Exp Brain Res (2002) 144:275–280
DOI 10.1007/s00221-002-1073-1

RESEARCH NOTE

James A. Danckert · Nadder Sharif
Angela M. Haffenden · Karen C. Schiff
Melvyn A. Goodale

A temporal analysis of grasping in the Ebbinghaus illusion: planning versus online control

Received: 9 November 2001 / Accepted: 21 February 2002 / Published online: 10 April 2002
© Springer-Verlag 2002

Abstract Recent work has shown that pictorial illusions have a greater effect on perceptual judgements than they do on the visual control of actions, such as object-directed grasping. This dissociation between vision for perception and vision for action is thought to reflect the operation of two separate streams of visual processing in the brain. Glover and Dixon claim, however, that perceptual illusions can influence the control of grasping but that these effects are evident only at early stages of the movement. By the time the action nears its completion any effect of illusions disappears. Glover and Dixon suggest that these results are consistent with what they call a 'planning and control' model of action, in which actions are planned using a context-dependent visual representation but are monitored and corrected online using a context-independent representation. We reanalysed data from an earlier experiment on grasping in the Ebbinghaus illusion in which we showed that maximum grip aperture was unaffected by this size-contrast illusion. When we looked at these data more closely, we found no evidence for an effect of the illusion even at the earliest stages of the movement. These findings support the suggestion that the initial planning of a simple object-directed grasping movement in this illusory context is indeed refractory to the effects of the illusion. This is not to suggest that more deliberate and/or complex movements could not be influenced by contextual information.

Keywords Ebbinghaus illusion · Visuomotor planning and control · Grasping

J.A. Danckert (✉) · N. Sharif · A.M. Haffenden · K.C. Schiff
M.A. Goodale
CIHR Group on Action and Perception, Department of Psychology, Social Science Centre, University of Western Ontario, London, Ontario N6A 5C2, Canada
e-mail: jdancker@uwo.ca
Tel.: +1-519-6612111 ext. 88532, Fax: +1-519-6613961

Introduction

We have previously demonstrated that size-contrast illusions, which by definition have clear effects on conscious perception, have only minimal effects on the scaling of grasping movements directed at targets embedded in those illusions (Aglioti et al. 1995; Haffenden and Goodale 1998, 2000; Haffenden et al. 2001). For example, when subjects reach out to pick up a target disc in the middle of an Ebbinghaus illusion, their maximum grip aperture in flight is largely unaffected by the illusion. Manual estimates of the target's size, however, show a strong and robust effect, indicating that subjects perceive the discs to be bigger or smaller than they really are. Even the small effect on grasping that is sometimes seen disappears when the gap between the target and the small-circle annulus is altered. Thus, in a recent experiment (Haffenden et al. 2001), we showed that there was no difference in the effect of small- and large-circle displays on grip aperture when the distance between the targets and their surrounding annuli were made equivalent by increasing the size of the gap between the target and the small-circle annulus (Fig. 1A). Nevertheless, a strong effect on the manual estimations of target size was still evident, despite the increase in the distance between the target and the surrounding annulus in the small-circle display (Fig. 1A). These results suggest that the small effect on grasping that is sometimes seen with traditional Ebbinghaus displays is not due to the illusion but is due instead to the tendency of the visuomotor system to treat the 2D elements surrounding the target disc as potential obstacles. In other words, the visuomotor system appears unable to distinguish easily between real obstacles and 2D contours close to the target. As a consequence, subjects make adjustments in the trajectory of the finger and thumb to avoid these virtual 'obstacles' (see Haffenden et al. 2001 for a more detailed discussion of this point).

