Do visual illusions probe the visual brain?
Illusions in action without a dorsal visual stream

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Abstract

Visual illusions have been shown to affect perceptual judgements more so than motor behaviour, which was interpreted as evidence for a functional division of labour within the visual system. The dominant perception–action theory argues that perception involves a holistic processing of visual objects or scenes, performed within the ventral, inferior temporal cortex. Conversely, visuomotor action involves the processing of the 3D relationship between the goal of the action and the body, performed predominantly within the dorsal, posterior parietal cortex. We explored the effect of well-known visual illusions (a size-contrast illusion and the induced Roelofs effect) in a patient (IG) suffering bilateral lesions of the dorsal visual stream. According to the perception–action theory, IG’s perceptual judgements and control of actions should rely on the intact ventral stream and hence should both be sensitive to visual illusions. The finding that IG performed similarly to controls in three different illusory contexts argues against such expectations and shows, furthermore, that the dorsal stream does not control all aspects of visuomotor behaviour. Assuming that the patient’s dorsal stream visuomotor system is fully lesioned, these results suggest that her visually guided action can be planned and executed independently of the dorsal pathways, possibly through the inferior parietal lobule.

Keywords: Vision; Perception; Action; Visual illusion; Dorsal–ventral pathways; Optic ataxia

The idea of a functional division of labour within the visual system has received a great deal of support over the past 20 years from studies of both brain damaged and healthy individuals. The convergent opinion suggests that at least two functional aspects within the visual system must be dissociated, that is ‘vision-for-action’ and ‘vision-for-perception’. One means of probing this dissociation has involved comparisons of explicit perceptual judgements versus visuomotor processing within illusory spatial configurations (Milner & Goodale, 1995; Rossetti & Pisella, 2002). Visual illusions are a class of visual objects (or scenes) characterised by the fact that specific arrangements of the elements composing those objects lead to an erroneous perception of their physical aspects. There are several instances of such visual illusions affecting the perception of either object location (e.g. the induced Roelofs effect) or object size (e.g. the Müller–Lyer or Ebbinghaus–Titchener illusions, referred to here as the size-contrast illusion) while leaving spatial performance unaffected when considering the same objects for visuomotor control. For the induced Roelofs effect, presenting a visual target within an off-centred surrounding reference frame biases judgments of the egocentric location of that target while leaving spatial performance unaffected when considering the same objects for visuomotor control. For the induced Roelofs effect, presenting a visual target within an off-centred surrounding reference frame biases judgments of the egocentric location of that target when estimates are made verbally. However, no effect of the off-centred reference frame was observed when the target was the goal of a reaching response (Bridgeman, 1991, 2000). Similar outcomes have been reported with other illusions, though weak effects of the illusory configuration on motor behaviours have been described for some illusory contexts (Aglioti, DeSouza, & Goodale, 1995; Gentilucci, Chieffi, Deprati, Saetti, & Toni, 1996). Moreover, the effect of visual illusions have been shown to be dependent on the experimental context, as the magnitude of the effect could be manipulated by statistical criteria (Carey, 2001), attentional requirements (Fischer, 2001), matching of the different
responses (Franz, 2001; Puvani, Boscaglì, Benvenuti, Rabuffetti, & Farnè, 1999) implicit structure of the visual scene (Haffenden & Goodale, 2000; Haffenden, Schiff, & Goodale, 2001), control strategies (Heath, Rival, & Neely, 2006) or frames of reference (Bruno, 2001; Heath, Rival, Neely, & Krigolson, 2006). As mentioned above, repeated demonstrations of dissociations between perception and action within illusory contexts have nonetheless been interpreted within the framework of dual neural pathways for processing of visual information for perception and action (Bridgeman, Kirch, & Sperling, 1981; Goodale, Milner, Jakobson, & Carey, 1991; Jeannerod & Rossetti, 1993; Paillard, 1987). Consequently, it has been assumed that one of the main aspects of the visual system for perception is that it deals with explicit holistic descriptions of the visual input, even when such information leads to errors in spatial processing. Conversely, the visual system for action deals with the absolute metrics of the visual input that are relevant for specifying actions (e.g. reaching or grasping, Ganel & Goodale, 2003; Rossetti & Pisella, 2002), and thus remains unaffected by the same illusory contexts that nevertheless lead to erroneous perceptual judgements.

Within the context of these findings, Goodale and Westwood (2004) recently suggested that one of the ongoing challenges for neurobiologists is to map the behavioural findings discussed above onto the brain and reconcile them with what we already know about the dorsal and ventral streams of visual processing from primate neurophysiology and human neuropsychology. Based on the seminal observation of two distinct cortical streams originating from the primary visual cortex in monkeys (Ungerleider & Mishkin, 1982), Milner and Goodale’s reformulation suggested that the role of each stream must be understood not only from the point of view of the visual inputs received, but also in terms of the outputs generated within each stream (Goodale & Milner, 1992). Thus, the visual inputs projecting from primary visual cortex (area V1) to posterior parietal cortex – the so-called dorsal stream1 – are thought to mediate the visual control of actions, while projections from V1 to inferotemporal cortex – the so-called ventral stream – are thought to be important for conscious perception, object recognition and scene parsing (Goodale & Milner, 1992; Milner & Goodale, 1995). This reformulation of the dual-pathway model received support from neuropsychological observations that contrasted optic ataxia, a condition in which patients with dorsal stream damage have difficulty reaching towards visual targets, and visual agnosia, a condition in which recognition of objects based solely on visual input is specifically impaired following damage to the ventral stream. Though this theory is routinely invoked to explain the differences observed in perception and action in healthy individuals faced with the kinds of pictorial illusions discussed above, the effects of such illusory contexts have never been explicitly tested in patients with either optic ataxia or visual agnosia. Indeed, despite a substantial body of research exploring the dissociation between visuomotor and visuo-perceptual functions in patients with lesions of either stream (Goodale & Milner, 1992; Goodale et al., 1991; Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003; Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999; Milner & Dijkerman, 2001; Pisella et al., 2000; Rossetti et al., 2005; reviews: Milner & Goodale, 1995; Pisella, Ota, Vighetto, & Rossetti, in press, chap. 21; Rossetti & Pisella, 2002), the effects of such localised brain lesions on visual illusions have not been explored in this way.

