that participants learn to better perform egocentric encoding over repeated trials. However, they seem to do so more efficiently when the task already favored this type of encoding.

These findings have several implications for the current debate on the immunity of actions from perceptual illusions. First, and largely in accord with the hypothesized independence of vision-for-action from vision-for-perception, they demonstrate that pointing is substantially immune from ML-family illusions when programmed on the basis of vision and within an egocentric spatial reference frame. Interestingly, this general conclusion also suggest that sensory feedback plays only a marginal contribution to improve pointing accuracy under these conditions. This is perhaps not so surprising given the fast, quasi-ballistic nature of rapid pointing, but it was unexpected to us in light of previous findings (Gentilucci et al., 1996; Glover, 2002). In particular, it has been proposed (Glover, 2004) that immunity from actions depends on the difference between action programming and control. Within this proposal, programming uses a perceptually based representation whereas control performs online corrections based on visual and kinesthetic feedback about hand position (as in classical closed-loop theory; Adams, 1971). Thus, the prediction is made that illusion effects should be smaller when vision of the stimulus is allowed (either with or without vision of the hand). As shown in the current review, however, when the effect of feedback is separated from that of condition at the programming phase, the data suggest that feedback plays only a marginal role in reducing the illusion effect.

A second implication of these results concern the role of different frames of reference when planning the action (see Bruno, 2001). Planning a movement ultimately requires a specification of the target location in body-relative coordinates. Under certain task demands or viewing conditions, however, this specification might also be influenced by stimulus features coded in object-relative coordinates. The results of the present review confirm that, other things being equal, subtle features of the pointing task can make the relevance of such coding more or less large. In accord with previous proposals (de Grave et al., 2004), for instance, starting near the shaft endpoint to move along the direction of the shaft seems to make object-relative coding more salient, relative to starting outside and moving orthogonally to the shaft direction. As shown by the interaction plotted in Fig. 5, however, this tendency seems to be affected in different ways by practice. When the task tends to favor exclusive egocentric encoding, illusion effects appear to decrease rapidly with more trials. When the task makes object-relative encoding more salient, the effect of trials is more gradual.

The effect of practice might be based on coding the position of the target using increasingly accurate eye movements. Consider the following scenario. Before the initiation of hand movement, participants saccade to the endpoint of the segment; an internal model of the saccadic movement is passed on to the motor program for hand movement; this is then used to guide the action to the correct location (see also Post and Welch, 1996). However, there is ample evidence that saccadic eye movements, unlike pointing, are affected by the Müller-Lyer illusion as much as perceptual reports (Bernardis et al., 2005; Binsted and Elliott, 1999; de Grave et al., 2006; Knox and Bruno, 2007). In addition, pointing can be essentially immune from the illusion even when the instructions explicitly prevent saccading to the target (Bruno and Bernardis, 2003).

Another, more plausible mechanisms might be based on focal attention. Over repeated trials, the visuomotor system might learn to focus on the target endpoint while excluding the illusion-inducing arrows. Such process would reduce the opportunity for relative encoding of segment lengths and effectively privilege egocentric target positions, counteracting the illusion. The idea that the deployment of spatial attention and motor processes may be tightly linked is not new (i.e., the premotor theory of attention; Rizzolatti and Craighero, 1998). Within this context, the involvement of attention might play an important role in motor preparation in analogy to what shown for action selection by van Doorn et al. (2007). One interesting possibility in this regard lies in recognizing that action-related functions served by the parietal lobes may go beyond the mere control of primitive object-oriented movements (Jeannerod and Jacob, 2005; Rizzolatti and Matelli, 2003; Rizzolatti and Gallese, 2006). To the extent that these functions include higher-level attentional processes related to actions, it seems reasonable to assume that they should allow for different learning processes within different spatial reference frames. If these attentional functions are involved in processes that call into play the ventral system, this might eventually explain why the attenuation of illusion effects over repeated presentations occurs not just in visuomotor responses, but also in perception. As already reported in a previous section of our analysis, this has been known to happen for at least a century (Eysenk and Slater, 1958; Judd, 1902; Köhler and Fishback, 1950; Lewis, 1908; Porac, 1994; Predebon, 1998, 2006; Schiano and Jordan, 1990). If so, consideration of these potential interactions between vision-for-action and vision-for-perception might be needed before behavioral data are brought to bear on the functional interpretation of anatomically separable visual streams.

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Appendix A

A summary of mean effects in the studies we have examined is presented in Table A1.

Appendix B

The 11 remaining papers which used either variants of the methods of adjustment, such as drawing the perceived extent or setting the length of a variable shaft, or used verbal estimations of length is given in Table B1.

Table A1

n	Reference	Exp. or group	Ave.%
1	Bernardis et al. (2005)	3	7
2	Binsted and Elliott (1999)	1	0.2
2	Binsted and Elliott (1999)	2	1.6
2	Binsted and Elliott (1999)	3	−0.3
3	Bruno and Bernardis (2003)	2	−2.6
3	Bruno and Bernardis (2003)	4	0.1
3	Bruno and Bernardis (2003)	5	−1.4
4	de Grave et al. (2004)	1	2
5	de Grave et al. (2006)	3	33.2
5	de Grave et al. (2006)	4	23.8
6	Elliott and Lee (1995)	1	5.5
6	Elliott and Lee (1995)	2	1.9
7	Gentilucci et al. (1996)	1	1.9
7	Gentilucci et al. (1996)	2	3.7
7	Gentilucci et al. (1996)	3	4.3
7	Gentilucci et al. (1996)	4	10
8	Gentilucci et al. (1997a)	1	2.3
9	Gentilucci et al. (2001)	1	5.3
9	Gentilucci et al. (2001)	2	5.9
10	Glazebrook et al. (2005)	2	3.8
11	Mack et al. (1985)	1	4.6
11	Mack et al. (1985)	2	12.3
12	Meegan et al. (2004)	1	6.8
12	Meegan et al. (2004)	2	2.2
13	Mendoza et al. (2005)	1	8.4
14	Mon-Williams and Bull (2000)	1	2
15	Post and Welch (1996)	1	17.5
16	Predebon (2005)	1	1.2
16	Predebon (2005)	2	1.9
17	Rival et al. (2003)	1	1
17	Rival et al. (2003)	2	4.7
17	Rival et al. (2003)	3	5.3
18	Welch et al. (2004)	1	4.3

Table B1

n	Reference	Exp. or group	Ave. %
1	Bernardis et al. (2005)	1	22.3
3	Bruno and Bernardis (2003)	1	16.4
3	Bruno and Bernardis (2003)	3	22.8
4	de Grave et al. (2004)	1	23
9	Gentilucci et al. (2001)	1	33.5
10	Glazebrook et al. (2005)	1	18
11	Mack et al. (1985)	1	26.7
14	Mon-Williams and Bull (2000)	1	4
15	Post and Welch (1996)	1	20
15	Post and Welch (1996)	2	36.7
18	Welch et al. (2004)	1	4.3

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