Although we have argued that the control of grasping is impervious to the perceptual effects of the Ebbinghaus size-contrast illusion (Aglioti et al. 1995; Haffenden et al. 2001; Haffenden and Goodale 1998), the possibility

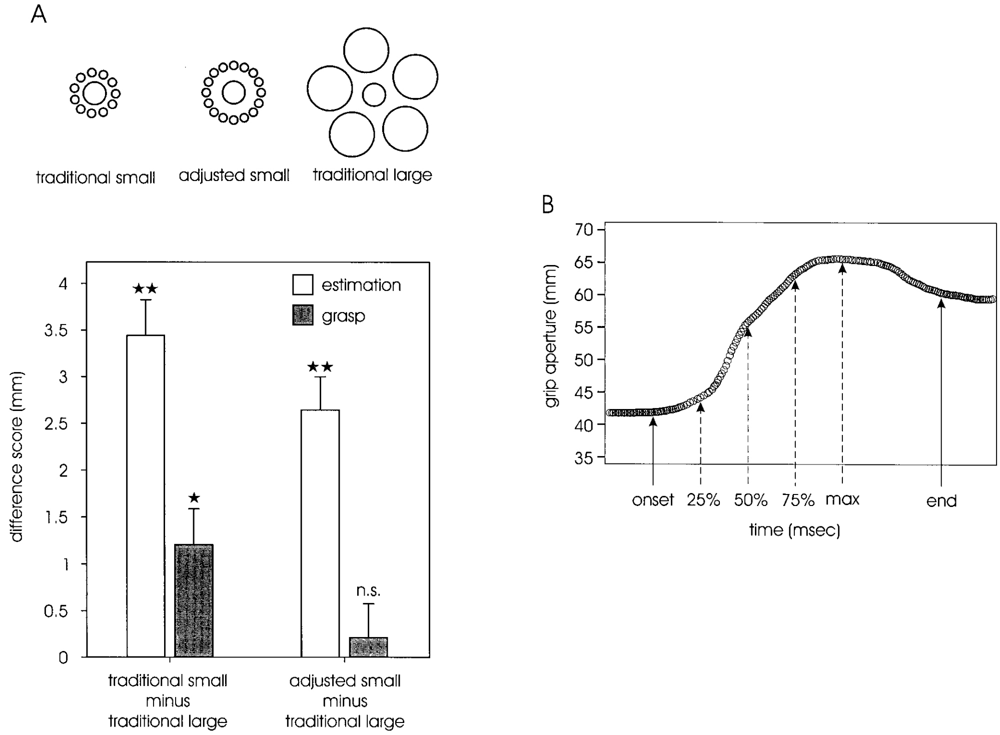

Fig. 1 **A** Schematic representation of the stimulus displays used. Note that the distances between the targets and the annuli are equivalent for the traditional large- and adjusted small-circle displays. Mean (+SE) grip aperture and perceptual estimation difference scores (see "Materials and methods") are presented below the schematic. [This is a subset of the data from the Haffenden et al. study (2001).] Although a large effect was observed for perceptual estimations of target size, only a very small effect was observed for grasping (Haffenden et al. 2001). When data from the adjusted small-circle display were compared with data from the traditional large-circle display there was no significant effect of the illusion on grasping. **indicates a significant difference at $P<0.001$, *indicates a significant difference at $P<0.01$, *n.s.* non significant. **B** Schematic representation of a grasping profile taken from a single trial by one subject in the current study. Typically, the hand opens wider than the actual target size before closing in on the object to complete the grasp ('end' of the movement in the figure). The point of maximum aperture ('max' in the figure) occurs around 70% of the way through the movement. The analysis for the current study divided the time taken to reach maximum aperture into four time points at 25%, 50% and 75% of the time taken to reach maximum aperture, as well as the maximum aperture point itself

remains that illusions could influence the grasp at earlier stages of the movement, well before maximum grip aperture is achieved. This suggestion was recently put forward by Glover and Dixon (2001), who proposed that the initial movement plan is based on context-dependent information and is therefore susceptible to the influence of illusory contexts. But once the hand has begun to move, its trajectory is then adjusted or controlled online by making use of context-independent information. They termed this a 'planning and control model' of prehension. In developing these ideas, they used a version of the tilt illusion, in which subjects grasped rods placed against background gratings oriented at different angles with respect to the rod (i.e. which creates a perceptual illusion such that the rod appears to be tilted in a direction opposite to that of the grating). In their experiment, the earliest stages of the grasping movements directed at the rods were indeed influenced by the illusory context, but no such influence was observed later in the movement (Glover and Dixon 2001).