In this respect, it is worth mentioning that some recent findings in optic ataxia, a disorder arising from dorsal stream damage (including IPS and SPL), have suggested the possible involvement of the ventral stream in visuomotor control for these patients. Indeed, the immediate control of actions is impaired in patients with optic ataxia (review: Rossetti, Pisella, & Vighetto, 2003), but improves dramatically when the action is pantomimed or performed following a delay (Milner et al., 1999, 2003; Milner & Dijkerman, 2001; Rossetti et al., 2005). Based on these results and the reciprocal finding made in visual agnosia (Goodale, Jakobson, & Keillor, 1994), it was suggested that the preserved visual guidance of coordinated arm-hand movements for delayed actions relied on processing within the ventral stream, which may contribute to the control of actions, at least in the absence of a functioning dorsal stream (Milner et al., 2003, see also Lee & Van Donkelaar, 2002). According to the perception–action theory then, perceptual judgements and the control of actions in ataxic patients should both be sensitive to visual illusions, as the two tasks would rely on visual processing within the ventral stream. However, neuropsychological and neuroimaging data have recently suggested that many aspects of motor planning might rely on the inferior parietal lobule, which receives projections from the primary visual cortex but also from both the ventral and dorsal visual streams and may thus constitute the locus for a third visual system involved in visuomotor transformations (Boussaoud, Ungerleider, & Desimone, 1990; Glover, 2004; Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006; Rizzolatti & Matteli, 2003). Accordingly, the involvement of the IPL in feed-forward control of actions may mean that the visuomotor performance of ataxic patients would not necessarily diverge from that of healthy controls in the presence of visual illusions, since only the visual processes within the superior parietal lobe are impaired in these patients (the classical dorsal stream).

In order to evaluate the consequences of suppression of dorsal activity in processing visual information for perception and action, we compared the perceptual judgements and visuomotor performances in patient IG who suffered bilateral lesions of the posterior parietal cortex (mainly SPL and IPS) and control subjects in the presence of visual illusions that influenced either object location (the induced Roelofs effect, Bridgeman, 1991, 2000) or object size (the size-contrast illusion, Aglioti et al., 1995). Both illusions are known to influence perceptual judgements much more so than the immediate control of reaching movements (see also Brenner & Smeets, 1996; Dyde & Milner, 2002; Franz, Gegenfurtner, Bülthoff, & Fahe, 2000; Van Donkelaar, 1999 for research demonstrating specific effects of different illusory contexts on action).

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1 As stated by Milner and Goodale (1995) the dorsal stream includes the intraparietal sulcus (IPS) and the superior parietal lobule (SPL). The inferior parietal lobule (IPL) was thought to be outside the ventral and dorsal streams (p. 183).
1. Experiment 1a: induced Roelofs effect in the left–right dimension

1.1. Methods

1.1.1. Participants

1.1.1.1. Healthy controls. Seven healthy right-handed subjects participated (two males, five females; age range 24–37 years). All subjects had normal or corrected-to-normal vision. They were self-declared volunteers for the study and were naive as to its purpose.

1.1.1.2. Case report: patient IG. IG is a well-documented 29-year-old patient with a bilateral lesion of the posterior parietal cortex (see Milner & Dijkerman, 2001; Milner et al., 2003; Pisella et al., 2000 for a detailed description). Magnetic resonance imaging revealed a hyperintense signal on T2 sequencing located in the posterior parietal and upper and lateral occipital cortico–subcortical regions (Fig. 1a). Visual fields showed a partial right inferior homonymous quadrantanopia with temporal crescent sparing. Smooth pursuit eye movements showed normal gain, direction and velocities. She exhibited no signs of hemineglect but demonstrated prototypical bilateral optic ataxia. The left lesion of IG affected most of both POJ and mIPS, areas activated for pointing, respectively, in peripheral and central vision as shown by Prado et al. (2005) (see Fig. 1b). Importantly this does not imply that she does not see at all objects in central and peripheral vision, although she may exhibit both perceptual and visuomotor deficits (Rossetti et al., 2005). Reaching and grasping inaccuracy predominated for her right hand in her right peripheral hemifield. During reaching, her hand posture was often inappropriate in terms of aperture and orientation, and she usually corrected her grip only through tactile reafferences after she had completed the movement. However, visually elicited hand movements were only marginally impaired when performed in foveal vision (Gréa et al., 2002; Milner et al., 2003; Pisella et al., 2000; Rossetti & Pisella, 2002). As in most patients with optic ataxia (Pisella et al., 2006; Rossetti et al., 2003), IG’s deficits in everyday life situations are not characterised by overwhelming visuomotor problems. Indeed, under normal visual control, she can reach and grasp appropriately a simple object presented in fixed positions (Gréa et al., 2002; Milner & Dijkerman, 2001; Milner et al., 2003; Pisella et al., 2000). However, in reaching tasks performed in the absence of direct visual control, she demonstrated greater scatter of reaching endpoints both horizontally and in depth when compared to controls (Khan, Pisella, Rossetti, Vighetto, & Crawford, 2005). Similarly, in a grasping task using a virtual environment, she also differed from controls in that she was less successful in grasping the object firmly and often had to perform a second approach to lift the object (Himmelbach, Karnath, Perenin, Franz, & Stockmeier, 2006). In addition her on-line visuomotor corrections were impaired when centrally viewed objects were moved during her ongoing pointing or grasping action (Gréa et al., 2002; Pisella et al., 2000).

