

Figure 1 (Brouwer et al.). Hitting a moving disc when the direction of motion is misperceived. Schematic illustration of the disc's predicted final positions (A), the direction of hand movement (B), and the scaled magnitude of the effect of the illusion (C). The hand was simulated to move for 250 msec (which was about the average movement time in our experiment). **A:** The solid line indicates the lateral position over time of a disc that moves straight down but is perceived to move at an angle of 9.5 degrees from the vertical. The dashed lines indicate the disc's extrapolated movement at time samples of 0, 50, 100, 150, and 200 msec after the hand started to move. The disc's correctly perceived position and its misperceived direction of motion are used for the extrapolation. The white dots represent the disc's predicted final positions. **B:** The lateral position of the hand over time when hitting (a) a disc that moves straight down (vertical velocity of 18 cm/sec, horizontal velocity of 0 cm/sec) with a correctly perceived direction of motion, indicated by the black solid line, (b) a disc that moves at an angle of 9.5 degrees (vertical velocity of 18 cm/sec, horizontal velocity of 3 cm/sec) with a correctly perceived direction of motion, indicated by the grey solid line, and (c) a disc that moves straight down, but is perceived to move at an angle of 9.5 degrees (an illusory horizontal velocity of 3 cm/sec), indicated by the curved dashed line. For this disc, the straight dashed lines indicate that at each time sample, the hand moves straight towards the disc's final position as predicted at that time sample. The dashed line for the first time sample overlaps the solid grey line. **C:** The effect of the illusion over time. This is the lateral hand position for hitting a disc with an illusory direction of motion of 9.5 degrees divided by the lateral hand position for hitting a disc with an actual direction of motion of 9.5 degrees. The effect of the illusion decreases during the movement.

effect of the illusion arises because of a timing difference between the increase in grip aperture caused by a larger approach parameter and that caused by a larger target. Additionally, the illusion necessarily decreases to zero because the digits continue to move to the intended contact positions. In a similar vein, the model can account for the dynamic effect of the Müller-Lyer illusion (a larger approach parameter for the line with the inward directed arrows, to avoid the protrusions). The model is also consistent with the observed decrease in the effect of an orientation illusion on the hand's orientation during grasping (Smeets et al. 2002).

In conclusion, we believe that the dynamic illusion effect in action does not justify the assumption of different visual representations for planning and control, or even the use of different sources of information before and during a movement. We have shown that the dynamic illusion in both interception and grasping can be explained without assuming a change in the information used.

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Planning and controlling action in a structured environment: Visual illusion without dorsal stream

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Abstract: Some data concerning visual illusions are hardly compatible with the perception–action model, assuming that only the perception system is influenced by visual context. The planning–control dichotomy offers an alternative that better accounts for some controversy in experimental data. We tested the two models by submitting the patient I. G. to the induced Roelofs effect. The similitude of the results of I. G. and control subjects favoured Glover's model, which, however, presents a paradox that needs to be clarified.

Since the pioneering work carried out by Woodworth (1899), a recurrent issue in the studies relating to visuomotor control concerns the way visual inputs are used to locate a target in the reaching space. A large body of data in the recent scientific literature has underlined the fact that planning a movement requires that many spatial aspects of not only the target but also of the surrounding contextual elements have been previously considered together. As an illustration, a luminous target in a dark context is perceived as being closer than its actual position and is undershot when reached manually with no visual feedback about the hand trajectory (Conti & Beaubaton 1980; Foley 1980). By contrast, spatial performance improves when the visual environment is structured; merely adding a textured background in the workspace improves movement terminal accuracy (Coello et al. 2000).

Another line of evidence is the fact that having the hand and the target in the visual field simultaneously improves the visuomotor performance, which indicates that an accurate assessment of the gap separating the hand and the target is one of the main determinants of spatial performance (Rossetti et al. 1994). In agreement with the latter point, the location of contextual information in relation to the self and the target plays a crucial role in determining reaching accuracy, with elements placed in the space through which the reach occurs conferring the most benefit (Coello 2002; Grealy et al. 2003). Interestingly, structuring the visual field has a broad effect on the control of movement amplitude but leaves the control of movement direction unaffected (Coello & Magne 2000). We recently reported that unexpectedly append-

ing a textured background in the action space had an instantaneous concomitant effect on movement amplitude and peak velocity (Magne & Coello 2002), indicating that the improvement in the motor performance was mainly the consequence of a more accurate visual system.