To examine whether or not the kinematics of grasping are influenced by the Ebbinghaus illusion at the earliest stages of the movement, we compared grip aperture to targets embedded in the small- and large-circle displays at four different time points during the course of the movement (25%, 50%, and 75% of the total time to reach maximum aperture, and maximum grip aperture itself, which typically occurs well before the hand contacts the target; Fig. 1B).

Materials and methods

The apparatus and procedure for this study have been described in detail elsewhere (Haffenden et al. 2001). In short, 18 right-handed subjects (9 males and 9 females) with normal or corrected-to-normal vision completed both the manual estimation and grasping versions of the Ebbinghaus task. All subjects gave informed consent prior to testing and the experimental protocol was approved by the institutional ethics committee. For the grasping task, subjects were asked to grasp the disc embedded in the display (Fig. 1A), with maximum grip aperture (i.e. the distance between forefinger and thumb) as the dependent measure. For perceptual estimations, subjects were asked to open their forefinger and thumb to a distance they felt was equivalent to the size of the target disc along the sagittal axis. For the present study we are concerned only with the grasping condition. For this task, subjects completed 60 grasping trials, with the four target disc sizes (28, 30, 31, 32 mm diameter) and three annulus arrays (traditional small-circle, adjusted small-circle and traditional large-circle; Fig. 1A) being randomized (see Haffenden et al. 2001 for the precise dimensions of the annuli used). This led to five trials per

