

No double-dissociation between optic ataxia and visual agnosia: Multiple sub-streams for multiple visuo-manual integrations

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Abstract

The current dominant view of the visual system is marked by the functional and anatomical dissociation between a ventral stream specialised for perception and a dorsal stream specialised for action. The “double-dissociation” between visual agnosia (VA), a deficit of visual recognition, and optic ataxia (OA), a deficit of visuo-manual guidance, considered as consecutive to ventral and dorsal damage, respectively, has provided the main argument for this dichotomic view. In the first part of this paper, we show that the currently available empirical data do not suffice to support a double-dissociation between OA and VA. In the second part, we review evidence coming from human neuropsychology and monkey data, which cast further doubts on the validity of a simple double-dissociation between perception and action because they argue for a far more complex organisation with multiple parallel visual-to-motor connections:

1. A dorso-dorsal pathway (involving the most dorsal part of the parietal and pre-motor cortices): for immediate visuo-motor control—with OA as typical disturbance. The latest research about OA is reviewed, showing how these patients exhibit deficits restricted to the most direct and fast visuo-motor transformations. We also propose that mild mirror ataxia, consisting of misreaching errors when the contralesional hand is guided to a visual goal though a mirror, could correspond to OA with an isolated “hand effect”.
2. A ventral stream-prefrontal pathway (connections from the ventral visual stream to pre-frontal areas, by-passing the parietal areas): for “mediate” control (involving spatial or temporal transpositions [Rossetti, Y., & Pisella, L. (2003). Mediate responses as direct evidence for intention: Neuropsychology of Not to-, Not now- and Not there-tasks. In S. Johnson (Ed.), *Cognitive Neuroscience perspectives on the problem of intentional action* (pp. 67–105). MIT Press.])—with VA as typical disturbance. Preserved visuo-manual guidance in patients with VA is restricted to immediate goal-directed guidance, they exhibit deficits for delayed or pantomimed actions.
3. A ventro-dorsal pathway (involving the more ventral part of the parietal lobe and the pre-motor and pre-frontal areas): for complex planning and programming relying on high representational levels with a more bilateral organisation or an hemispheric lateralisation—with mirror apraxia, limb apraxia and spatial neglect as representatives. Mirror apraxia is a deficit that affects both hands after unilateral inferior parietal lesion with the patients reaching systematically and repeatedly toward the virtual image in the mirror. Limb apraxia is localized on a more advanced conceptual level of object-related actions and results from deficient integrative, computational and “working memory” capacities of the left inferior parietal lobule. A component of spatial working memory has recently been revealed also in spatial neglect consecutive to lesion involving the network of the right inferior parietal lobule and the right frontal areas. We conclude by pointing to the differential temporal constraints and integrative capabilities of these parallel visuo-motor pathways as keys to interpret the neuropsychological deficits.

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1. Introduction: A brief history of the functional dissociations within the visual system

The cortical processing of visual information is topographically organised along several stimulus dimensions (Hubel & Wiesel, 1968). A particularly influential distinction has been made between an occipito-temporal pathway (“ventral stream”) and an occipito-parietal pathway (“dorsal stream”) (reviews: Danckert & Rossetti, 2005; Jeannerod & Rossetti, 1993; Milner & Goodale, 1995; Rossetti & Pisella, 2002). Even though the dorsal and the ventral streams of visual processing have been shown to be directly and indirectly inter-connected, topological analysis of the complex cortical connectivity has supported the privileged status of these two visual pathways (Nowak & Bullier, 1997). Based on a review of human neuropsychology and monkey connectivity and electrophysiology, this paper addresses the issue of whether it is possible to delineate more refined functional and anatomical circuits for visuo-motor processing, in particular within the posterior parietal cortex (PPC, dorsal occipito-parietal stream).

The most amazing discoveries about the functions of the visual system come from the examination of patients with brain lesions. In the early 1970s, patients with a lesion of the primary visual cortex, who are diagnosed as—and consider themselves to be—blind on a part of their visual field, have been shown to retain some residual ability to perform visually-guided movements with the eyes or the hand (Perenin & Jeannerod, 1975; Pöppel, Held, & Frost, 1973; Weiskrantz, Warrington, Sanders, & Marshall, 1974; review: Danckert & Rossetti, 2005). This first finding demonstrated that visuo-motor capacities can be dissociated from visual awareness (“Blindsight”), and was confirmed by other studies in patients (e.g. Danckert et al., 2003; Perenin & Rossetti, 1996) as well as by sophisticated psychophysical experiments performed in healthy individuals (Pélisson, Prablanc, Goodale, & Jeannerod, 1986). The second major discovery is that one patient (referred to as DF) with a bilateral lesion of the occipito-temporal cortex who presented with a strong visual form agnosia (VA)—a deficit for recognizing the form of visual objects—could nevertheless perform accurate visually-guided actions toward these objects (Goodale, Milner, Jakobson, & Carey, 1991). This original study was followed by a rich series of experiments exploring the visuo-motor capacities of this patient (e.g. Goodale, Jakobson, & Keillor, 1994; Milner et al., 1991) as well as of another similar patient SB (Dijkerman, Le, Demonet, & Milner, 2004). While the first discovery allowed to make the case for a degraded but preserved visuo-motor system in the absence of conscious processing of the visual input, the second finding revealed that a close-to-normal visuo-motor performance—i.e. the ability to orient the hand or to size the finger grip in a way that is appropriate to the object—can be observed in spite of the complete deficit for object recognition.

The neurobiological interpretation of Blindsight was first based on the anatomical distinction made between cortical and subcortical vision (Danckert & Rossetti, 2005). The interpretation given to the visuo-motor abilities found in DF pointed to the role of the dorsal stream of visual processing and emphasised the cortical dissociation described within the visual system. The

dorsal and ventral visual pathways have been assigned roles for answering different questions about the object. The initial proposal, based on monkey lesions experiment (Ungerleider & Mishkin, 1982), was that the dorsal and the ventral stream would respectively answer to the ‘Where’ and to the ‘What’ questions. Patient DF, as other classical cases of VA, was in agreement to the idea that the ventral stream is in charge of a ‘what’ system. However, her preserved visuo-motor performance prompted a revision of the role of the dorsal visual stream. The dorsal stream is not merely responsible for processing visuo-spatial attributes of an object (‘Where’) but rather for guiding the hand towards visual objects (‘How’) (Goodale & Milner, 1992; Jeannerod & Rossetti, 1993; Milner & Goodale, 1995). A crucial argument was made from the case of optic ataxia (OA), a neurological condition where patients have difficulties to reach towards visual objects presented in their peripheral visual field (e.g. Garcin, Rondot, & de Recondo, 1967; Perenin & Vighetto, 1983; Vighetto, 1980). We and other authors have argued in the past that VA and OA should be considered to form a double-dissociation that reveals an anatomical segregation in the brain between perception and action (review in Milner & Goodale, 1995). VA is characterised as a deficit in object recognition with intact visuo-motor capacities. Reciprocally, OA is considered as a deficit in visuo-motor functions with other visual functions preserved (including object recognition). The aim of the following section will be to reconsider the available evidence that demonstrate a double-dissociation between VA and OA and to review the limits to the original claims.