These observations are partly in agreement with Glover's contention that motor planning process depends on a number of factors including the object of the action (spatial and nonspatial characteristics), the surrounding environment, and the internal state of the actor, while control process focuses mainly on the on-line minimisation of the spatial error of the movement (sects. 1.1.1, 1.1.2). Adjusting the planning process in flight, the control system is restricted to the spatial characteristics of the target and is thus immune to the interference of visual context (sect. 1.1.3). The idea of a certain independence of planning and control processes is supported by numerous data and has been already suggested in the past (e.g. Pisella et al. 2000). However, assuming together that (1) context information plays a crucial role in target coding (as shown above), and that (2) the function of the control system is to amend the planning process in flight on the basis of only the spatial characteristics of the target, leads to a neglected paradox. Disregarding the situation where direct visual control is available, one may wonder what would be the benefit of a control system adjusting the displacement of the hand (estimated through proprioceptive signal and efferent copy) towards a visual target that is perceived at an erroneous distance (which is the case when contextual information is not included in target coding). Furthermore, providing contextual information in the form of a textured background was found to improve the planning process – but also the on-line control process. Indeed, the benefit of providing contextual information during both movement planning and movement execution (in the form of a textured background) was exactly equal to the sum of the benefit of providing contextual information during only movement planning or only movement execution (see Fig.1). This additive effect cannot be accounted for by the fact that the planning system overlaps the control system during movement execution (sect. 1.1.4).

Furthermore, the magnitude of the effect was higher in the execution than in the planning stage. This outcome supports the idea of an independent use of visual information during planning and control processes, in agreement with Glover's model, but demonstrates that the control process cannot be considered to be immune to the interference of visual context (sect. 1.1.3), at least not when distance coding is taken into account.

This parametric framework is of paramount importance to understand the dissociation between perception and action. As indicated by Glover, the dominant theory during the past decade has been the one propounded by Milner and Goodale (1995). According to this theory, a single visual representation is considered to subserve actions, whereas a separate representation subserves perceptions (sect. 2.6.1). The core idea of the theory is that the processing of visual information is thought to involve independent streams from the primary visual cortex. Visual processing for goal-directed behaviour is predominantly supported by the occipito-parietal pathway (dorsal stream), while visual processing for conscious perception is performed through the occipito-temporal pathway (ventral stream). These two types of processing have been assumed to give rise to the independent "sensorimotor" and "cognitive" representations of visual space (Paillard 1987; Rossetti 1998).

Many findings are consistent with the idea that visual illusions influence perception more than action. The first evidence came from the Induced Roelofs Effect (IRE; Bridgeman 1991b). Observers were asked to estimate the egocentric position of a luminous target appearing inside a surrounding frame at various locations along the fronto-parallel axis. When the frame had a lateral offset, the target was misperceived to be in the contralateral direction when estimated verbally but not when located with a manual reaching response. The interpretation of such dissociation was that the cognitive system dealing with relative positions elaborates an explicit qualitative representation, which includes information