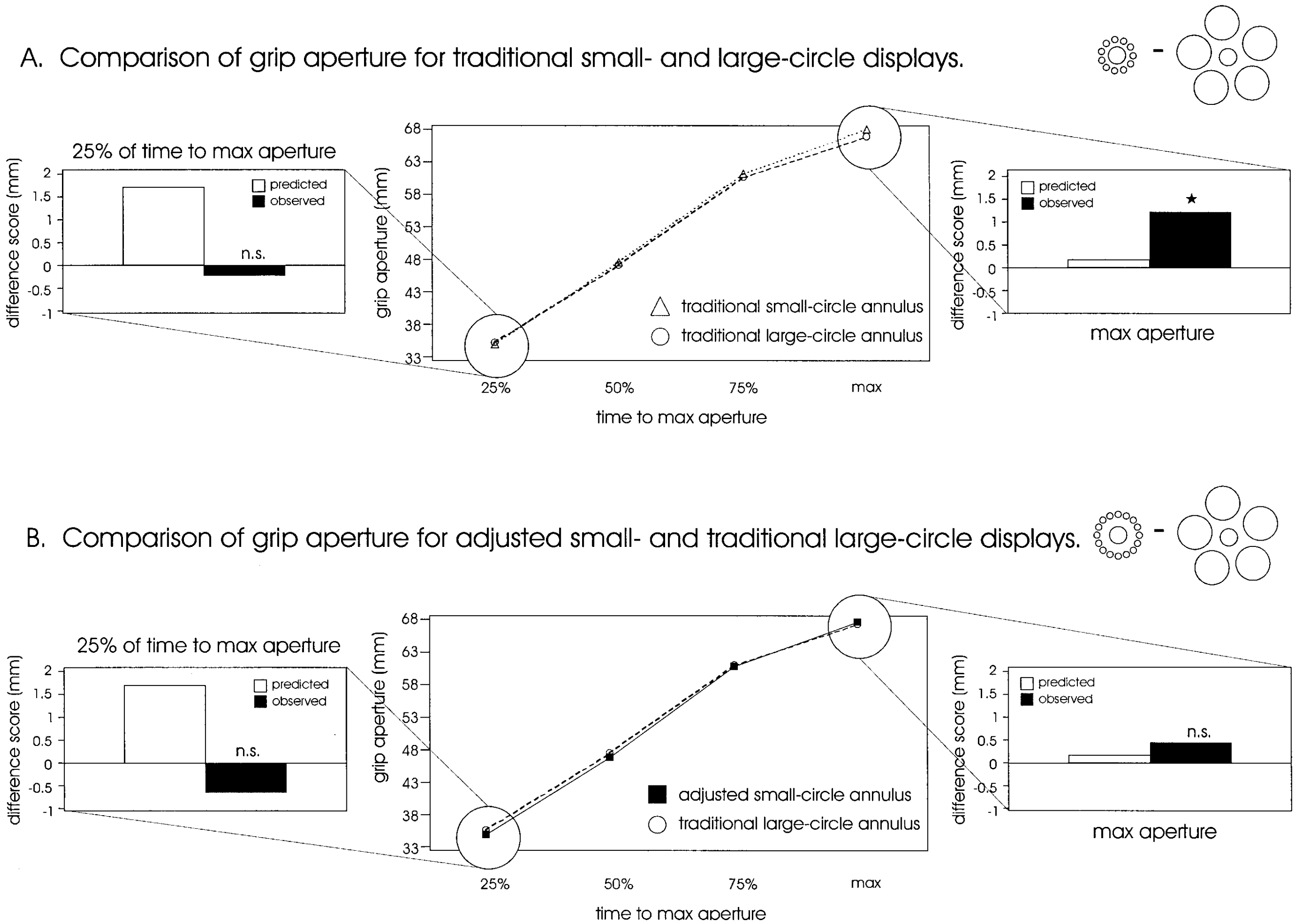

Fig. 2 A Mean grip aperture over the four time points for the traditional small-circle display (*open triangles*) and traditional large-circle display (*open circles*). **B** Mean grip aperture over the four time points for the adjusted small-circle display (*filled squares*) and traditional large-circle display (*open circles*). *Beside each figure to the left* are the predicted (*open bars*) and observed (*filled bars*) resultant difference scores between grasps to the small- and large-circle displays at 25% of the way through the movement. *On the right of each figure* are the resultant difference scores at the point of maximum aperture. The standard error for the difference scores of the observed data ranged from 0.32 to 0.48 mm and was not systematically influenced by the display type. Predicted scores are based on Glover and Dixon's (2001) planning and control model, which predicts a large effect of the illusion (i.e. a significant positive difference score) early in the movement and no effect (i.e. a difference score approaching zero) later in the movement. The predicted effect for the early time point is based on the effect of the illusion observed for perceptual estimations of size (Fig. 1A; note that this is a conservative estimate adjusted for the differences in slope observed for scaling estimations vs scaling grip aperture; see Haffenden et al. 2001 for details). For the maximum aperture time point, we assumed a non-significant difference as a predicted score (i.e. a difference score that approached zero – for illustration purposes we have depicted a positive score that approaches zero; however, there is no a priori reason for choosing this). *indicates a significant difference at $P<0.01$

condition. Finger and thumb position (as well as wrist position) were recorded using a three-camera Optotrak (Northern Digital) system that monitors infrared light-emitting diodes in real time and three-dimensional space. Subjects wore PLATO liquid crystal goggles (Translucent Technologies) that changed from clear to opaque upon movement onset, thereby creating an open-loop condition in which the subject's view of their hand and the target were occluded after movement onset. Subjects were instructed to initiate their movements as soon as they saw the target and speed was not emphasized. Instead subjects were asked to make natural grasping movements to the near and far axes of the target discs.