2. Questioning the double-dissociation between visual agnosia and optic ataxia

“Dissociation” is the main key word of neuropsychology. The separation of compound psychological functions into their primary elements has proved to be an important source of knowledge and theories about the organisation of the human mind. In this context, dissociation is viewed as the demonstrations that separate systems or structures are responsible for the two given variables (see Rossetti & Revonsuo, 2000). Single case studies have provided new directions and improved our understanding of the relationship between the brain and the mental structures. Their interpretation “has proved to be nothing less than revolutionary” (Code, 1996). For most of the important classic cases described in the literature, the focus of interest has been the dissociation of function (cf. Code, 1996). For example, visual agnosia has been regarded as a dissociation of higher (disruption of the cognitive aspects of vision) and lower (intact primary visual aspects) visual functions (e.g. Teuber, 1955). The positive and negative behavioural consequences of a given restricted lesion may be partially explained by the reorganisation of surrounding intact brain tissue. Consequently, the specificity of the effect of a given single lesion is often questionable. A stronger case is provided by an anatomical “double-dissociation”, for which a lesion of structure X will specifically disrupt function A while sparing function B, and a lesion of structure Y will specifically affect function B while function A would remain intact. Teuber (1955) termed this experimental tool ‘double-

dissociation', and used it for both animal and human studies, arguing that it indicates some specificity of function, e.g. between anterior and posterior brain lesions. It is still widely acknowledged that strong neuropsychological evidence for the existence of neurologically distinct functional systems depends on double-dissociation of function (for a review, see also Rossetti & Revonsuo, 2000), although criticisms have been raised to the validity and relevance of double-dissociations to anatomically localize cognitive processes (Passingham, Stephan, & Kotter, 2002).

2.1. Central versus peripheral vision

These definitions imply that “double-dissociated” patients have to be tested in identical conditions. Let us consider here the case of OA and VA in the light of the results presented in Table 1. Table 1 can be examined in two ways. First, one can look at within-pathology dissociations between perception and action. Let us consider the case of OA. It is widely acknowledged that these patients are impaired for reaching to visual objects (by definition) but this deficit is mostly observed in peripheral vision even in bilateral patients (e.g. Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999; Perenin & Vighetto, 1988; Ratcliff, 1990; Rossetti, Pisella, & Vighetto, 2003; Rossetti, Goldenberg, & Rode, 2005a; Rossetti et al., 2005b). Unfortunately, visual perception has not been extensively explored in these patients. Formally, it is not warranted to claim that OA is an action-specific impairment, as action and perception have been explored under different conditions. Two recent papers indicate that perception is impaired in the peripheral visual field of optic ataxia

patients (Michel & Hénaff, 2004; Rossetti et al., 2005a,b). If these results are confirmed, then OA cannot be taken as an evidence for dissociated perceptual and motor functions. One of the possible alternatives is that OA is a dissociation between central and peripheral vision (Rossetti et al., 2003). If we consider the case of VA, there is good evidence that patients are impaired at object recognition (by definition) in natural exploration condition, whereas it has been shown that they may exhibit preserved visuo-motor ability when simple goal-directed actions are performed in central vision under laboratory conditions (e.g. Goodale et al., 1991). Therefore, it can be concluded that VA may be viewed as an instance of dissociated vision-for-perception and vision-for-action systems. In fact, lesion of the ventral stream certainly impairs visual recognition but also has heavy consequences for everyday actions (see the description of case SB in Lê et al., 2002), sometimes even more than OA itself in which peripheral reaching inaccuracy can be easily compensated by foveating the target goal objects and slowing the goal-directed movements (review in Rossetti et al., 2003).

Second, one can examine between patients dissociation and analyse how they relate to the perception-action issue. As highlighted in bold in Table 1, an impairment of action is emphasised in OA and a deficit of visual recognition in VA. But is the evidence sufficient to make the case for a proper double-dissociation? Patients with OA do not exhibit obvious deficit for object recognition in central vision. Therefore one can argue for a simple dissociation: patients with VA are impaired for visual object recognition in central vision while patients with OA are not. Note that object recognition has never been tested in peripheral vision neither in OA nor in VA. When vision-for-action is

Table 1
Main perceptual and visuo-motor results available on optic ataxia (OA) and visual agnosia (VA)

	Vision	Optic ataxia	Visual agnosia
Object Recognition	Central	Preserved ← → Impaired	Impaired
	Peripheral	Impaired ?	?
Reaching	Central	Preserved	Preserved
	Peripheral	Impaired	? →
Grasping	Central	Preserved	Preserved
	Peripheral	Impaired	? →
Delayed Reaching	Central	Impoverished	Impoverished
	Peripheral	Improved	?
Delayed Grasping	Central	?	Impoverished
	Peripheral	Improved	?
Pantomimed Grasping	Central	?	Impaired
	Peripheral	Improved	?

The shaded boxes highlight the main features of the two neurological conditions. These features have been used to argue for a double-dissociation between visual agnosia and optic ataxia. The black arrows indicate the dissociations described between OA and VA. However, this apparent pattern becomes questionable when one introduces the visual eccentricity parameter. It should be noted that reaching and grasping performances have been documented in different conditions. The large white arrows depict the necessary control conditions that remain to be investigated. Reaching and grasping are impaired in peripheral vision whereas they remain largely preserved in central vision. Actions to peripheral targets remain undocumented in VA. The other missing control is about visual perception of OA patients in peripheral vision. Preliminary evidence indicates that it may be impaired (Rossetti et al., 2005a,b). The last three couples of rows describe other conditions investigated in these patients, for which the eccentricity parameter is again crucial.

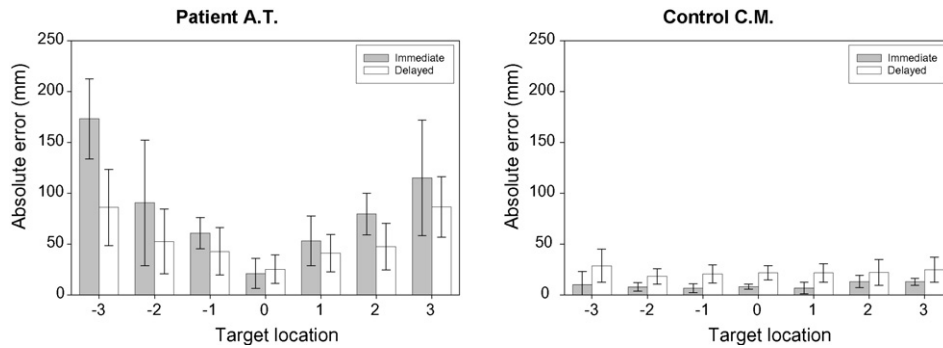


Fig. 1. Effect of delay on the pointing accuracy of a patient with bilateral optic ataxia (AT) in peripheral vs. central vision.

considered, it is obvious that the two types of patients have not been tested in identical conditions. While reaching movements are impaired in peripheral viewing conditions in OA, testing is only available in central vision for VA (see pointing and reaching lines in Table 1). The visuo-motor abilities of patients with OA in central vision have been recently studied (Gréa et al., 2002; Pisella et al., 2000) showing no or subtle visuo-motor reach-and-grasp deficits under basic conditions. Deficit of automatic/on-line visuo-motor control were revealed in central vision when a target jump was synchronised with the start of reach-and-grasp movement and asked for visuo-motor adjustments with high temporal constraint. In addition to central/peripheral vision, the effect of time on the visuo-motor abilities of OA patients will be discussed in the next section.