1.1.2. Apparatus, stimuli and procedure

The experimental device consisted of a rectangular box (60 cm high, 100 cm wide and 70 cm deep) divided horizontally by an upward-facing reflecting mirror (see Coello, Richaud, Magne, & Rossetti, 2003 for a detailed description). Resting the head on the upper part of the box, only the top half of the box was visible, but arm movements were possible in the bottom half. A computer monitor (20 in. Philips Trinitron) was placed upside-down on the top surface of the apparatus so that the image generated by the computer was reflected in the mirror and virtual information was available on the bottom surface. Direct visual control of the hand was precluded by the mirror, except when the hand was at the starting location.

Two red targets (diameter 8 mm) were presented successively in each trial. The first (reference) target was presented for a duration of 400 ms at either $0^\circ$ or $2.05^\circ$ (16 mm) from the sagittal axis along the fronto-parallel plane at a distance of 22.3 cm from the hand starting position and was centred according to a (96 mm × 38 mm) yellow rectangle (with a simultaneous onset for the target and rectangle). The centre of the second (test) target was positioned at ±20 mm, ±12 mm or 0 mm from the reference target (negative sign indicates a leftward deviation from the reference target). The test target was presented isolated on a dark background or within an off-centre frame to the right or to the left according

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Fig. 1. IG’s lesion. (a) Horizontal section through IG’s brain, visualised with structural MRI. Focal damage is present bilaterally in the posterior parietal lobes, including part of extrastriate areas (areas 18 and 19), superior parietal lobule (area 7), intraparietal sulcus and upper part of the angular gyrus (area 39). (b) Superimposition of IG’s lesion with the areas found to be activated for pointing to central ($0^\circ$) and peripheral ($5^\circ$ and $10^\circ$ targets) vision according to Prado et al. (2005). IG lesion comprises the most of POJ (peripheral vision) and mIPS (central vision).
to the body’s sagittal axis following an inter-stimuli interval (ISI) of 500 ms and was visible during 400 ms (Coello et al., 2003). When the test target was simultaneously presented with an off-centre frame, it was positioned at 8 mm with respect to the frame’s proximal side (the size of the whole stimulated visual field was thus 19.8°). The task consisted of comparing the location of a test target to the reference target presented earlier within a centred frame (perceptual task), or to point (pointing task), as quickly and accurately as possible, with the right hand to the test target (five positions × eight trials, the two tasks being performed in block session counterbalanced across subjects). A digitiser tablet (Wacom UD-1825, spatial resolution: 0.5 mm) was used to trigger the computer sequence (visual stimuli), and to register the (x, y) coordinates of an electromagnetic stylus held in the participant’s right hand (sample rate: 100 Hz).

1.1.3. Data recording and processing

In the perceptual task, the participant had to determine whether the test target was at the same location as the reference target, or to its right or left. Verbal responses were collected in real time by the experimenter. For each reference target and for each position of the frame, the location of the test target which was subjectively judged at the same location as the reference target was determined using a maximum likelihood fit procedure based on the second-order derivatives (quasi-newton method) to obtain the logit regression model that best fitted the responses of the subject (right, left or same) for the five positions of the target (±16 mm, ±8 mm, 0 mm from the reference target). The logistic function is represented by the following equation:

\[ y = \frac{e^{\alpha + \beta x}}{1 + e^{\alpha + \beta x}} \]

where \( y \) is the subject’s response, \( x \) the target location, \((-\alpha/\beta)\) the critical value of \( x \) at which the transition from one type of response (right) to the other type of response (left) occurs thus expressing the mean location of the target for response ‘same’ and \((\beta/\beta)\) is a measure of the slope at point \(-\alpha/\beta\) (not analysed in the present study).