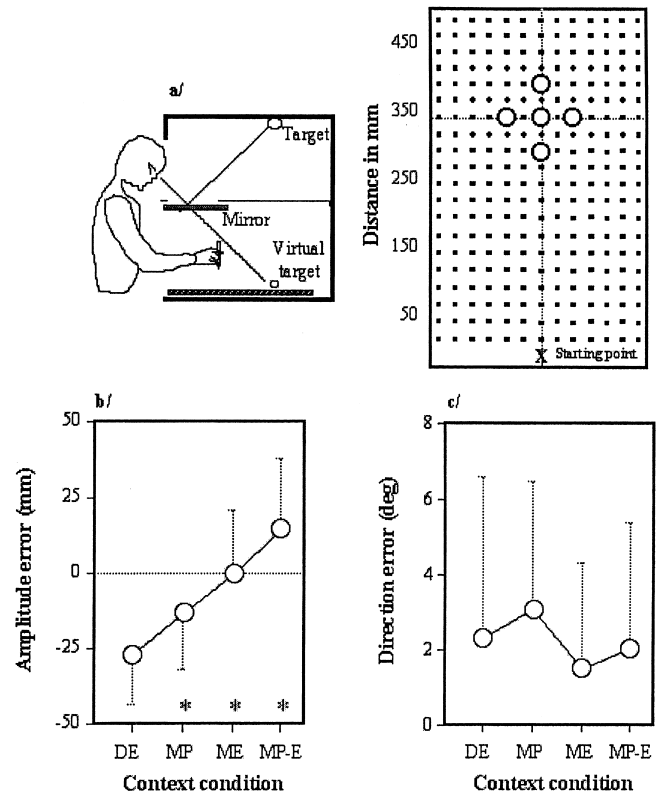


Figure 1 (Coello & Rossetti). (a) Apparatus and visual scene seen by the participant in presence of a textured background. (b) Mean amplitude error and (c) mean direction error of pointing movements as a function of the context condition: dark environment (DE), background during movement planning (MP), background during movement execution (ME), background during movement planning and movement execution (MP-E). (*) Indicates when performances were significantly influenced by the presence of a textured background, with respect to the dark condition. (Adapted from Coello & Magne 2000.)

relating to the whole visual scene even when the processing of contextual elements leads to localisation errors. Conversely, dealing with absolute positions, the sensorimotor system elaborates an implicit quantitative (metric) representation of visual space that is insensitive to contextual information (Bridgeman 1991b; 2000). According to Glover, the lack of effect of the contextual frame on the manual response might be due to the fact that the control system adjusts the motor performance in flight on the basis of a spatial analysis that remains immune to the interference of visual context (sects. 1.1.3 and 2.6.2). However, we recently reported data that support none of these interpretations (Coello et al. 2003). Using the IRE, but in slightly different experimental conditions, we found a dissociation in the influence of the off-centre frame on the motor response that was dependent on the spatial dimension tested. When the frame was displaced along the fronto-parallel axis, the target was misperceived along the same axis but in the opposite direction, while the manual capture of the target remained unaffected in keeping with the original study. However, the IRE interfered with perceptual and pointing responses in identical ways when the frame was displaced along the sagittal axis. Hence, the processing of visual information for action is not always immune to contextual influence, which appears to be dependent on the spatial dimension (direction or distance) that the task emphasises.

The crucial issue that remains to be addressed concerns the neurophysiological substrate which can subserve the distinct influence of visual context on distance and direction parameters. Based on a case study of optic ataxia, Mon-Williams et al. (2001)