2.2. The effect of delay: A role of the ventral stream in action?

In support to the idea of double-dissociation between OA and VA, the opposite effect of time on the behavioural dissociation between these two pathologies had been already described in the literature. The visuo-motor abilities of a VA patient vanished if the movement was delayed with respect to the object presentation (described for grasping by Goodale et al., 1994 and for reaching by Milner et al., 1999). Conversely, Milner et al. (1999, 2001, 2003) and Rossetti et al. (2005a,b) described a paradoxical improvement of visuo-motor abilities after a delay in OA patients (Fig. 1). However again, this reverse pattern of change with delay was observed in central vision for the VA patient and in peripheral vision for the OA patient. When a movement was planned in central vision, the OA patient did not show a pathological level of visuo-motor error and thus did not improve with delay (see figure in Milner et al., 1999; Rossetti et al., 2005a,b). This effect of delay, together with the lack of on-line motor control in these patients, was confirmed by further surprising phenomena: movement guidance toward a novel object (modified location or size) was based on the characteristics of the previous object shown 8 s before, rather than on the present characteristics of the novel object (Milner et al., 2001, 2003; Rossetti et al., 2005a,b). However, this effect was again observed in peripheral vision.

These simple observations suggest that we should have a closer look at the reputed “double-dissociation” between VA and OA (Table 1), and try to review the available neuroanatom-

ical evidence that may allow us to test this idea. It should also be highlighted that the performance of OA patients in delayed movements is still impaired with respect to normal performance in the same conditions (Himmelbach & Karnath, 2005; Milner et al., 1999, 2001, 2003; Rossetti et al., 2005a,b). The idea of a unique use of this ventral stream-to-motor pathway (preserved in OA) for delayed movements in normal brain as in patients does not account for these two aspects. An interaction between the dorsal and the ventral stream for guidance of delayed movements should rather be evoked (review: Rossetti & Pisella, 2002). The study of Smyrnis, Theleritis, Evdokimidis, Muri, and Karandreas (2003) is informative regarding how and when the two streams may interact for delayed action. Showing that a single pulse of Transcranial Magnetic Stimulation (TMS) applied to the PPC of healthy subjects 300 ms after target presentation did significantly affect the accuracy of movements started 3 s after target presentation, the authors have demonstrated that the initial coding of target or hand location (i.e. the early planning processes) crucially depend on the dorsal stream. In the condition of low temporal constraint, it can thus be proposed that in the normal brain the ventral stream can deal with a visual information pre-processed by the dorsal stream, whereas in OA patients the ventral stream has to process and transform the “raw” visual information, hence their still impaired performance in delayed tasks with respect to normal individuals.

The study of Jeannerod, Decety, and Michel (1994) has provided further arguments for a ventral stream-to-motor pathway by showing that OA patient can well guide grasping movements toward familiar objects in while their actions remain completely unadapted for unfamiliar objects. As suggested by Rushworth, Nixon, and Passingham (1997), contrary to simple goal-directed movements, conditional motor responses (i.e. “arbitrary” association between a visual stimulus and a motor response) may not rely on the PPC, at least not until they have become automatic (Grol, de Lange, Verstraten, Passingham, & Toni, 2006). They may involve projections from the infero-temporal area of the ventral stream to the dorsal striatum and ventral prefrontal cortex, and then to the pre-motor cortex (Passingham et al., 2002; Toni et al., 2002). Brain imaging studies have consistently revealed occipital and temporal responses when the task required delayed responses upon instruction, either in the context of arbitrary visuo-motor associations (Toni, Ramnani, Josephs, Ashburner, & Passingham, 2001a; Toni, Rushworth,

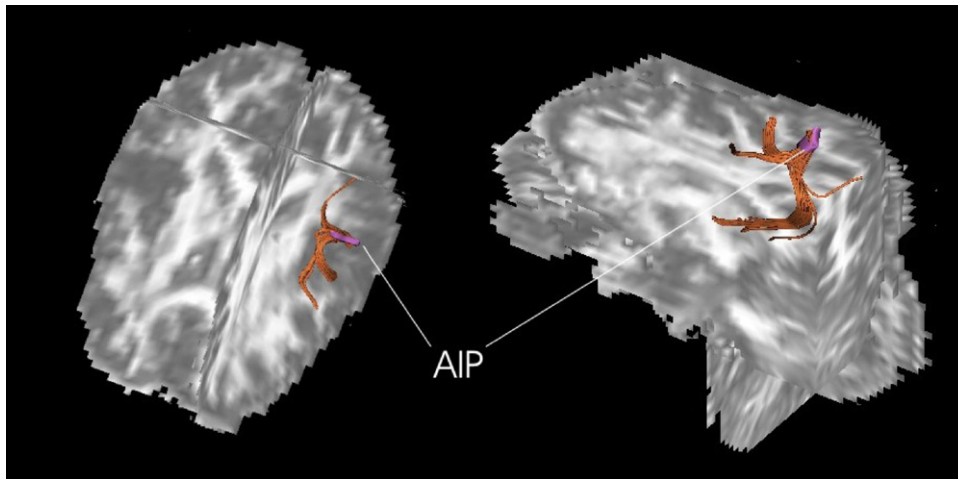


Fig. 2. Dorsal-ventral interaction tract in humans as revealed by diffusion tensor (DTI) tractography. The tractography data were measured on a 1.5 T Siemens SYMPHONY scanner using standard EPI sequences (TR: 6200, TE: 95, Fov: 384, voxel size: 3×3 mm; 40 slices; B0: 0, B1: 600; diffusion modus: MDDW, diffusion weighing: 2) in 18 spatial directions. Data analysis was performed using the DTI TASKCARD software Version 1.69 (Sørensen, MGH, Boston). The following parameters were used to depict the fibertracts: angle threshold 37° , FA threshold 0.3, step length 4.5 mm. This MR imaging technique allowed us to identify in vivo in humans the connections (non-direction specific) of a focused region localized manually with anatomical landmarks (here the anterior part of the intra-parietal sulcus, highlighted in purple for the anterior part of the intra-parietal area [AIP]). The horizontal slice shows the parieto-frontal tract with connection of AIP with a caudal intra-parietal area (CIP) more posteriorly and with pre-motor areas (two loci). The sagittal slice shows an example of interconnections between dorsal and ventral systems with connections of AIP with temporal areas, in addition to the same parieto-frontal tract (CIP, AIP, pre-motor regions).

& Passingham, 2001b; Toni, Thoenissen, & Zilles, 2001c; Toni et al., 2002) or in the context of imitative behavior (Decety, Chaminade, Grezes, & Meltzoff, 2002; Iacoboni et al., 2001). Conversely, a task requiring the planning of rapid hand movements found specific preparatory responses confined to the dorsal visuo-motor stream, including MT+/V5 (de Lange, Hagoort, & Toni, 2005). Although a direct intra-subject comparison between planning activity evoked by immediate and delayed responses has not been done yet, these findings provide further support for the hypothesis that delayed actions and immediate responses rely on different neural circuits.

The temporal lobe areas have anatomical links to the pre-frontal areas (for example the infero-temporal cortex projects to the ventral pre-frontal area) (Yeterian, & Pandya 1998; Webster, Bachevalier, Ungerleider 1994), making prefrontal regions a possible bridge between dorsal and ventral streams (review in Rossetti & Pisella, 2002; Rossetti, Pisella, & Pélisson, 2000). However, the cross-talk may also happen at other stages of the visuo-motor process, namely in the PPC. Such connections between the intraparietal and temporal areas can indeed be identified in vivo in humans by means of novel MR technique of diffusion tensor imaging (DTI) tractography as demonstrated in Fig. 2 (see also Rushworth, Behrens, & Johansen-Berg, in press).