In the pointing task, end-points of hand paths were determined from the two-dimensional coordinates (x, y) of the electromagnetic stylus. Constant terminal errors according to the test target (though the reference target was also presented) were decomposed into radial (the distance between movement vector length and target vector length, negative sign indicating an undershoot) and lateral error (the angle between the starting-position-to-target vector and the starting-position-to-end-movement-position vector, negative sign indicating a deviation to the right). To determine reaction time and movement time, movement onset and offset were defined as the point at which velocity exceeded 5 cm/s for more than 100 ms. In both response modes (verbal and manual pointing), angular values for lateral errors were transformed into millimetres by projecting the terminal pointing position onto the fronto-parallel axis crossing the target position for similar angular values. Only data for the target that was at the same location in experiments 1 and 2 (target number 1) are presented. Statistical analyses were carried out on variable means through a two-way analysis of variance (ANOVA: “response type” × “frame position”) with repeated measures on the two factors to test for principal effects. In the case the sphericity assumption was violated (i.e. epsilon smaller than 1), Huyn–Feldt adjustments of the p-values were reported.

1.2. Results

1.2.1. Control subjects

An effect of the frame location \(F(2, 12) = 7.80, p < 0.01\), an effect of response modality \(F(1, 6) = 20.66, p < 0.01\) and a significant interaction between stimulus type and response modality was observed \(F(2, 12) = 4.20, p = 0.04; \text{Fig. 2}\), replicating previous findings (Bridgeman, 1991, 2000; Coello et al., 2003). Perceptual judgements of target location in the absence of a reference frame were accurate (lateral error: 0.7 mm), showing that determining when the location of the test target corresponded or not to that of the reference target was quite straightforward. However, a right-sided off-centre frame induced a perceptual mislocation of the test target to the left (6.9 mm), whereas a left-sided off-centre reference frame induced a perceptual mislocation of the test target to the right (−6.85 mm), both performances being statistically different \((t(12) = 5.67, p < 0.01)\). In the pointing task, hand paths terminated on average 16.2 mm to the left of the test target in the absence of frame, but this lateral error was not modified by the presence of an off-centre frame (15.2 and 15.3 mm to the left for the right and left off-centre frames, respectively, \(t(12) = 0.02, p > 0.05\)). Interestingly, distance error was also not affected by the presence of a frame or its location \((F(2, 12) = 1.11, p > 0.05)\), mean radial error: −10.29 mm (S.D. 37 mm), −16.52 mm (S.D. 38 mm) and −14.14 mm (S.D. 43 mm) for right-displaced, left-displaced or absent frame, respectively). Movement duration in the pointing task was not influenced by the location of the frame \((F(2, 12) = 1.73, p > 0.05)\); mean MD: 414 ms (S.D. 26 ms), 425 ms (S.D. 31 ms) and 419 ms (S.D. 32 ms) for right-displaced, left-displaced or absent frame, respectively). Reaction time when pointing to the test target was also not influenced by the location of the frame \((F(2, 12) = 0.9, p > 0.05)\); mean RT: 439 ms (S.D. 117 ms), 476 ms (S.D. 175 ms) and 505 ms (S.D. 208 ms) for right-displaced, left-displaced or absent frames, respectively).

1.2.2. Patient IG

Similar to the observations made with controls, the off-centre location of the frame influenced IG’s perceptual judgement of target location but, surprisingly, not her pointing performance. Though her perceptual judgement of target location in the absence of a reference frame was quite accurate (lateral error: 0.1 mm), providing a frame led to misperception of the test target to the side opposite to the frame location (10.4 mm to the left when the frame was off-centre to the right and −6.8 mm to the right when the frame was off-centre to the left, the difference between the two conditions being at 0.28σ from the average control difference: 13.8 mm). For her visuomotor performance, no effect of the position of the frame was found (0.1 mm (σ = 11.5 mm) and 0 mm (σ = 3.5 mm) deviation when the frame was off-centre to the right or the left compared to the frame condition (7.18 mm, σ = 10.5 mm), the difference between the two conditions being at 0.01σ from the average control difference: −0.01 mm). Radial error was large but consistent across the experimental conditions (81.5 mm (σ = 18 mm), 86.3 mm (σ = 13.5 mm), 79 mm (σ = 15.5 mm) with the frame off-centre to the right, to the left or absent). Movement duration was also weakly affected by the reference frame (653 ms (σ = 43 ms), 676 ms (σ = 26.5 ms) and 673 ms (σ = 44.5 ms) with the frame off-centre to the right, to the left or absent) as well as reaction time (670 ms (σ = 154 ms), 605 ms (σ = 79 ms) and 540 ms (σ = 89 ms), respectively). The important finding here is that IG’s visuomotor system was not more sensitive to the illusion than the control group. In addition, she did not show any reduction in the effect of the illusion on her perceptual judgements as compared to controls, which demonstrates that the lack of an effect found for the motor response cannot be attributed to a purely perceptual deficit. Overall, her pattern of results is similar to the present control group and to previously reported data with healthy subjects (Bridgeman, 1991; Coello et al., 2003).
Fig. 2. (a) Apparatus, target display and sequence of stimuli presented to the participant with the induced Roelofs effect. The reference target was presented simultaneously with a centred frame for 400 ms at two possible locations with a distance of 8 mm between them (target 1 or 2). Following a blank period of 500 ms, a test target was presented at a position similar to that of the reference target, at ±8 mm, or at ±16 mm in the right-left dimension or (b) the near-far dimension. It was accompanied with an off-centre frame or presented alone. (c) Constant error (mm) in the perceptual and pointing tasks as a function of the location of the frame for healthy controls and IG in the right-left and (d) near-far versions of the illusion (error bars indicate standard errors for controls). Constant errors are presented in the left panel whereas relative errors according to the no frame condition are presented in the far right panel.