Data analysis

To determine the effect the illusion had on maximum grip aperture (and on perceptual estimations of size) difference scores were calculated by subtracting the responses made to the large-circle displays from the responses made to the small-circle displays. A positive difference score indicates that grip aperture to targets surrounded by the small-circle annuli were larger than grip aperture to targets surrounded by the large-circle annulus array, indicating that the subject perceived the disc presented in the small-circle display to be larger than discs of the same size presented in the large-circle display. To analyse this effect over time, we first calculated the time taken to reach maximum grip aperture for each subject on each trial. This figure was then divided into four time points at 25%, 50% and 75% of the time taken to reach maximum grip aperture, as well as the point of maximum aperture itself (note: time to reach maximum aperture was chosen rather than full movement time, as grip aperture tends to decrease after maximum aperture until point of contact with the target is made, at which time there will be no difference across conditions given physical contact with the target object has been made). The grip aperture at each of these time points was then entered into the analysis. For each subject, data were then collapsed across disc size, which had been shown previously not to interact with task (i.e., estimation vs grasping) or annulus array (Haffenden et al. 2001). Two separate ANOVAs were then conducted, one comparing grip aperture across time for the traditional annulus arrays and the second comparing grip aperture across time for the adjusted small-circle and traditional large-circle displays (Fig. 1A). Both ANOVAs had two factors: annulus array (small vs large) and time (25%, 50%, 75%, and 100% of time to reach maximum aperture). Main effects and interactions were compared with paired samples *t*-tests with Bonferroni corrections for the number of comparisons made. Difference scores were calculated for the purpose of display by subtracting grip aperture to the large-circle annulus from grip aperture to the two small-circle annulus displays separately (Figs. 1, 2).

Results

For grasps made to targets embedded in the traditional small- and large-circle displays, repeated measures analysis of variance (ANOVA) revealed a significant interaction ($F_{(1,3)}$=3.66, P<0.05) between illusory context (small-circle annulus vs large-circle annulus) and time (at 25%, 50%, 75%, and 100% of the total time to reach maximum aperture). Post hoc analysis showed that this interaction was entirely due to the significant difference in *maximum* grip aperture ($t_{(17)}$=3.17, P<0.01), which we had already seen in our earlier study (Haffenden et al. 2001; Fig. 2A). In other words, although maximum grip aperture was slightly larger when subjects were grasping targets in the small-circle annulus array as compared to when they were grasping the same targets in the large-circle annulus array, this difference was not evident at the three earlier time points (25% of max. aperture, $t_{(17)}$=–0.65, P=0.53; 50% of max. aperture, $t_{(17)}$=1.3, P=0.21; 75% of max. aperture, $t_{(17)}$=1.3, P=0.2; Fig. 2).

No significant effects or interactions were found when the same analysis was applied to data from the traditional large-circle and adjusted small-circle annuli (Fig. 2B). That is, there were no significant differences in grip aperture between the two displays at any of the time points tested, including maximum grip aperture (with a Bonferroni corrected alpha value of 0.0125; 25% of max. aperture, $t_{(17)}$=–1.5, P=0.14; 50% of max. aperture, $t_{(17)}$=–2.3, P=0.04; 75% of max. aperture, $t_{(17)}$=–0.83, P=0.4; max. aperture, $t_{(17)}$=1.26, P=0.22; Fig. 2B). Importantly, as was the case for the two traditional displays, there was no evidence of an early contextual effect of the illusion on grasping.

Discussion

Our reanalysis of how grip aperture evolves during the course of a grasping movement showed no evidence for an effect of the Ebbinghaus size-contrast illusion at early stages of the movement. According to Glover and Dixon's planning and control model, one would expect to see evidence of larger grip apertures to targets in the small-circle display than in the large-circle display at the beginning of the movement, and this difference would become smaller as the movement unfolded. As our data show, this was clearly not the case for either the comparison between the two traditional displays or for the comparison between the adjusted small-circle display and the traditional large-circle display (Fig. 2). In fact, given that the perceptual effect of the illusion was greater for the traditional rather than the adjusted displays, one might have expected that if the illusion had any effect on the initial planning of the movement, it would be most evident here. But as Fig. 2 shows, there was not even a hint of an early effect in either comparison.