3. Several dorsal sub-streams

As reviewed above, it is not possible to infer a complete double-dissociation between perception and action from the behaviour of OA and VA patients. Furthermore, OA has been considered as the typical visuo-motor deficit but there are numerous neuropsychological consequences that affect the visuo-motor function after a focal lesion. First, as reviewed above, the

ventral visual stream may provide an independent path to motor planning by means of its connections with pre-frontal areas. Second, the modularity of visuo-motor functions in the PPC will be evidenced in this second chapter suggesting the existence of several dorsal sub-streams achieving different visuo-motor transformations.

The idea of multiple visuo-motor occipito-parieto-frontal pathways has emerged from at least two different backgrounds. First, the theory of independent visuo-motor channels hypothesised that reach-to-grasp movements require independent coding of different object properties (location, size, orientation and shape) (Jeannerod, 1997). Second, anatomical studies have lent support to the idea that the transformation of these properties into appropriate movements of arm, finger and wrist is achieved by separated parieto-frontal pathways controlling the different body segments. For instance, anatomical studies have tended to confirm the existence of separate pathways within the dorsal system (Tanne-Gariepy, Rouiller, & Boussaoud, 2002), especially for reaching ($V6a \rightarrow PMd$: Galletti, Fattori, Gamberini, & Kutz, 2004) and for grasping ($CIP \rightarrow AIP \rightarrow PMv$). There have also been neuropsychological reports consistent with this hypothesis. For instance, Binkofski et al. (1998) have reported optic ataxia patients with specific grasping-related impairments. However, specific reach-related impairments have not been described so far, and this is one of the reasons why the hypothesis of functional independency of “visuo-motor channels” (Jeannerod, Paulignan, & Weiss, 1998) is still controversial (e.g. Smeets, Brenner, & Biegstraaten, 2002).

Recently, Rizzolatti and Matelli (2003) have further detailed the anatomy behind the idea of multiple parallel parieto-premotor circuits, suggesting that parieto-frontal circuits are organised in a dorso-dorsal pathway, running from V6 to V6a and MIP in the superior parietal lobule (SPL), and from here

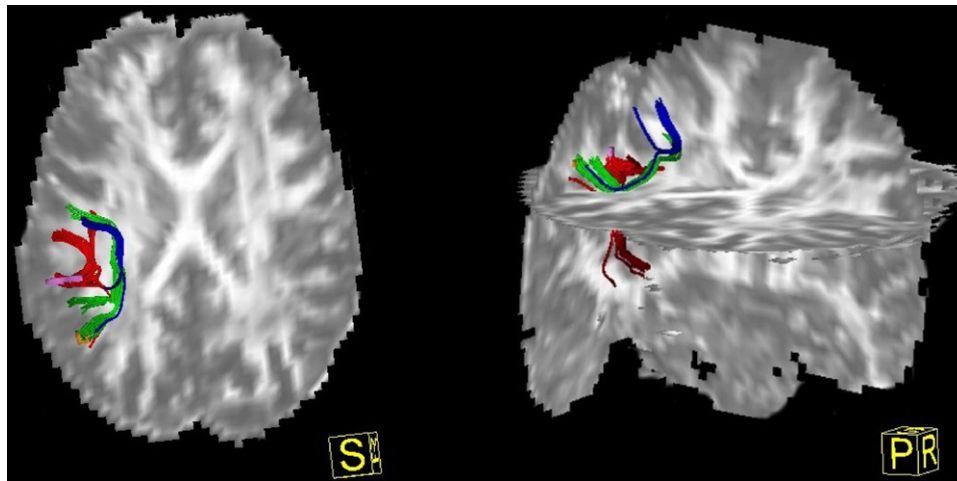


Fig. 3. Many dorsal sub-streams in humans as revealed by diffusion tensor (DTI) tractography. Tracts are provided on horizontal and sagittal slices. Connections (non-direction specific) of three focused regions localised manually with anatomical landmarks could be identified in vivo: (1) the parieto-occipital sulcus (POS) is highlighted in yellow. The green tract may correspond to the reaching pathway with connection of POS (V6a) with a medial intra-parietal region (MIP) and a pre-motor region (2). The frontal-eye-field (FEF) in the corner of the pre-central sulcus on the anterior bank is highlighted in dark blue. The blue tract may correspond to the pathway involved in eye movements with connection of FEF to two pre-rolandic loci, the most posterior one could correspond to a lateral intra-parietal region (LIP) (3). The anterior part of the intraparietal sulcus is highlighted in purple for area AIP. The red tract may correspond to the grasping pathway (already shown and described in Fig. 2).

to the dorsal pre-motor areas (F2vr and F7-non-SEF¹); and a ventro-dorsal pathway, running from medial superior temporal area (MST) to the inferior parietal lobule (IPL), and from here diverging further along a caudal route (PGm²—F7-non-SEF) and an intermediate route (F5-F2vr). Human neuroimaging data appear consistent with a modular architecture of the parietal lobes (for example Rushworth et al., *in press*; Seitz & Binkofski, 2003; and DTI tracts on Fig. 3). The neuropsychology of the parietal lobe also tends to confirm the existence of more than two dorsal sub-streams as well as ventral-dorsal interactions, as detailed below.

3.1. The dorso-dorsal stream (involving projections from SPL, the intra-parietal and occipito-parietal sulci to pre-motor and pre-frontal areas)

Optic ataxia (OA) can be considered as the specific impairment of the dorso-dorsal stream, i.e. of the most direct (immediate) visual pathway for action (Rossetti & Pisella, 2002, 2003). Indeed, the lack of on-line motor control demonstrated for the reaching (Gréa et al., 2002; Pisella et al., 2000; Rossetti et al., 2005a,b) and for grasping (Milner et al., 2001, 2003; Tunik, Frey, & Grafton, 2005) in these patients highlights the specificity of this most superior parietal region for direct goal-directed visuo-motor transformations involving short-lived processes (Rossetti, 1998). However, this pathology may not be a unitary deficit. The usual lesion causing OA is rather large and includes the SPL,

the intraparietal sulcus (IPS) and the occipito-parietal sulcus (POS).

The reach and grasp components constitute a first possible factor of dissociation. Two studies have converged toward the anterior part of the IPS (AIP) as the lesion site causing the distal grasping deficit (Binkofski et al., 1998; Tunik et al., 2005). Reversely, a recent neuro-anatomical study has proposed a more posterior and ventral site as a minimal lesion site causing the misreaching (Karnath & Perenin, 2005): the junction of the two sulci (IPS and POS), designed in another study as the parieto-occipital junction (POJ, Prado et al., 2005). Haaxma and Kuypers (1975) found marked deficits after deep leucotomies at the parieto-occipital junction. The common zone of lesion overlap in the Karnath and Perenin study includes the white matter around this area, suggesting that all connections from occipital to parietal are disrupted, hence the visuo-motor functions are markedly disturbed. However, this says little about the specific contribution of SPL or IPS areas suggested by several case studies, including cases of OA described in the present paper.

