The Role of Vision in the On-line Correction of Illusion Effects on Action

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Abstract In this study, participants reached out and picked up a bar placed on a background grating that induced an illusion in the perceived orientation of the bar. The illusion had a large effect on the orientation of the hand early in the reaches, but this effect decreased continuously as the hand approached the target. This pattern occurred whether or not participants were allowed vision of the hand and target while reaching. These results are consistent with a "planning/control" model of action, in which actions are planned using a context-dependent visual representation but monitored and corrected on-line using a context-independent visual representation. The hypothesized neural bases of these representations are discussed.

Résumé Lors de cette étude, les participants devaient atteindre et saisir une barre placée devant une grille qui produisait une illusion quant à l'orientation perçue de la barre. Cette illusion a eu un effet marqué sur l'orientation de la main lorsque s'amorçait l'atteinte de la cible, mais l'effet diminuait de façon continue à mesure que la main approchait de la cible. Ce patron se manifestait que les participants aient pu ou non voir leur main et la cible en tentant d'atteindre cette dernière. Ces résultats sont conformes au modèle d'action de type « planification/contrôle », selon lequel les actions sont planifiées à partir d'une représentation visuelle dépendante du contexte, mais sont contrôlées et adaptées « en ligne » à l'aide d'une représentation visuelle indépendante du contexte. Les bases neurologiques qui sont supposées permettre ces représentations sont examinées.

Studies of the effects of context-induced optical illusions on action reveal a complex pattern. Whereas some indices of action appear to be relatively immune to the perceptual effects of illusions (e.g., maximum grip aperture, Aglioti, DeSouza, & Goodale, 1995; pointing accuracy, Bridgeman, Perry, & Anand, 1997; saccadic accuracy, Wong & Mack, 1981), other indices appear to be just as affected by illusions as are perceptually based judgments (e.g., lifting force, Brenner & Smeets, 1996; posture choice, Glover & Dixon, in press a; movement times, van Donkelaar, 1999). In the present study, we show that a context-induced orientation illusion has a diminishing effect on the trajectory of the hand as participants reach out to grasp a bar. Further, the removal of vision coincident with the signal to reach has no discernible impact on this effect. These results suggest that separate visual representations are involved in the planning and control of action (Glover & Dixon, in press a; 2001a; Glover, 2000).

Woodworth (1899) was the first to hypothesize separate stages of action underlying planning and control. According to Woodworth, the early portions of a reach reflected an "initial adjustment" stage that was entirely pre-planned and ballistic. At some point after movement initiation, the "current control" stage began, in which visual and proprioceptive feedback were used to correct errors in the trajectory. Since Woodworth's seminal work, much research has gone into characterizing these two stages of action (e.g., Keele & Posner, 1968; Meyer, Abrams, Kornblum, Wright, & Smith, 1988), and the two-stage dichotomy has become generally accepted as a principle of human motor control (Jeannerod, 1988; Rosenbaum, 1991).

In the planning/control model (Glover & Dixon, in press a; 2001a; Glover, 2000), we hypothesize that separate visual representations are used in each stage of action. On the one hand, the visual representation underlying planning is assumed to encode the relationship between the target and its surrounding visual context. This contextual information is used, for example, in planning movement trajectories that avoid obstacles and in computing affordances for interacting with the target. On the other hand, the visual representation used during on-line control is designed for the fast and accurate corrections that occur in flight (e.g., Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991; Savelsbergh, Whiting, & Bootsma, 1991; Zelaznik, Hawkins, & Kisselburgh, 1983). We assume that this visual representation is focused almost exclusively on the target itself and its relationship to the effector. As a result, this representation of the target is independent of the contextual relationships that induce many visual illusions. The distinction between the two visual representations we posit here implies that context-induced illusions should have large effects on planning processes but little or no effects on on-line control processes.