Given that we chose to explore fixed time points in the course of the movement based on the time taken to reach maximum aperture, one possibility for the absence of any difference in grip aperture at these time points could be that the different illusory contexts influenced how long subjects took to reach maximum aperture in some systematic way. For example, subjects may have taken longer to reach maximum aperture under the small annulus array than the large annulus array, making any comparison of fixed time points based on time to reach maximum aperture invalid. To address this issue we analysed the time to reach maximum aperture across the different displays (e.g. traditional small and large annulus displays, as well as the adjusted small annulus array). We found no significant differences in the time taken to reach maximum aperture, suggesting the different displays used in the current study did not influence the time taken to reach maximum aperture. Furthermore, if one suspects that subjects were taking *longer* to reach maximum aperture under some conditions than others, then the concern for Glover and Dixon's planning and control model would be that our method of analysis might mask any effects very early on in the movement (i.e. before the point where 25% of the time taken to reach maximum aperture had elapsed). Closer examination of Glover and Dixon's findings, however, shows that in their study the effects of the slant illusion on grasping were significant well beyond 25% of the overall movement duration (Glover and Dixon 2001 – see their Fig. 7). Therefore, our method of analysis would presumably have uncovered any early effects had they been there. Moreover, although we did not examine explicitly the differences at earlier timepoints in the movement (i.e. prior to 25% of the time taken to reach maximum aperture), there is no indication at all that any differences were present (Fig. 2).

As we have already emphasized, the small difference in maximum grip aperture seen for the traditional Ebbinghaus displays (i.e. in which the gap between targets and the large- and small-circle annuli are not equivalent; Fig. 1A) was not due to the size-contrast illusion. Instead, we suggest that this effect is due to an attempt by the visuomotor system to avoid 'obstacles' surrounding the target.[1] Support for this conjecture comes from our observation that there is no difference in maximum grip aperture when the gaps between the target and the surrounding elements for small- and large-circle annuli

[1] There is evidence that the visuomotor system will treat 2D objects as obstacles during the performance of a grasping or aiming movement (see Haffenden and Goodale 2000 for a review of this literature)

are made equivalent (Haffenden et al. 2001). Importantly, for data obtained using the adjusted small-circle annulus, there was also no evidence of an early effect of the illusion on grasping. Therefore, the current reanalysis of grasping data in the Ebbinghaus illusion provides strong evidence that the initial programming of the grasp was based on the real dimensions of the target, not its perceived size.

Glover and Dixon asked subjects to grasp rods placed against gratings oriented at different angles with respect to the rod (i.e. the tilt illusion). This display results in an orientation-contrast illusion, such that the rod appears to be tilted more than it really is (in a direction opposite to the orientation direction of the grating). When subjects reached out to grasp the rod in this display, the illusion exerted a large effect on hand posture at the early stages of the movement. By the time the hand was about to make contact with rod, however, all effects of the illusion had disappeared. It was this result that led Glover and Dixon to formulate their planning and control model, in which they suggested that the initial programming of movements makes use of visual representations that take into account the surrounding context, while online mechanisms which make use of context-independent visual representations correct for any contextual effects later on in the movement. Why then did we not see any effect of illusory context on grip aperture at early stages of the movement in our experiment? We would suggest that the crucial difference between the two studies lies in the nature of the elements inducing the illusion. In the case of the tilt illusion, the inducing elements of the illusion – the contrast between the edges of the rod and the background grating – are likely to depend on local inhibitory interactions between groups of neurons tuned to different orientations, probably occurring at the level of primary visual cortex (Hubel and Wiesel 1968; Sengpiel et al. 1997). The early locus of the source of the illusion means that the processing of orientation in both ventral and dorsal extrastriate visual areas will be affected. In contrast, the inducing elements of the Ebbinghaus size-contrast illusion are thought to depend on object processing that occurs in ventral extrastriate areas well beyond primary visual cortex (see Milner and Goodale 1995 for review). Thus, local processing of the target by dorsal stream mechanisms is unaffected by this illusion.