However, the “double-dissociation” between reaching and grasping deficits has not been described yet and most OA patients exhibit deficits on the grasp components as well as misreaching with a PPC lesion sparing AIP. The lack of observable isolated reaching deficits (contrary to the reverse dissociation that seems to emerge from the isolated lesion of AIP: Binkofski et al., 1998) may simply be due to the combined reach and grasp activities found in the POS (Fattori, Breveglieri, Amoroso, & Galletti, 2004) and/or to the close localisation of area CIP (caudal part of the intraparietal sulcus) with respect to the lesion site revealed for misreaching (Karnath & Perenin, 2005). By using event related fMRI, CIP has been shown to process the information about the spatial orientation of objects (and maybe also other spatial features of objects), which is then forwarded to AIP. Information in AIP may be processed to prepare adequate actions on these

¹ SEF, supplementary eye field.

² PGm: cortex on the gyrus ventral and caudal to the cingulate sulcus (nomenclature used by Pandya & Seltzer (1982) in reference to Von Economo (1929)), also referred to as 7m (Cavada & Goldman-Rakic, 1989a). This region can be distinguished from Péc dorsally, and PO caudally on the basis of its lighter myelination.

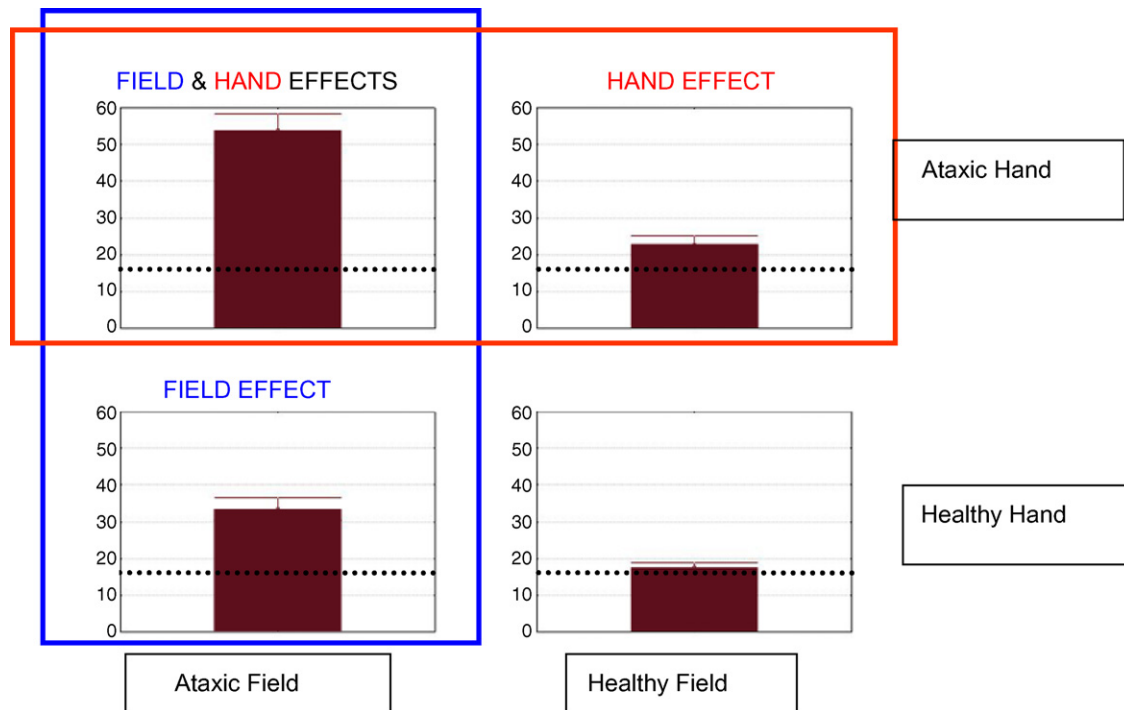


Fig. 4. Field effect and hand effect in unilateral optic ataxia in a task of pointing to peripheral visual targets in the dark. Columns represent the means and standard deviations of the endpoints errors for each four combination of visual hemifield and pointing hand for two unilateral patients as a group. Except for the condition in which the ipsilesional hand points toward the ipsilesional visual field ($Z_{\text{adjusted}} > 0.6$ and $p > 0.2$ for both patients), the mean pointing error appears significantly larger than the standard deviations of the control group represented by the grey rectangle ($Z_{\text{adjusted}} < -2.35$ and $p < 0.05$ in the three conditions and for both patients). Furthermore all conditions are significantly different when compared by pairs within patient (all $F(1, 8) > 10.4$ and $p < 0.05$). This pattern of performance in the visual pointing task reveals, for both patients a combination of a hand effect and a field effect (Blangero et al., 2006).

objects (Shikata et al., 2003). In more detail, subjects were asked either to discriminate spatial orientation of discs, or to imagine to reorient the hand according to the orientation of the discs, or to actively reorient the hand accordingly. In all conditions the CIP activation level was the same, whereas in AIP the activation increased from discrimination to motor imagery and was the highest in execution. Therefore, CIP is participating in spatial discrimination (independent from condition) and AIP is transforming this information into suitable grasp actions but the lesion of CIP is the minimal condition for observing grasping deficit.

The existence of “field effect” and “hand effect” (Perenin & Vighetto, 1988) constitutes the second factor of possible dissociation within OA. As illustrated in Fig. 4, unilateral optic ataxia patients exhibit reach-and-grasp errors when the object is presented in their contralesional visual field with either hand (“field effect”) and when they use their contralesional hand toward either hemifield (“hand effect”). Only the condition in which the object is presented in the ipsilesional visual field and grasped with the ipsilesional hand is normally accurate. This pattern has been considered as the complex expression of a unique deficit at the visuo-manual interface (Perenin & Vighetto, 1988). Interestingly however, these two types of errors appear to be additive, errors being larger in the condition of reaching toward the contralesional field with the contralesional hand (Blangero et al., 2006). Such additive character of errors may suggest dissociated origins.

Along this line, recent results have provided a differential functional interpretation for these two components of the mis-

reaching pattern. Errors linked to the field effect appear to be linked to oculo-centric spatial representations of visual target within the PPC (Gaveau et al., 2006; Khan et al., 2005a; Khan, Pisella, Rossetti, Vighetto, & Crawford, 2005b; Ota et al., 2002, 2006). Errors linked to the hand effect appear to be related to a mislocalisation of the contralesional (ataxic) arm based on impairment of high-level processing of proprioceptive information (Blangero et al., 2006). In addition, comparing pointing errors in the dark versus in the light in a patient with right unilateral optic ataxia, Blangero et al. (2006) have revealed a significant interaction effect of Vision X Hand but not of Vision X Hemifield. Planned comparisons have shown that condition of visual feedback of the hand significantly and specifically reduced the hand effect. This suggested that movements toward objects performed in central vision are preserved especially when they are performed with vision of the hand, which compensates for the proprioceptive mislocalisation deficit evoked above. Conversely, when reaching is performed with the ataxic hand in the dark the visuo-motor transformation has to rely on the comparison of the location of the visual target and of the unseen hand, this latter being necessarily informed from the impaired proprioceptive integration. This logically leads to the conclusion that, contrary to the “field effect” errors, the “hand effect” errors are present when the reaching movement is performed in central vision as well as in peripheral vision.