Evidence in favour of the planning/control model comes from studies in which the effects of an illusion are measured throughout the course of a movement. In one paradigm involving an orientation illusion (Glover & Dixon, in press a; 2001a), there was a large effect of the illusion on the trajectory of the hand in the early portions of a movement as participants reached out to grasp a bar. However, the effect of the illusion decreased continuously as the hand approached the target. By the end of the reach, the effect of the illusion on the hand was minimal, allowing the participants to grasp the bar without difficulty. A study employing the Ebbinghaus size-contrast illusion replicated this "dynamic illusion effect" with grasping (Glover & Dixon, in press b). Presumably, the large effect of the illusion at the outset of the reach in these studies reflected planning processes prior to the initiation of the movement, whereas the decline in the effect over the movement trajectory reflected the contribution of on-line control processes.

In the present study, we examined the role of visual feedback of the hand and continuous vision of the target in the on-line correction of the orientation illusion's effect on reaching. In principle, on-line control might use several sources of information. These include visual feedback of the moving hand, visual information regarding the target, proprioception, and efference copy. Although it is intuitive to suspect that the contribution of visual information to the on-line correction of illusion effects on action is important or even paramount, the available evidence is mixed. Whereas some studies have found important effects of visual feedback and continuous vision of the target during movements (e.g., Gentilucci, Chieffi, Daprati, Saietti, & Toni, 1996; Glover & Dixon, 2001b), others have suggested that denying participants visual information during reaching has little impact on the magnitude of an illusion's effect (e.g., Bridgeman et al., 1997; Glover & Dixon, in press b; Haffenden & Goodale, 1998). Given this ambiguity, it was important to investigate this issue further.

The task used here required participants to reach out and pick up a bar lying on a table in front of them. The orientation of the bar is critical to the action because the orientation of the hand must accommodate that of the bar by the end of the reach in order for the bar to be grasped effectively (Jeannerod, 1981; Stelmach, Castiello, & Jeannerod, 1994). The perceived orientation of the bar was manipulated by placing the bar against a background grating that was slightly misaligned with the participant's sagittal plane. When the grating was rotated clockwise from sagittal, it induced the illusion that the bar was more counterclockwise than it actually was, and vice versa. This effect has been found to be roughly 2° in a perceptual adjustment task (Glover & Dixon, in press a; 2001a). In a reaching task, we have found that the effect of this illusion on the orientation of the hand is large during the initial portion of the reach but negligible by the time the hand reaches the bar. In the present study, we investi-