2. Experiment 1b: size-contrast Illusion

2.1. Methods

2.1.1. Participants

Four healthy controls all with normal or corrected to normal vision participated (two males, two females, age range from 22 to 28 years). Informed consent was obtained from all participants prior to commencing the experiment. Although this is admittedly a very small sample size, especially when dealing with the small but consistent effects of illusory contexts on perception, our intention was not to challenge previous findings but to demonstrate that our experimental protocol led to the same pattern of results observed in previous studies.

2.1.2. Procedure

Two target disc sizes were used (30 and 32 mm diameter) that were embedded within two annulus arrays (small (circle of 70 mm) and large (circle of 180 mm)) with target size and annulus array randomised across trials (see Haffenden et al., 2001 for a detailed description). The angular size of the whole stimulated visual field was 11.3° and 22.8° for the small and large annulus arrays, respectively, thus stimulating both the central and peripheral retina. Target discs were placed within the annulus on each trial by the experimenter. The task required participants to estimate the width of target circles presented within an annulus of larger or smaller circles using either a grasping movement or a manual estimation (described in detail below). Participants completed 8 trials per condition, thus 32 trials for grasping targets and 32 for estimating target size. They stood at a table top looking down on the target and annulus display. Targets were approximately 30 cm from the subject’s starting position directly in front of their body’s midline. Prior to commencing a trial, the display was occluded by an opaque board, which was removed once the target was placed within the annulus. Subjects then initiated ‘natural’ precision grasping movements to the near and far axes of the targets. For estimations, subjects were asked to place their hands at a point midway between where the target disc would appear and where their initial starting point had been for grasping trials. When the target became visible they were instructed to raise their hand above the table top and open their thumb and forefinger to a distance they felt approximated the target’s size along the near and far axis. Grasping and estimating trials were performed in separate blocks counterbalanced across subjects and were measured using infrared light-emitting diodes attached to the forefinger and thumb (Optotrak; Northern Digital; sampling rate 250 Hz).

2.1.3. Data recording and processing

The critical variable of maximum grip aperture was calculated by subtracting the vector position of the IRED attached to the forefinger from the vector position of the IRED attached to the thumb, thereby providing a measure of the vector distance between the two digits. Typically, maximum grip aperture...
occurs at roughly 70% of the way through the movement, prior to any contact being made with the target. Thus, this measure allows us to examine any potential influence of the illusory context on grip aperture free from confounds such as haptic feedback. For controls, a mean aperture was calculated for each condition (target size by annulus; eight trials per condition). To further address the effects of the annulus size on grip aperture or estimation, difference scores were calculated for each individual subject. Difference scores were calculated by subtracting grip aperture under the large annulus array (in which the illusion should lead to the perception of a smaller target size) from grip aperture under the small annulus array (in which the same target size should appear to be larger). Thus, a positive difference score would indicate that the illusion has influenced performance (in either the grasping or estimating task), while a difference score not significantly different from zero would indicate that the illusion had no influence on performance (Haffenden et al., 2001). To determine reaction time and movement time, movement onset and offset were defined as the point at which velocity exceeded 5 cm/s for more than 10 consecutive time frames.

2.2. Results

2.2.1. Control subjects

In the perceptual matching task, a main effect of the size of the target (F(1, 3) = 83.69, p < 0.05) but also the surrounding annulus (F(1, 3) = 12.96, p < 0.05) was observed in healthy controls. The interaction between the two factors was not significant (F(1, 3) = 1.66, p = 0.24). This demonstrates that subjects made smaller estimations for targets embedded within the large annulus array (small target–large annulus mean estimations, 42.52 mm; large target–large annulus mean estimations, 54.28 mm) when compared to their size estimates for targets embedded in the small annulus array which were consistently larger (small target–small annulus mean estimations, 44.09 mm; large target–small annulus, 60.73 mm). In contrast, analysis of actual grasping showed a main effect of target size on grip aperture (i.e. the distance between forefinger and thumb; F(1, 3) = 11.12, p < 0.05) such that subjects opened their hand wider for the larger target when compared to the smaller target (small target–small annulus mean grip aperture, 60.96 mm; small target–large annulus mean grip aperture, 61.31 mm; large target–small annulus mean grip aperture, 64.61 mm; large target–large annulus mean grip aperture, 64.79 mm). This effect was completely independent of the surrounding annulus (F(1, 3) = 0.05, p = 0.83) and no interaction between the two factors was observed (F(1, 3) = 0.35, p = 0.57; Fig. 3). Movement duration did not differ across the four conditions (small target/small annulus mean, 922 ms (S.D. 139 ms); small target/large annulus mean, 895 ms (S.D. 140 ms); large target/small annulus mean, 865 ms (S.D. 150 ms); large target/large annulus mean, 889 ms (S.D. 196 ms), p > 0.05). Reaction time was also quite consistent across the experimental conditions (small annulus/small target, 469 ms (S.D. 85 ms); small annulus/large target, 394 ms (S.D. 40 ms); large annulus/large target, 460 ms (S.D. 52 ms); large annulus/small target, 432 ms (S.D. 56 ms), p > 0.05).