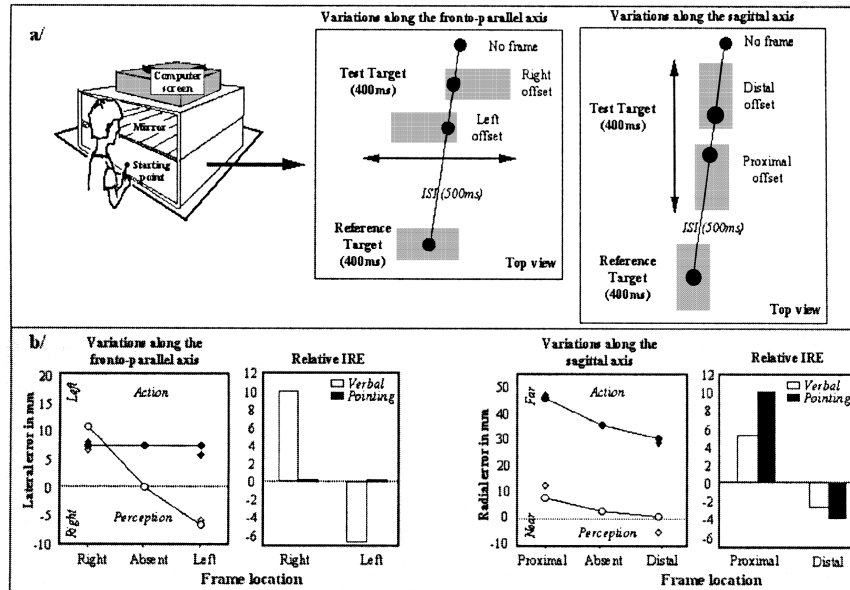


Figure 2 (Coello & Rossetti). (a) Apparatus and sequence of stimuli presented to the patient I.G. The Reference Target was presented simultaneously with a centred frame for 400 msec at two possible locations. Following a blank period of 500 msec, a Test Target was presented at a position similar to that of the Reference Target, at ± 8 mm, or at ± 16 mm along the fronto-parallel axis, or along the sagittal axis. It was accompanied with an off-centre frame or was presented alone. The task was to determine whether the Test Target was at the same position or not, compared to the Reference Target position, or to point towards the Test Target (for a detailed presentation of the method, see Coello et al. 2003). (b) Induced Roelofs effect along the fronto-parallel axis (left) and sagittal axis (right) for the patient I.G. Considering the fronto-parallel dimension, the induced Roelofs effect influenced the verbal response (open circle) but not the pointing response (filled circle) though the patients showed a constant bias to the left. Considering the sagittal dimension, the induced Roelofs effect influenced both the verbal response (open circle) and the pointing response (filled circle), the latter showing a constant overshoot of the target. Control performances (adapted from Coello et al. 2003) are indicated by the diamond, but normalised with respect to the no frame condition in order to allow a direct relative comparison of effect size in IG and controls.

suggested that the ventral stream is responsible for extracting distance information from monocular retinal cues, such as shading, texture, and perspective, while the dorsal stream has access to binocular information from disparities and vergence. This makes our results compatible with the Milner and Goodale model. Thus, the lack of dissociation between perception and action along the sagittal axis with the IRE could be interpreted as a greater participation of the ventral stream in distance processing, independent of the type of response or the viewing condition. However, according to Glover's model, the ventral system is involved in any aspect of motor planning. In this model, simple movements, such as reaching and grasping, tend to rely on the IPL for movement planning. Visual information can be projected to the IPL via the temporal lobe (which carries out information about spatial and non-spatial characteristics of a target and the surrounding context) and the "third" visual stream (sect. 1.2.2; but see review: Rossetti et al. 2000; Rossetti & Pisella 2002).

One way to contrast these two models would be to evaluate the performance of a patient with an impaired dorsal stream when confronted with the IRE. According to the ventral-dorsal dichotomy, an impaired dorsal stream would lead the patient to be unable to perform accurate motor acts considering the strong implication of the dorsal stream in motor control. Previous observations have shown, however, that this is not the case (Rossetti et al. 2003). Another possibility would be that the participation of the ventral stream is strengthened in the organisation and control of the motor acts in order to compensate for the impaired dorsal stream (Milner & Dijkerman 2001; Rossetti & Pisella 2002). One would therefore expect an effect of the IRE in both the fronto-parallel and the sagittal axes. By contrast, according to the planning-control dichotomy, the ventral stream participates in movement planning in all aspects and therefore, no discrepancy between the patient and the control participants is expected. We recently tested patient I.G., a 31-year-old woman who had suf-

fered bilateral parieto-occipital infarction one and a half years ago, resulting in a severe bilateral ataxia (see Pisella et al. [2000] for a detailed description). As shown in Figure 2, when submitted to the IRE, I.G. showed a pattern of results very similar to that of the control subjects, which stands in support for Glover's model.

In conclusion, many of the recent data concerning visual illusions are hardly compatible with the simple perception-action model, assuming in particular that only the perception system is subjected to context influence. The planning-control dichotomy offers an alternative that better accounts for the apparent controversy in experimental data related to visual illusions. However, to provide a general framework, it seems imperative to solve the paradox in the model, which originates from the fact that the role of the control system is thought to reduce spatial errors denying context information, while it nonetheless has been demonstrated that visual context broadly contributes to the accurate coding of target location.

The planning-control model and spatio-motor deficits following brain damage

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Abstract: Glover's planning-control model accommodates a substantial number of findings from subjects who have motor deficits as a consequence of brain lesions. A number of consistently observed and robust findings are not, however, explained by Glover's theory; additionally, the claim that the IPL supports planning whereas the SPL supports control is not consistently supported in the literature.