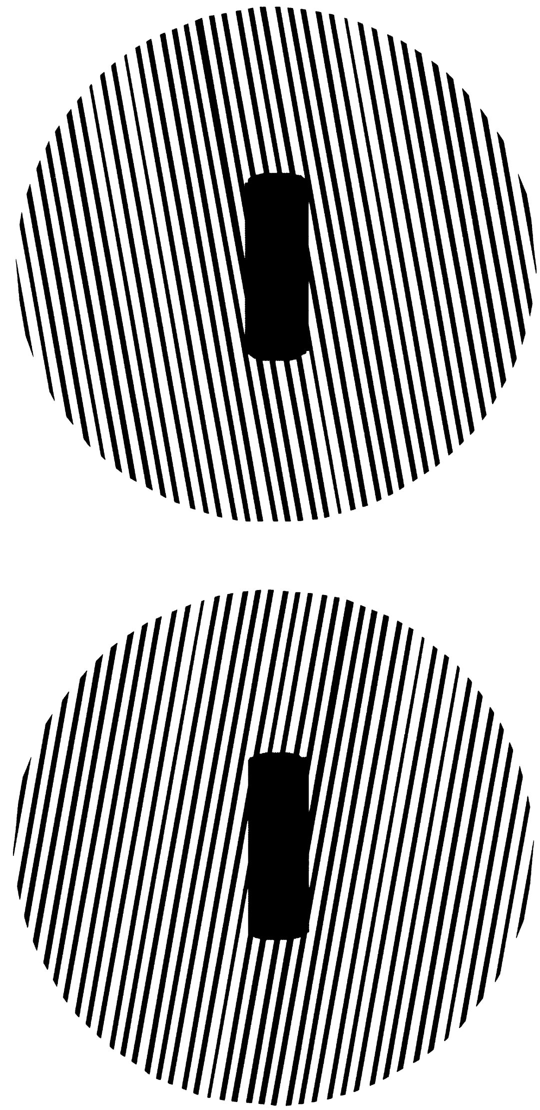

Figure 1. The orientation illusion used in the reaching and perception tasks. On the top, the grating is oriented -10 degrees clockwise from sagittal, on the bottom, the grating is oriented at +10 degrees clockwise from sagittal. Both bars are drawn vertical, yet appear slightly misoriented in the direction opposite the grating.

gated the role of visual information during reaching by comparing conditions in which visual information was either available or unavailable during the movement.

Method

PARTICIPANTS

Twenty-four University of Alberta undergraduates served as participants in the experiment. All participants reported having normal or corrected-to-normal vision, and all were strongly right-handed using a modified version of the Edinburgh inventory (Oldfield, 1971). All participants were naive as to the exact purpose of the study, and all gave their informed consent prior to testing.

APPARATUS

Participants sat on an adjustable chair at a 100 x 60 cm table and viewed the table top through a 4 x 7 cm rectangular area in the centre of a two-way mirror. The ability of the participants to see through the mirror was manipulated by switching on or off the table lighting. When the display was visible, participants had a view of the stimulus through the rectangular viewing area. A high-frequency black-and-white grating was centred within the participant's field of view (Figure 1). A target bar was set on top of the grating; this bar was an 8 x 2 cm (7.0° x 1.8° visual angle) black wooden dowel. An 8 x 2 cm starting bar was attached to the table, directly in front of the participant, with its long axis parallel to the participant's saggital plane. The distance between the centre of the starting and target bars was exactly 20 cm, and the distance between the centre of the starting bar and the participant's midsection was approximately 20 cm.

The table top was monitored by an infrared video camera mounted overhead, which fed information into an Iscan tracking system. The tracking system was calibrated using a method adapted from Haggard and Wing (1990). The calibration procedure involved fixing an ired to either end of a 12-cm bar and sweeping the bar forwards and sideways across the workspace from various starting positions, while recording the reported distance between the two ireds. The standard deviation in these measurements was less than 1.2 mm in both the forward and horizontal dimensions.

PROCEDURE

Half of the participants were assigned to the vision condition, and the other half to the no vision condition. The basic procedure was the same in both conditions. Participants wore two ireds attached to their right hand, just back of the base of the first (index) and fourth fingers, and roughly one-third of the distance from the knuckles to the wrist. The ireds were alternately illuminated at a rate of 60 Hz, and the position of the lit ired was detected by the camera and recorded for analysis off-line. Participants in both groups began each trial by pinching the starting bar with the thumb and index finger. The task was to reach out and pick up the bar near its centre using the thumb and index finger, with the finger on the left side of the target bar. The instructions did not emphasize speed. The wrist and about half of the hand could be seen under the frame prior to the start of the movement.

Participants in the *vision* condition were allowed to reach as soon as the table lighting was switched on. Participants in the vision condition were given six practice trials prior to the test trials. While reaching, vision of the hand was occluded by the apparatus for roughly the first two-thirds of the reach after it left the starting bar.

Participants in the *no vision* condition followed the same procedure as those in the vision condition with the following exceptions: in the no vision condition, participants were first allowed a two-second preview of the stimulus display. Following this, the lights were extinguished and participants had to execute their reaches without vision of their hand or the target (the extinguishing of the lights also served as the cue to reach). Due to the greater difficulty of the no vision task, participants in the no vision condition were given 12 practice trials instead of six.

In both vision and no vision conditions, participants were exposed to eight repetitions of each of seven bar orientations (ranging from +5° to +35° clockwise from the participant's sagittal plane, inclusive) and two grating orientations (+10° and –10°), for a total of 112 randomly ordered trials. Participants were allowed a brief rest after half of the reaching trials were completed.