2.2.2. Patient IG

Similar to control performance again, IG perceptually estimated targets embedded in the small annulus array to be larger than targets embedded in the large annulus array (mean small

annulus estimates, 52.41 mm and mean large annulus estimates, 48.4 mm, the difference between the two conditions being at 0.76σ from the average control difference, 3.48 mm). When grasping target circles, IG opened her grip wider for the larger target than she did for the smaller target independent of the surrounding annulus array (mean grip aperture small target, 60 mm (σ = 5.1 mm) in the small annulus and 58.3 mm (σ = 7.5 mm) in the large annulus array; mean grip aperture large target, 64.9 mm (σ = 4.4 mm) for the small annulus and 65.86 mm (σ = 4.6 mm) for the large annulus array, the difference between the two annulus conditions being at −2.14σ from the average control difference, 1.25 mm). Once again, IG’s performance with the size-contrast illusion was very similar to that of the healthy controls, i.e. the illusory context affected her perception without contaminating her visuomotor responses. Despite the fact that movements were performed at lower velocity than controls, movement duration for IG remained quite stable in the various conditions tested (small target–large annulus, 1528 ms (σ = 528 ms); small target–small annulus, 1470 ms (σ = 463 ms); large target–large annulus, 1362 ms (σ = 685 ms); large target–small annulus, 1140 ms (σ = 439 ms)). Moreover, reaction time was also quite consistent across all experimental conditions (small target–large annulus, 1000 ms (σ = 326 ms); small target–small annulus, 1089 ms

![Diagram](image-url)
2.3. Discussion

These two studies were a replication of previous work in healthy individuals investigating either the induced Roelofs effect (Coello et al., 2003) or the Titchener–Ebbinghaus illusion (Aglioti et al., 1995), and contrasted those performances with that of a patient suffering bilateral lesions of the posterior parietal cortex encompassing the visual dorsal stream. Altogether, the two experiments demonstrate that impaired neural activity through the dorsal visual stream does not alter the perceptual or visuomotor sensitivity to visual illusions in the predicted way according to the perception–action theory. Although the dorsal–ventral anatomical framework has been referred to by most authors in search for explanations for the weak effects of visual illusions on action, our results suggest thus that the anatomical and functional dissociations cannot be simply mapped on to each other. Spared functional visual processing in the absence of the dorsal stream appeared then to produce similar outcome in the presence of visual illusions, independently of whether the purpose of the output was related to perception or action. However, it is worth noting that the lack of any effect of the illusions on IG’s actions might result from differences in the way she performed the tasks as compared to healthy controls. IG’s movements were indeed on average 58% (induced Roelofs effect) and 35% (size-contrast illusion) slower than those of controls. However, it is acknowledged that such an increase of movement duration should favour spatial processing within the ventral stream associated with longer time constraints, and this should further enhance the effects of the illusory contexts on the control of action (Gentilucci et al., 1996; Milner et al., 1999, 2003; Rossetti et al., 2003, 2005). Thus, the absence of any effect of the illusions on IG’s actions cannot simply be explained by non-equivalent movement time between the control subjects and patient IG.

In addition, there has been some debate in the literature concerning the effect of illusory contexts on action (Brenner & Smeets, 1996; Danckert, Sharif, Haffenden, Schiff, & Goodale, 2002; Glover & Dixon, 2001; Pavani et al., 1999; Van Donkelaar, 1999). In particular, some have suggested that the lack of an effect of the illusory contexts on action might come about as a consequence of on-line feedback during the course of the movement (Glover, 2004; Glover & Dixon, 2001). That is, an effect of illusory contexts of this kind can be observed early on in a movement’s trajectory but is corrected late in the movement by recourse to on-line visual feedback (Glover & Dixon, 2001). In contrast, a recent re-analysis of grasping data in the Titchener circles illusion found no evidence for an effect of the illusion on action even when grip aperture was examined at the very early stages of the movement trajectory (i.e. 25% of the way towards maximum aperture, Danckert et al., 2002). This result suggests that the planning phase of movements is relatively resistant to the effect of illusory contexts. We conducted a similar analysis on IG’s data and although statistical power is dramatically reduced in a single case analysis of this kind, we still found no evidence that IG was using visual feedback to correct her grip aperture during the course of movements made within the Titchener circles illusory context (Fig. 4). This is perhaps not so surprising given previous research demonstrating impaired use of visual feedback to modify movements on-line in IG (Gréa et al., 2002; Pisella et al., 2000). Finally, several authors have suggested that the presence or absence of haptic feedback may be an important factor in determining the differential effects of illusions on perception (no haptic feedback) and action (haptic feedback, Vishton, Rea, Cutting, & Nunez, 1999). Although haptic feedback is undoubtedly an important factor in visuomotor control, it cannot have informed the current set of results with IG for several reasons. As noted above, when looking at her grip aperture throughout her movement trajectory there was very little evidence of an effect of illusions on grip aperture early in the movement and certainly no effect of the illusion prior to receiving haptic feedback. Presumably, if her accurate performance depended largely on haptic feedback this would not have been the case (i.e. an effect of the illusion should have been obvious early in the movement and up until the point of contact with the target). Second, our dependent measure was always maximum grip aperture which typically occurs well before contact is made with the target and thus before any haptic feedback is received.