Given that the two illusions depend on mechanisms at very different levels of the visual system, it is perhaps not surprising that different patterns of visuomotor control are observed. Indeed, a recent study by Dyde and Milner (2002) directly compared the effects of a low-level illusion (the tilt illusion) with those of a higher-level 'pictorial' illusion (the 'rod and frame' illusion) on both perceptual judgements and visually guided actions. They found that the tilt illusion had an equivalent effect on perception and action, whereas the rod and frame illusion affected only perception. This result fits nicely with the argument we are making here that the level at which the inducing elements of an illusion are processed will determine the extent to which visuomotor control escapes the effects of the illusion. Thus, the manifestation of the illusion in the early stages of the movement in the Glover and Dixon study need not imply that the initial programming of skilled actions is influenced by contextual information surrounding the target object. Instead, we would argue that the earlier in the visual system the illusion 'emerges', the greater the likelihood that the illusion will exert some influence on the control of actions (as well as influencing perceptual judgements).

In the original study by Aglioti and colleagues (1995) using the Ebbinghaus illusion, the relative insensitivity of grip scaling to the illusion was taken as evidence that the visual control of actions depends on visual pathways that are quite separate from those mediating our perception of the world. Since that paper was published, a large number of studies have pursued this finding and have explored in detail the effects of different illusions on perception and action (Brenner and Smeets 1996; Bridgeman et al. 2000; Dyde and Milner 2002; Franz et al. 2000; Gentilucci et al. 1996; Glover and Dixon 2001; Goodale and Milner 1992; Haffenden et al. 2001; Haffenden and Goodale 1998; Jackson and Shaw 2000; Marotta et al. 1998; Mon-Williams and Bull 2000; Pavani et al. 1999; van Donkelaar 1999). The story that is emerging is not a simple one – but one that is nevertheless quite consistent with the original two-visual systems proposal. Although some investigators have shown no difference between the effects of their illusory stimulus on action and perception, this by itself does not constitute evidence against the two-visual systems model. There are many reasons why actions can be influenced (or at least appear to be influenced) by perceptual illusions. As we have already seen, for example, the surrounding elements in the Ebbinghaus display can be treated as 'obstacles' and thus influence grip aperture (Haffenden et al. 2001; see also Mon-Williams et al. 2001 and Howard and Tipper 1997). Some illusions, like the tilt illusion, may demonstrate an influence on action by virtue of the fact that the illusion arises in primary visual cortex, thereby exerting an influence on both the ventral and dorsal streams (Dyde and Milner 2002). Timing is also critical. If there is a delay between viewing the target and initiating the action, then illusions that do not affect actions in real time may now do so, presumably because the subject is utilizing a remembered (and thus perceptual) representation of the target (Bridgeman et al. 1979; Goodale et al. 1994; Hu and Goodale 2000). The action parameter that one measures is also important. Grip aperture, which is largely determined by information that is available on the retina, is much less likely to be influenced by context than initial grip force, which will be based on expectation or prior experience with the target object (Brenner and Smeets 1996; Jackson and Shaw 2000). In addition, some actions, like pointing, may be more likely to be influenced by illusions than others, such as grasping. When pointing to the 'centre' of a line in the context of the Müller-Lyer or Judd illusions, for example, one is indicating where one perceives the centre to be. In contrast, when grasping a rod in the context of the same illusions, one is simply trying to pick up the rod. Not surprisingly, pointing shows greater influence from these illusions than grasping (Gentilucci et al. 1996; Mon-Williams and Bull 2000; van Donkelaar 1999). Finally, it should be noted that some visual displays can induce adjustments in target-directed movements with only small (or non-existent) changes in perception (Goodale et al. 1986; Yamagishi et al. 2001).

In conclusion, the present study shows no evidence for an effect of the contextual information in the Ebbinghaus size-contrast illusion on grip aperture, even at early stages of the movement. This finding adds to the growing body of evidence that the visual control of skilled actions, such as grasping, depends on visual processing that is quite separate from that leading to our perceptual representations of the world. We would suggest, however, that the performance of an action in an illusory context will be influenced by many different factors, not all of which are perceptual, and for this reason the demonstration that visual context can influence action does not necessarily contradict the two-visual systems hypothesis.

Acknowledgements This work was supported by a grant from the Canadian Institutes of Health Research to M.A.G. The authors would like to thank Dr. David Westwood for insightful comments on an earlier version of this manuscript.