Accordingly, the hand and field effects may be respectively confronted to the two neural networks recently evidenced by the imaging study of Prado et al. (2005): a medio-parietal network



Fig. 5. This 68-year-old patient H.S. presented with a small atypical intracerebral bleeding in the region of the middle right intraparietal sulcus. At the initial presentation some signs of left sided visual neglect could be found. When tested under the mirror the patient exhibited a slight mirror ataxia in his left arm. His major complaint was misreaching with his left arm, in absence of paresis and primary sensory deficits. This “hand effect” was observed in both visual fields (upper panels) when the classical clinical testing of optic ataxia was performed (Perenin and Vighetto, 1988), whereas no misreaching could be observed with the ipsilesional arm in either hemifield (no “field effect”).

was activated when reaching was performed in both central and peripheral vision and an additional network, more caudal in the PPC (called POJ: parieto-occipital junction), was activated only when reaching was performed in peripheral vision. Despite these recent arguments, no case of OA with isolated field effect or isolated hand effect has been reported so far in the literature, to our knowledge (but see the mirror ataxia patient described below and on Fig. 5).

3.1.1. Mirror ataxia: Mildly affected patients may exhibit optic ataxia with an isolated hand effect

Mirror ataxia is characterised by misreaching of objects presented through a mirror. The patients usually transport their arm

to the rough position of the object in the real space but misreach it and need several corrections depending on the severity of the disorder. As for OA, mirror ataxia may not be a unitary deficit. The original description from Binkofski, Buccino, Dohle, Seitz, and Freund (1999b) distinguished two “subtypes” or “levels” of impairment; the severely affected patients had larger and more posterior parietal lesions while the less affected patients had smaller and more anterior lesions.

A prominent feature of the performance of severely affected patients was the large number of corrections they needed to grasp the object. Although they could direct their arms away from the mirror and roughly toward the object, they often failed to reach it. In these instances they even produced some dystonic-

like hand and arm movements. Otherwise they tried to approach the object by changing their trajectories several times, finally being unable to find a direct way toward the real object. They were not able to conceive the direct movement trajectory and therefore looked for other points of reference or approached the target by trial and error. At the beginning the patients could even direct their arms to the virtual location of the target object in the mirror.

The less severely affected patients were all able to extrapolate the mirror space into real space from the beginning. Contrary to the severely affected patients, they always hit the object with the ipsilesional hand. With the contralesional hand, they needed several corrections of their movement path before reaching the real object while viewing the object through the mirror. Only two patients failed to finally hit the object in some trials but subsequently learned to direct the movement trajectory to the exact spatial position of the real object.

Mirror ataxia manifests itself only in presence of a mirror and most patients do not exhibit classical OA. The reason for this might be that the visuo-manual guidance through a mirror requires a specific visuo-motor transformation. The lesions causing mirror ataxia are rather localised in the anterior IPL and not in the SPL (Binkofski et al., 1999a,b). However, the deficit of the less severely affected patients following a unilateral lesion only concerns the contralesional hand and the question of the dissociation between mirror ataxia and OA is then less clear. We would like to propose here that mild mirror ataxia may correspond to OA with an isolated hand effect. At least one patient with mirror ataxia observed by Binkofski (Binkofski & Fink, 2005) showed only the hand effect of OA (error with the contralesional hand in both visual fields and no error in the contralesional visual field with the ipsilesional hand, see Fig. 5). Furthermore, the recent demonstration of a mislocalisation of the ataxic (contralesional) hand in a proprioceptive-pointing task has led to identify the hand effect as a specific deficit to extract the position of the ataxic hand from proprioceptive information for guidance of goal-directed movement (Blangero et al., 2006). Accordingly, the hand effect was causing large misreaching errors in conditions in which the vision of the hand was not available (in the dark). Similarly, this mislocalisation deficit may also cause large misreaching errors in the condition of guidance through a mirror, since the visual location of the hand in the mirror is erroneous visual information.

3.1.2. Prospects

Note that the two listed factors of dissociation within OA (reach versus grasp and field versus hand effect) seem to be grossly organised along an anterior-posterior gradient inside the PPC. Whether they are distinct or superimposable factors will be worth investigating. For example, one could speculate that the grasping deficits in OA may be only related to a hand effect, consistent with the more frequently observed grasping deficits in central vision. Furthermore, anterior lesions (e.g. around AIP) tend to produce more lateralised effects (i.e. lateralised grasping deficits (Binkofski et al., 1998) but also mild reaching deficits of mirror ataxia restricted to the contralesional hand (Binkofski et al., 1999a,b). More posterior lesions produce more bilateral

deficits—for example severe cases of mirror ataxia observed with either hand (Binkofski et al., 1999a,b) and mirror apraxia (described below), by nature bilateral, resulting from even more posterior lesions. This might rely on the organisation of inter-hemispheric communication between the parietal lobes. The anterior structures (i.e. post-central gyrus with the primary sensory cortex and the adjacent areas) are more strongly lateralised (exception is the secondary somatosensory area that is especially organised in a bilateral manner) than the posterior areas of the SPL (for example area V6a in the POS has a bilateral representation of the whole visual field: Galletti, Fattori, Kutz, & Gamberini, 1999). The posterior IPL is also strongly bilaterally organised—as will be described below (ventro-dorsal streams), mirror apraxia, limb apraxia and hemineglect affect both sides of the body.

3.2. The ventro-dorsal streams (involving projections from IPL to pre-frontal and pre-motor areas)

In contrast to the dorso-dorsal stream is the ventro-dorsal stream supposed to underlie more advanced processing of sensorimotor information. Lesions of the ventro-dorsal streams produce impairments at cognitive levels, i.e. after unilateral lesion patients do not exhibit deficits lateralised to the contralesional limb.

3.2.1. Mirror apraxia—A pathway for reaching with spatial transposition involving the posterior IPL bilaterally

In comparison to mirror ataxia, mirror apraxia is associated with more ventral and caudal lesions of the PPC. Patients with mirror apraxia, as originally described by Binkofski et al. (1999a,b) were unable to distinguish between the real and the mirror space. These patients perceived the object as located in or behind the mirror and guided each of their hands directly toward the virtual object image in the mirror. They were not able to reach toward the real object as long as it was presented through a mirror. Most of these patients directed each hand to the mirror in all trials without hesitation and without any attempt to correct the movement path. There was no change in the performance of these patients when the position of the target object was changed from trial to trial. Moreover, common to all these patients was the inability to make use of proprioceptive information provided by passive movements imposed by the experimenter toward the real object, irrespective of whether this was done while the patient watched the procedure or while the patient kept his eyes closed. After this exertion, they strikingly continued to reach toward the mirror object.

To test for the influence of the visual environment on the perception of object position, the target was presented to one patient through a mirror as a dim light in complete darkness. In this new situation (without visual information about the background), the patient continued to direct his arm toward the virtual object in the mirror. Kinematic recording showed that movements directed toward an object viewed through a mirror were performed with the same trajectory and the same peak velocity than movements directed toward real objects under direct visual control and with no additional corrections.

Binkofski et al. (2003) further showed that mirror apraxia seems to affect the peripersonal space more than the personal space. Objects localised on or very near the body surface are reached without any difficulties. When the same objects are lifted several centimetres away from the body, the patients reach again towards the virtual object in the mirror.

In addition, mirror apraxia manifests itself not only in the central, but also in the peripheral vision (Patients were presented with two targets in the mirror and were asked to fixate the target that was presented in the centre and to reach for the second target, which was presented in the right or left periphery. In both cases they continued to reach for the virtual object in the mirror).