An alternative explanation for the current set of results would suggest that damage in the dorsal stream disrupted not only visuomotor integration but also the integration of contextual cues within the visual system when coding target location or size for action. According to this assumption, visuomotor planning in IG that is obviously under the control of the ventral stream due to the absence of appropriate dorsal activity, would also take into account the relevant aspects of spatial information that need to be processed depending on the purpose of the behaviour. In other words, simply grasping or pointing to targets may not require any processing of the surrounding context,
whereas avoiding obstacles obviously does, suggesting that IG is only impaired relative to controls for motor tasks that require such contextual processing. There are several kinds of contextual effects. For instance, structuring the workspace with a textured background has been shown to improve distance coding (Magne & Coello, 2002) and to affect egocentric perception of target distance (Coello & Iwanow, 2006) even with illusory configurations (Coello et al., 2003). To examine the possibility of a specific deficit in context processing in IG, we explored another version of the induced Roelofs effect, which is known to influence perception and action equally. Indeed, when presented along the near-far rather than the left–right dimension, the off-centred frame was found to induce a misjudgement of target location in both the perceptual and the motor task (Coello et al., 2003).

3. Experiment 2: induced Roelofs effect in the near-far dimension

3.1. Methods

3.1.1. Participants

Control participants were those that participated in Experiment 1a. IG also participated in this experiment.

3.1.2. Apparatus, stimuli and procedure

Using the same apparatus as in Experiment 1a, two red targets (diameter 8 mm) were presented successively in each trial. The first target (reference target) was presented at 20.7 or 22.3 cm from the starting position of the hand and was centred according to a rectangle aligned with the sagittal axis. The test target was positioned at ±16 mm, ±8 mm or 0 mm from the reference target along the sagittal axis and could be either presented alone, or within an off-centre frame displaced in proximal or distal space. When the test target was simultaneously presented with an off-centre frame, it was positioned at 8 mm with respect to the frame’s proximal side. The reference target appeared at one of the possible locations for a duration of 400 ms. The test target then appeared following an inter-stimuli interval of 500 ms and was visible for 400 ms. Participants were instructed in blocked sessions counterbalanced across subjects to verbally estimate the test target location according to the reference target or to point to the test target (five positions × eight trials). All other aspects of this experiment were identical to Experiment 1a.

3.2. Results

3.2.1. Control subjects

An effect of the frame location ($F(2, 12) = 13.60, p < 0.01$), but no effect of the response modality ($F(1, 6) = 0.31, p > 0.05$) and no interaction between the frame location and the response modality ($F(2, 12) = 0.13, p > 0.05$; Fig. 2) was observed, replicating previous findings (Coello et al., 2003). Perceptual judgement of target location in the absence of a reference frame was accurate (radial error: $-0.27$ mm). However, a proximal off-centre frame induced a perceptual overestimation of target location ($8.31$ mm), whereas a distal off-centre frame induced a perceptual underestimation of target location ($-7.41$ mm), both performances being statistically different from zero ($t(12) = 6.89, p < 0.01$). In the pointing task, the mislocation of the target in the presence of the frame was $7.52$ and $-9.62$ mm with the proximal and distal off-centre frame, respectively, these two values being statistically different from zero ($t(12) = 7.51, p < 0.01$), whereas it was $-2.52$ mm in the no frame condition. Interestingly, lateral error was not influenced by the frame location ($F(2, 12) = 0.31, p > 0.05$, mean lateral error: $16.85$ mm (S.D. 10.5 mm), $17.46$ mm (S.D. 10 mm) and $18.84$ mm (S.D. 9 mm) for the proximal, distal or absent frame, respectively). Movement duration in the pointing task was not influenced by the location of the frame ($F(2, 12) = 0.79, p > 0.05$; with $419.5$ ms (S.D. 24 ms), $412.5$ ms (S.D. 12 ms) and $419$ ms (S.D. 13 ms) with a proximal off-centre frame, a distal off-centre frame or no frame, respectively). Similarly, reaction time when pointing to the test target was not influenced by the location of the frame ($F(2, 12) = 0.02, p > 0.05$; with $521$ ms (S.D. 151 ms), $527$ ms (S.D. 162 ms) and $521$ ms (S.D. 157 ms) with a proximal off-centre frame, a distal off-centre frame or no frame, respectively).

3.2.2. Patient IG

IG was similarly influenced by the location of the frame when comparing perceptual and visuomotor performance. Thus, IG, as was the case for healthy controls was influenced by the position of the frame in the near-far dimension both when providing perceptual judgements of target location and when pointing to visual targets (perceptual judgment: $5.1$ and $-2.1$ mm with the proximal and distal off-centre frame, respectively, with $2.96$ mm in the no frame condition, the difference between the two conditions being at $-0.72$ from the average control difference: $15.72$ mm). She was also influenced by the frame location for her visuomotor performance: $10.5$ mm ($\sigma = 10.5$ mm) and $-4.83$ mm ($\sigma = 7.16$ mm) with the proximal and distal off-centre frame, respectively, compared to the no frame condition ($35.66$ mm, $\sigma = 18.30$ mm), the difference between the two conditions being at $-0.16$ from the average control difference: $17.14$ mm). Lateral error was small and quite consistent across the experimental conditions ($0.72$ mm ($\sigma = 4.2$ mm), $3.59$ mm ($\sigma = 5.04$ mm), $-2.15$ mm ($\sigma = 4.52$ mm) with the distal off-centre frame, the proximal off-centre frame or the no frame condition, respectively). Movement duration appeared to be weakly affected by the reference frame ($658$ ms ($\sigma = 25$ ms), $627$ ms ($\sigma = 36$ ms) and $625$ ms ($\sigma = 34$ ms) with a proximal off-centre frame, a distal off-centre frame or no frame, respectively), and the reaction time was $620$ ms ($\sigma = 72$ ms), $717$ ms ($\sigma = 47$ ms) and $605$ ms ($\sigma = 60$ ms), respectively.

