

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.

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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 loca-

tion (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 judgements 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

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responses (Franz, 2001; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farné, 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, Kirsh, & 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, neurophysiological 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 & Matelli, 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, Bühlhoff, & Fahle, 2000; Van Donkelaar, 1999 for research demonstrating specific effects of different illusory contexts on action).

¹ As stated by Milner and Goodale (1995) the dorsal stream includes the intra parietal 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).

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