DATA ANALYSIS

The dependent variable in this experiment was the orientation of the hand throughout the course of the reach. Data were analyzed by passing the position recordings through a custom filter that excluded artifacts. For each recording, the position of the ired that was not lit during that frame was interpolated between the measurements for the preceding and following frames. The orientation between the two ireds was then computed for each sample. A criterion velocity of 0.025 m/s was used for the onset and offset of the movement. Trials were excluded if the reaction time was less than 150 ms, if the movement time was less than 250 ms, or if either the reaction time or movement time was greater than 1,500 ms. One participant was excluded because she produced less than 85% usable trials. A total of 95.5% of the trials from the remaining 23 participants were included.

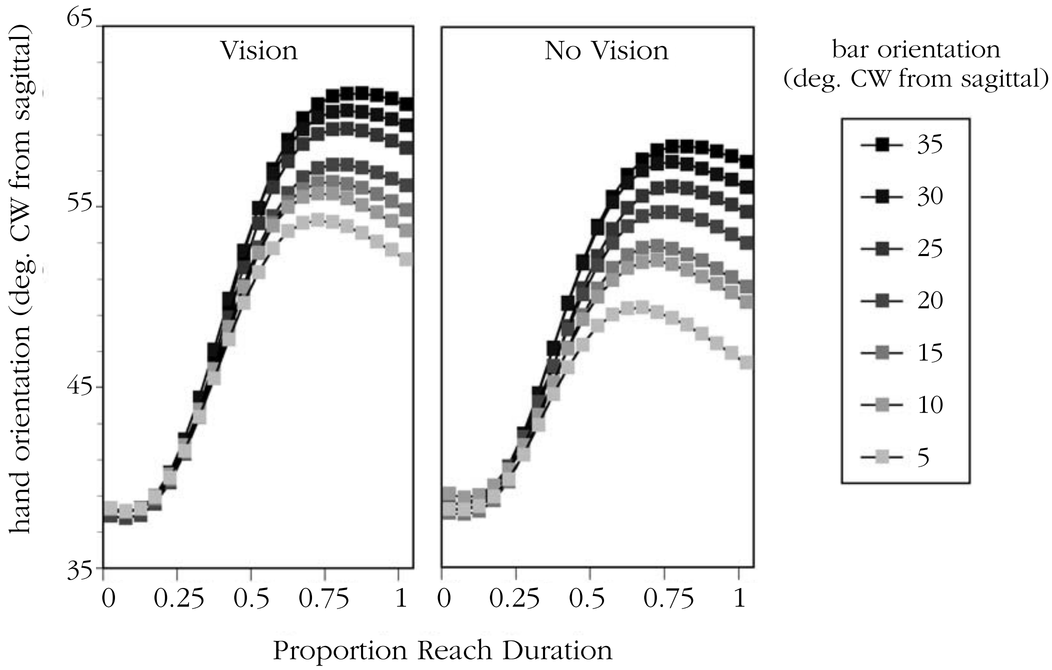

Figure 2. Hand orientation as a function of orientation of the bar and time in the closed-loop (left) and open-loop (right) conditions. The orientation of the hand is shown in degrees clockwise from sagittal from t=0.0 to t=1.0.

For each trial, the orientation of the hand was computed at 21 equally spaced intervals from onset to offset, inclusive. These time-normalized data were averaged for each participant, grating, and bar orientation. The raw illusion effect (the difference in hand orientation between the two grating conditions) was scaled by the corresponding effect of bar orientation at each time interval. This was done in both the perception and reaching tasks. In data of this sort, successive observations in time tend to be highly correlated. In order to minimize this problem of nonindependence, only a few, widely spaced points in time were used in the statistical analysis of the reaching trajectory. Further, because the scaled illusion effect was variable early in the reach, only data from the second half of the movements were used, corresponding to 50%, 75%, and 100% of the movement duration.