Importantly, after a unilateral lesion (either the right or the left posterior parietal cortex), the impairment concerns both hands; mirror apraxia is thus a high-level cognitive impairment, suggesting that it is the spatial mediation itself that is impaired and that it may necessarily involve a tight interaction between the two hemispheres.

3.2.2. *Limb apraxia—Lateralised ventro-dorsal stream of the left hemisphere (left IPL: Spatio-temporal organisation of movements)*

Limb apraxias affect imitation, pantomime of object use and use of real objects. According to OA being regarded as a typical disorder of the dorso-dorsal stream, online motor performance should be preserved by definition in limb apraxia. A Positron Emission Tomography (PET) imaging study showed that reaching towards targets with various locations in space and presented through the mirror engages preferentially dorso-dorsal stream areas, especially V6a (Binkofski et al., 2003), confirming a possible partial dissociation between the more “simple” on-line dorso-dorsal and the more complex integrative ventro-dorsal functions. Despite this frequent clinical observation however, there is little systematic evidence for preserved abilities concerning sequential imitation and online action performance in patients with limb apraxia. Jason (1983) found that patients with limb apraxia can achieve the same maximal frequency as controls in the “Luria sequence” (fist–palm–edge of hand) task while imitating it synchronously.

Why is the left IPL so important for processing of complex actions, especially object-oriented actions? Clinical neuropsychology classifies disorders of tool use as being the core symptom of ideational apraxia (De Renzi & Luchelli, 1998; Morlaas, 1928; Poeck, 1982). The observation that only patients with left brain damage encounter problems with single familiar tools or tool/object pairs is unequivocal. It suggests that the integration of tools with purpose, recipient, action, and the inference of function from structure are both based on the integrity of the left hemisphere. Indeed it has been shown that only patients with left brain damage commit errors when asked to match objects to actions demonstrated without an object (Vaina, Goodglass, & Daltroy, 1995; Varney, 1978; Vignolo, 1990), to pantomime the action associated with an object (Barbieri & De Renzi, 1988; Goldenberg, Hartmann, & Schlott, 2003; Goodglass & Kaplan, 1963) or to match objects subserving the same purpose (De Renzi, Scotti, & Spinnler, 1969; Rumiati, Zanini, Vorano, Shallice, 2001; Vignolo, 1990). Inference of possible func-

tions from structure has been tested by asking patients to apply novel tools which are linked to their complementary objects by transparent mechanical relationships (Goldenberg & Hagmann, 1998; Heilman, Maher, Greenwald, & Rothi, 1997), or by asking them to discover alternative uses of familiar tools (e.g. a coin for screwing, Heilman et al., 1997; Roy & Square, 1985), which was also found to be impaired only in patients with left brain damage. However, recent series of studies investigating “naturalistic” multi-step tasks involving several tools and objects like preparing coffee and fixing a cassette recorder have shown that the right hemisphere is also important for these complex functions (Hartmann, Goldenberg, Daumüller, & Hermsdorfer, 2005).

Inside the left hemisphere, lesion studies have confirmed that the IPL plays a crucial role for making correct inferences about the function of an object from its structure (Barbieri & De Renzi, 1988). Tool-responsive regions in the ventro-dorsal pathway (also in the left hemisphere) consist of an anterior portion of the intraparietal sulcus (IPS) in the IPL and of the ventral premotor cortex (PMv) (Binkofski et al., 1999a,b; Chao & Martin, 2000; Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003; Johnson-Frey, 2004; Kellenbach, Brett, & Patterson, 2003). However, the wealth of information about objects stems from the temporal cortex (ventral stream). It is therefore conceivable that these two systems have to exchange information in order to generate object-related actions. Accordingly, tools elicit activity in a distributed network of brain areas, concentrated within the left hemisphere (Johnson-Frey, 2004). This network is active across presentation format (pictures, visual words or auditory words) and processing task (viewing objects, naming objects, retrieving information about tools and their action-related properties, performance of the object-appropriate action). Like all object categories, tools evoke activity in posterior ventral temporal cortex. Tool-related activity in this region is strongest in the medial portion of the fusiform gyrus, located between face-preferring regions more laterally and houses/place-preferring regions more medially (Chao, Haxby, & Martin, 1999). Greater activity to tools than to other object categories in the medial fusiform gyrus has been replicated a number of times using both pictures and words (Beauchamp, Lee, Haxby, & Martin, 2002, 2003; Devlin, Rushworth, & Matthews, 2005). A second focus of tool-related activity is found in left posterior lateral temporal cortex. This region is located on the lateral surface in the middle temporal gyrus and inferior temporal sulcus (abbreviated MTG). Because of the selectivity of the left MTG response to action word generation, and its proximity to the visual motion area MT/V5, it was suggested that information about the motion properties associated with object actions may be stored in this region (Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). Impaired tool recognition can be found after left MTG damage (Tranel, Damasio, & Damasio, 1997). The association between action word generation, tool naming, and activation of the posterior region of the left MTG has been replicated numerous times using different imaging methods and experimental paradigms (Devlin et al., 2002; Martin, 2001) as well as the association between tool and action knowledge deficits and left MTG lesions (Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003). The

consistency of these findings suggests that the left MTG is a critical node in the neural circuitry underlying knowledge of tools and their associated actions. These temporal regions are the best candidates for providing the necessary tool-related information for integrating it with appropriate actions inside the intended? IPL and for the junction between the ventral and dorsal streams.

3.2.3. Spatial neglect—Lateralised ventro-dorsal stream of the right hemisphere (right IPL: Spatio-temporal organisation of mental representations)

Spatial neglect is classically considered as a syndrome functionally affecting the left space in the domains of perception, representation and action. However, if the underlying attentional component is usually acknowledged in parietal neglect, the intentional component is still controversial. A difficulty to initiate and guide movements toward the left space has been raised by several authors (e.g. Mattingley, Husain, Rorden, Kennard, & Driver, 1998) and has been proposed as a “motor or intentional” component of hemineglect (see Coulthard et al., in this issue).

As a matter of facts, the visuo-motor deficits of patients with parietal neglect have mostly been observed on the timing parameters of leftward movements, irrespective of both the space where the movement is performed and the arm used for the movement: bradykinesia corresponds to slow leftward movements, directional akinesia to increased reaction time for leftward movements (Mattingley, Phillips, & Bradshaw, 1994; Mattingley et al., 1998). Accuracy problems (directional hypokinesia: hypometry of leftward movements) have been described for limb as for ocular movements but are very controversial (see Niemeier & Karnath, 2000). Most tests have confounded the factor of spatial perception of the goal (spatial attention) and the factor of movement performance toward the left space (spatial intention). Therefore, these “motor deficits” expressed in time have often been attributed to the more acknowledged pole of hemineglect, i.e. to attentional (perceptual) deficits of processing of the cue or of the goal (materialised or not) of the action. The protocol of Mattingley et al. (1998) involved internally-generated movements and therefore was supposed to prevent from such contamination from attention. However, the theoretical debate between the parietal involvement in attention or intention (Andersen & Buneo, 2002; Colby & Goldberg, 1999) can even concern the mental representation of the location of the goal. Accordingly, the following experiment (Fig. 6) shows that the motor impairment is not directly linked to the movement direction and is thus demonstrative of the high-level motor impairment in unilateral neglect. In response to a central visual cue (rightward or leftward arrow), the patients were instructed to grasp a ball located straight-ahead (first movement) and, then to bring it into the right or the left basket respectively (second movement). In both cases, the first movement was aimed straight-ahead toward the ball. However, when the cue indicated the left basket as the final goal of this sequential action, the first movement was slower than when the cued indicated the right basket (Rode, Rossetti, Farne, Boisson, & Bisiach, 2000; Rossetti et al., 2005a,b). The final lateralised intention or attention did thus affect the execution of the first non-lateralised grasp movement. This suggested that (1) the whole movement