3.3. Discussion

On the basis of this experiment, the hypothesis that damage in the dorsal stream disrupts not only visuomotor processing but also the integration of contextual cues within the visual system when coding target location for action can be rejected. IG, like controls, was influenced by the position of the frame both when providing a verbal estimate of target location and when pointing to it in the near-far dimension. This finding, in agreement with previous observations (Coello et al., 2003), clearly demonstrates that IG’s performance was not different from that of control subjects for visual illusions affecting either size or spatial location irrespective of the spatial reference frame tested (fronto-parallel or sagittal). For the three illusions explored in this study, IG behaved surprisingly in the same manner as healthy
controls when probing both perceptual and motor responses. Interestingly, a similar pattern of results was found whether or not on-line vision of the limb was available (Experiments 1a and 1b), indicating that the observed effect was not due to specific control strategies. It could be argued that if IG has a sparing of dorsal stream visuomotor systems dedicated to the central visual field as previously suggested (Pisella et al., 2006; Rossetti et al., 2003), then she would be able to respond manually to the targets in our experiments using these spared regions, without the surrounding stimuli having any effect on her movements (Experiment 1). However, we do not believe that this idea can account for our data. First, IG’s performance in depth with the induced Roelofs effect indicates that she was far from being as accurate as control subjects when pointing to visual targets. Indeed, IG consistently overshot the target (by 82 mm in Experiment 1a (33% of the distance), and 36 mm in Experiment 2 (14.5% of the distance), the values being −13.7 and −11.2 mm for the controls). Such results corroborate previous observations made with IG showing greater scatter of movement endpoints both horizontally and in depth compared to controls when performing reaching movements in the absence of direct visual control (Khan et al., 2005).

Second, the lesion in the dorsal stream encompasses most of the POJ and mIPS areas found to be activated during reaching in peripheral and central vision, respectively (Prado et al., 2005; see Fig. 1b). Surprisingly, IG and most optic ataxia patients, do not complain about simple everyday life actions (Rossetti et al., 2003). This is compatible with the results of experimental investigations performed in the simplest of situations, in which no or only minor deficits are reported (Gréa et al., 2002; Milner et al., 1999, 2003; Pisella et al., 2000; Rossetti et al., 2005). However, several experimental situations have also revealed abnormal performance in central vision, when the need for on-line control was stressed (Gréa et al., 2002; Pisella et al., 2000), or when visual open loop conditions (Khan et al., 2005) or virtual feedback (Himmelbach et al., 2006) were used. We may conclude that IG’s optic ataxia is clearly dominant in peripheral vision but not strictly restricted to it, and results from a near-complete lesion of dorsal-stream visuomotor mechanisms. Finally, IG’s motor performance was influenced by contextual information in the near-far version, but not in the right-left version of the induced Roelofs effect. This result argues against the influence of visual illusions on motor performance depending only on a lesioned dorsal stream. Consequently, our data strongly suggest that the distinction in the processing of visual inputs for perception and action may not strictly depend on a simple segregation of the visual system into a ventral and a dorsal stream.

The question that remains to be addressed concerns the possible pathways lying in between the dorsal and ventral streams that may be implicated in action control, at least in the absence of a functioning dorsal stream. As suggested above, one possible candidate is the ventro-dorsal pathway through the inferior parietal lobule (Mattingley, Husain, Rorden, Kennard, & Driver, 1998; Rizzolatti & Matelli, 2003), which may constitute the locus for a third visual system (Boussaoud et al., 1990; Glover, 2004; Pisella et al., 2006; Rizzolatti & Matelli, 2003) involved both in perception and organization of motor activities (Deiber, Ibanez, Sadato, & Hallett, 1996; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti & Matelli, 2003). This area receives projections from V1, as well as from the temporal lobe (Boussaoud et al., 1990), and may participate in the computation of environmental features (e.g. depth cues, Carey, Dijkerman, & Milner, 1998) and semantic meaning (e.g. tool use, Glover, 2004). It also receives projections from the superior parietal lobe, the frontal and somatosensory cortex. Furthermore, IPL projects to areas of the ventral premotor cortex and to the prefrontal cortex (Rizzolatti & Matelli, 2003). An alternative visuomotor route through the IPL is thus one possible explanation for the lack of illusory effects on IG’s reaching and grasping in the two first experiments, using systems that may in the normal brain be concerned with action planning. As perturbation occurs mostly in peripheral vision, it might be, that IG is more impaired in the control of reaching movements in that part of the visual field (Ishihara et al., 2004; Milner et al., 2003; Rossetti et al., 2005), as well as in on-line visuomotor control (Gréa et al., 2002; Pisella et al., 2000), underlining the importance of distinguishing between “planning” and ‘controlling” visuomotor acts. Notwithstanding the necessary speculations about the reported findings, what the present study clearly shows is that projections from or to the dorsal stream proper (including IPS and SPL) are not responsible for the immunity of the visuomotor system to visual illusions.

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