The results were assessed by comparing the fit of nested linear models. The relative quality of two fits was evaluated by computing the maximum likelihood ratio – that is, the likelihood of the data based on one model divided by the likelihood of the data based on the other model. This statistic provides an easily interpretable measure of the relative quality of the two model fits. Likelihood ratios of this type are closely related to the statistics used in null hypothesis testing, and the null hypothesis would generally be rejected when the likelihood ratio is 10 or greater (Dixon, 1998; Dixon & O'Reilly, 1999). A likelihood ratio of 10 would be classified as "moderate" evidence using the criterion suggested by Goodman and Royall (1988).

Results

Figure 2 shows the effects of the orientation of the bar on hand orientation in the vision (left) and no vision (right) conditions. It is evident that in both conditions, the orientation of the hand became increasingly dependent on the orientation of the target as the reaches progressed, a typical finding in this paradigm (Glover & Dixon, in press a; 2001a).

Figure 3 shows the scaled effects of the orientation illusion on the orientation of the hand in the vision (left) and no vision (centre) conditions. A third panel (right) compares the overall effect of the illusion in the two vision conditions. When a model including a constant effect of the illusion was compared to a null model, the likelihood ratio was large, l = 15.5. That is, the data were more than 15 times as likely on the assumption that there was an effect of the illusion on hand orientation than on the assumption of no such effect. Adding in the effect of time improved the fit dramatically, l = 55.9, replicating the dynamic illusion effect found in other studies (Glover & Dixon, in press a, b; 2001a). Although there appeared to be some beneficial effects of performing the task in the vision condition (Figure 3, right), adding in the effects of vision and the time x vision interaction improved the fit only slightly, yielding a likelihood ratio of l = 2.8. This is

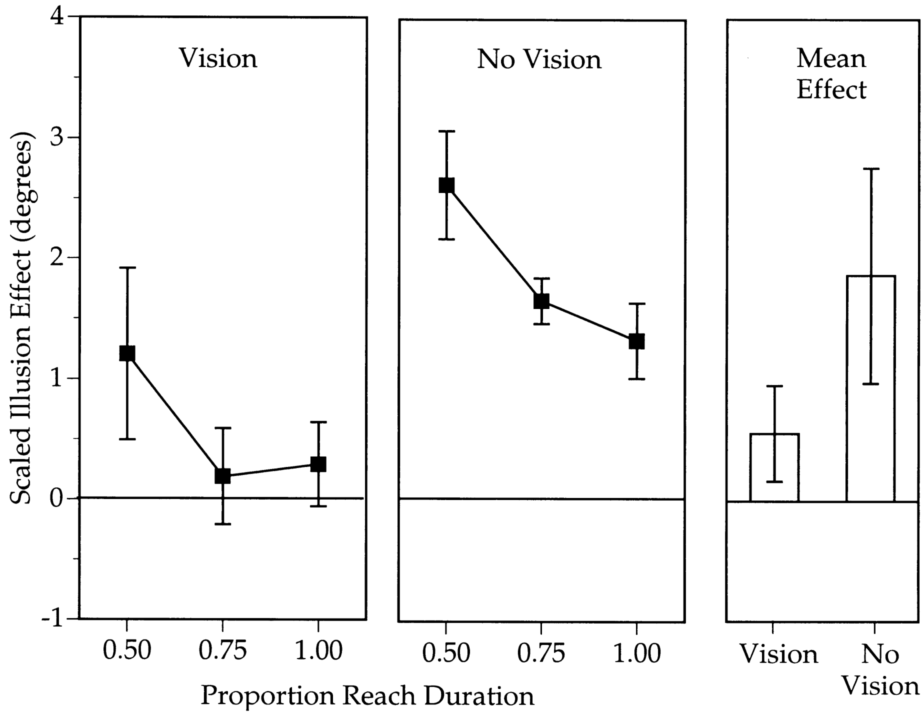

Figure 3. The scaled effect of the illusion on hand orientation. The left and centre panels show the effect at each quartile of the reach in the vision and no-vision conditions, respectively; for these panels the error bars represent standard errors of the mean based on within-subjects variation and are appropriate for comparisons across time (Loftus & Masson, 1994). The right panel shows the mean effect for the vision and no-vision conditions; in this case, the error bars represent standard errors of the mean based on between-subjects variation and are appropriate for comparisons between groups and relative to zero.