References

Aglioti S, DeSouza JFX, Goodale MA (1995) Size-contrast illusions deceive the eye but not the hand. Curr Biol 5:679–685

Brenner E, Smeets JB (1996) Size illusion influences how we lift but not how we grasp an object. Exp Brain Res 111:473–476

Bridgeman B, Lewis S, Heit G, Nagle M (1979) Relation between cognitive and motor-oriented systems of visual position perception. J Exp Psychol Hum Percept Perform 5:692–700

Bridgeman B, Gemmer A, Forsman T, Huemer V (2000) Processing spatial information in the sensorimotor branch of the visual system. Vision Res 40:3539–3552

Dyde R, Milner AD (2002) Two illusions of perceived orientation: one fools all of the people some of the time; the other fools all of the people all of the time. Exp Brain Res (in press)

Franz VH, Gegenfurtner KR, Bülthoff HH, Fahle M (2000) Grasping visual illusions: no evidence for a dissociation between perception and action. Psychol Sci 11:20–25

Gentilucci M, Chieffi S, Daprati E, Saetti MC, Toni I (1996) Visual illusion and action. Neuropsychologia 34:369–376

Glover SR, Dixon P (2001) Dynamic illusion effects in a reaching task: evidence for separate visual representations in the planning and control of reaching. J Exp Pyschol Hum Percept Perform 27:560–572

Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. Trends Neurosci 15:20–25

Goodale MA, Pélisson D, Prablanc C (1986) Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. Nature 320:748–750

Goodale MA, Jakobson LS, Keillor JM (1994) Differences in the visual control of pantomimed and natural grasping movements. Neuropsychologia 32:1159–1178

Haffenden AM, Goodale MA (1998) The effect of pictorial illusion on prehension and perception. J Cogn Neurosci 10: 122–136

Haffenden AM, Goodale MA (2000) Independent effects of pictorial displays on perception and action. Vision Res 40: 1597–1607

Haffenden AM, Schiff KC, Goodale MA (2001) The dissociation between perception and action in the Ebbinghaus illusion: nonillusory effects of pictorial cues on grasp. Curr Biol 11: 177–181

Howard LA, Tipper SP (1997) Hand deviations away from visual cues: indirect evidence for inhibition. Exp Brain Res 113: 144–152

Hu Y, Goodale MA (2000) Grasping after a delay shifts size-scaling from absolute to relative metrics. J Cogn Neurosci 12: 856–868

Hubel DH, Wiesel TN (1968) Receptive fields and functional architecture of the monkey striate cortex. J Physiol 195:215–243

Jackson SR, Shaw A (2000) The Ponzo illusion affects grip-force but not grip-aperture scaling during prehension movements. J Exp Pyschol Hum Percept Perform 26:418–423

Marotta JJ, DeSouza JFX, Haffenden AM, Goodale MA (1998) Does a monocularly presented size-contrast illusion influence grip aperture? Neuropsychologia 36:491–497

Milner AD, Goodale MA (1995) The visual brain in action. Oxford University Press, New York

Mon-Williams M, Bull R (2000) The Judd illusion: evidence for two visual streams or two experimental conditions? Exp Brain Res 130:273–276

Mon-Williams M, Tresilian JR, Coppard VL, Carson RG (2001) The effect of obstacle position on reach-to-grasp movements. Exp Brain Res 137:497–501

Pavani F, Boscagli I, Benvenuti F, Rabuffetti M, Farné A (1999) Are perception and action affected differently by the Titchener circles illusion? Exp Brain Res 127:95–101

Sengpiel F, Sen A, Blakemore C (1997) Characteristics of surround inhibition in cat area 17. Exp Brain Res 116:216–228

van Donkelaar P (1999) Pointing movements are affected by size-contrast illusions. Exp Brain Res 125:517–520

Yamagishi N, Anderson SJ, Ashida H (2001) Evidence for dissociation between the perceptual and visuomotor systems in humans. Proc R Soc Lond Biol 268:973–977