substantially below the criterion of 10:1 suggested by Dixon and O'Reilly (1998; see also Goodman & Royall, 1988) as providing good evidence for one model over the other. Thus, there was no strong evidence for an effect of vision or a time x vision interaction in this experiment.

The dynamic illusion effect was also evident in a separate analysis of the data from the no vision condition. A model that included a constant effect of the illusion provided a much better fit than the null model, $l >$ 1,000. When an effect of time was added in, the fit was better still, $l = 41.7$. This analysis shows that a dynamic illusion effect occurred in the absence of vision and suggests that the on-line correction of illusion effects on actions can be accomplished effectively using some combination of proprioception, stored visual information, and efference copy.

Discussion

The results of the present study support the planning/control model in that the effect of an orientation illusion on the orientation of the hand was larger earlier in the reach than later. In the planning/control model, context-induced optical illusions affect how actions are planned but not how they are monitored and corrected on-line. The dynamic illusion effect found here replicates several previous findings, both with the orientation illusion used here (Glover & Dixon, in press a; 2001a), and with the Ebbinghaus illusion (Glover & Dixon, in press b).

The dynamic illusion effect was also evident in a separate analysis of the no vision condition, showing that the on-line correction of the effects of the orientation illusion did not require visual feedback of the hand or continuous vision of the target during reaching. This result suggests that a large part of the correction process, in the present case at least, relies on some combination of proprioceptive feedback, stored visual information, and efference copy. However, our conjecture is that the type of illusion used may have a large impact on the role of this variable. For example, whereas the impact of removing vision has been found to be rather small or non-existent in studies employing the Ebbinghaus illusion (Glover & Dixon, in press b; Haffenden & Goodale, 1998), Roelef's effect (Bridgeman et al., 1997), and the orientation illusion used here, greater effects have been found in studies using the Muller-Lyer illusion (Gentilucci et al., 1996;

Glover & Dixon, 2001b; Westwood et al., 2000). This may occur because the Muller-Lyer illusion owes its effects not only to the contextual relations between the target and its visual surround, but to other factors as well, such as blurring of the contact points between the shaft and the arrows (see, e.g., Coren & Girgus, 1978).

One possible methodological concern with the present study is that participants in the no vision condition were allowed a 2-s preview of the display prior to the signal to reach. One might suppose that this preview allowed participants to notice and adjust for the effect of the illusion. However, the present pattern of results does not support this interpretation: The illusion actually had a larger overall effect in the no vision condition than in the vision condition, suggesting that the planning of the movement was more affected by the illusion during the brief period between when the lights were extinguished and the movement was initiated. More generally, it is possible that the nature of the illusion changed as a function of the 2-s preview. For example, the delay may enable participants to alter the manner in which the orientations of the bar and the background are encoded. However, the critical result from our perspective is that regardless of the nature of the illusion at the outset of the reach, the illusion had little effect by the time the hand reached the bar. Thus, the control mechanisms can accurately guide the hand to the target even in the absence of visual feedback.

Although the results of the present study support the planning/control model, alternative models of the effects (and noneffects) of context-induced optical illusions on action also exist. One such alternative is the perception/action model (Aglioti et al., 1995; Haffenden & Goodale, 1998; Milner & Goodale, 1995). In the perception/action approach, the context plays a much larger role in shaping perceptions than it does in controlling actions. Cases in which illusions have large effects on action are argued to result from an interaction between the two systems. In these cases, the ventral (perception) stream is said to contribute a large input into how the action is planned and presumably controlled by the dorsal (action) stream.

In order to account for the dynamic illusion effect, however, a proponent of the perception/action model would have to hypothesize a significantly larger role of the ventral stream in action than is commonly assumed (Milner & Goodale, 1995). Presumably, the ventral stream would have to play a dominant role in the planning of the movement, after which the dorsal stream would be responsible for the balance of its execution. Although this would explain the dynamic illusion effect, we believe that interactions of this sort tend to undermine the parsimony of a fundamental distinction between visual representations for perception and action. We contend that a distinction between planning and control provides a more straightforward account of the dynamic illusion effect.

The planning/control model can also be interpreted in terms of human neural organization (Glover, 2000). We argue that a putative third visual stream (Boussuoad, Ungerleider, & Desimone, 1990), terminating in the inferior parietal lobule in humans, is critical for action planning. On the other hand, we argue that the dorsal stream is most heavily involved in the on-line monitoring and control of actions. The data from PET imaging studies of action support this dissociation. In the period preceding the onset of the movement, increased neural activity has been observed in the inferior parietal lobule (Deiber, Ibanez, Sadato, & Hallett, 1996; Grafton, Fagg, & Arbib, 1998; Krams, Rushworth, Deiber, Frackowiak, & Passingham, 1998). During execution, a greater increase in activity has been observed in the superior parietal lobule (e.g., Grafton, Mazziota, Woods, & Phelps, 1992; Krams, Rushworth, Deiber, Frackowiak, & Passingham, 1998).

Evidence from human neuropsychology is also consistent with the proposed neural bases of the visual representations underlying planning and control. For example, damage located in the superior parietal lobule has been linked with optic ataxia, and such patients show the greatest impairments in the visual guidance of actions (e.g., Jakobson, Archibald, Carey, & Goodale, 1991; Jeannerod, 1986). Ataxia can thus be argued to represent a deficit in on-line control. Complementary to the ataxic syndrome is ideomotor apraxia, in which patients show a deficit in the performance of purposeful actions, typically following damage to the left inferior parietal lobule or its visual inputs (Clark, Merians, Kothari, Poizner, Macauley, Gonzalez Rothi, & Heilman, 1994; Poizner, Clark, Merians, Macauley, Gonzalez Rothi, & Heilman, 1995).

Although it is mere speculation at this time, we would hypothesize that contextual information is preferentially passed from the ventral "perceptual" stream to the third "planning" stream. This notion draws support from the fact that direct connections exist between the ventral and third streams (Boussuoad et al., 1990). Further, extensive interaction between these perceptual and planning systems would seem necessary because other information important for action planning (such as the function of the target) is also computed in the ventral stream. As such, we would argue that the direct ventral-third stream connection plays a critical role in action planning.

In sum, a variety of evidence on human neural function suggests that the planning mechanism hypothesized here depends on visual information processed in the inferior parietal lobule, whereas the control mechanism depends on information processed in the superior parietal lobule. Further, the planning operations carried out by the inferior parietal lobe in humans may depend on contextual and object-related information obtained through direct connections with the ventral stream.

Conclusions

In the present study, we found that visual feedback of the hand and continuous vision of the target were not required for a dynamic illusion effect to occur. The dynamic illusion effect replicates several previous studies involving optical illusions and action (Glover & Dixon, in press a, b; 2001a). The failure to find an effect of immediate visual information suggests that this source of information plays at most a minor role in the on-line correction of the orientation illusion's effects on action. In contrast, the results emphasize the importance of proprioception, stored visual information, and/or efference copy in the on-line correction process.

The results of the present study are consistent with a planning/control model of action, in which actions are planned using a context-dependent visual representation, but are monitored and corrected using a context-independent visual representation. As a consequence, illusions affect the initial planning of actions but not their subsequent control. This interpretation accounts for the effects of illusions on actions and fits well with a description of the neural bases of the two visual representations. We suggest that the planning/control model represents a suitable framework for the interpretation of a wide variety of phenomena related to human motor control.

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