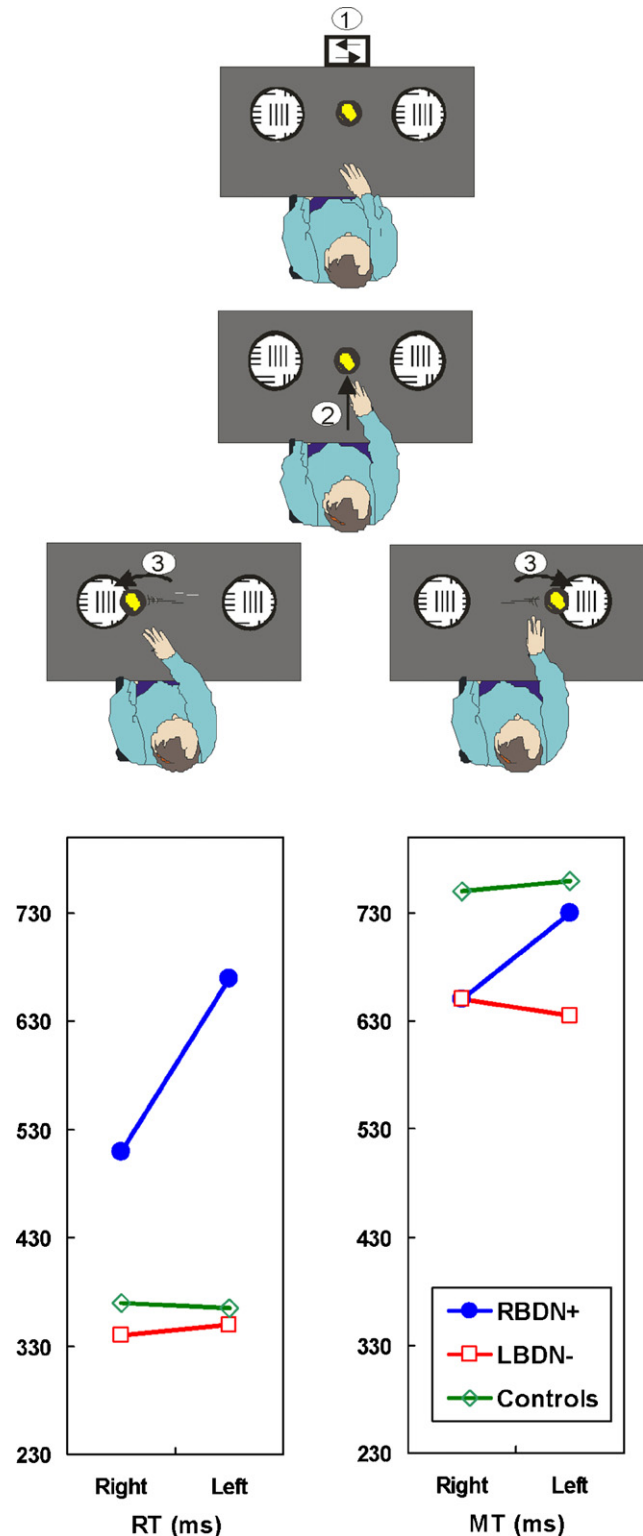


Fig. 6. Spatio-motor impairment in hemineglect. Upper panel: illustration of the protocol used to test sequential movements in hemineglect. Lower panels: mean reaction time (RT) and mean movement duration (MT) of the first movement directed to the central location of the ball when the final goal basket was in the left versus in the right space. The results of three groups are presented for comparison: right brain-damaged patients with neglect, left brain-damaged patients without neglect and a control group of aged-matched healthy subjects. Only the group of patients with neglect did show a significant left-right difference in RT and MT.

sequence is planned prior to starting the movements and (2) the deficit is at the representational level of the final goal, which may be higher than the classical view of attention as perceptual function and intention as motor planning of a single movement.

3.2.4. Prospects

Recent evidence from behavioural (Bersalou, 1999), neuropsychological (Tranel et al., 2003) and neuroimaging investigations (reviewed in Martin & Chao, 2001) have provided support for the old idea that object concepts are grounded in perception and action (Broadbent, 1878; Lissauer, 1890). This idea posits that the concept of a particular object is represented within the same sensory and motor systems engaged when we learned about, or interacted with, the object. Accordingly, a supramodal representation of tools could recently be identified not only in the posterior fusiform gyrus, but also in the bilateral PMv (Binkofski, Buccino, Zilles, & Fink, 2004).

The dynamic of the process of building up representations of tools and of tool-related actions has not yet been studied by means of neuroimaging (but see Toni et al., 2002). Limb apraxia probably results from damage of integrative, computational and working memory (WM) capacities of the left IPL. Interestingly, WM has also emerged recently in the literature of spatial neglect, i.e. of the right hemisphere. Husain et al. (2001) showed that during visual search, a patient with spatial neglect re-explored and re-considered previously cancelled targets as if they were new targets. The authors called this “amnesic” aspect of exploration “re-visiting behaviour”. Re-visiting was revealed in a series of experiments by using carbon paper or computerised version (using a mouse click instead of a pen) of the classical cancellation task (Husain et al., 2001; Wojciulik, Husain, Clarke, Driver, 2001). These displays prevented the patient from seeing the marks he previously made on the sheet and consequently increased the tendency to re-select and re-mark previously visited object locations (thus mostly ipsilesional right targets) after having explored further toward the neglected side; this latter element being important to rule out a perseverative behaviour. This re-visiting was observed even though the instruction explicitly asked to mark each target only once. The authors also created a variant cancellation task where all the elements presented on the screen/sheet were different (drawings of different objects and animals). In this task, each visited location could be encoded by a perceptual image and the results consequently showed a drastic decrease of re-marking/re-clicking behaviour. This last experiment ruled out the presence of a general WM deficit. The authors concluded that neglect patients may exhibit a spatial WM deficit.

Re-visiting behaviour may reveal a deficit of building a coherent representation of visual space across exploratory saccades (Husain et al., 2001; Driver & Husain, 2002; Pisella & Mattingley, 2004). Along this line, Pisella, Berberovic, and Mattingley (2004) observed a spatial WM deficit specifically in neglect patients with lesion including the PPC. They further postulated (Pisella & Mattingley, 2004) that manifestations like re-visiting behaviour could be accounted by a disorder of spatial trans-saccadic remapping processes, as such deficit has been shown to be specifically a parietal dysfunction by Heide, Blankenburg, Zimmermann, & Kömpf (1995). Remapping pro-

cesses operate in higher-level oculocentric maps of the PPC to ensure visual integration of the successive retinal images over time and space. Indeed, in primary occipital visual areas, retinotopic maps are renewed and thus overwritten at each new ocular fixation. The right hemispheric specialisation of these parietal remapping processes in humans have been confirmed in following studies (Heide et al., 2001; Pisella et al., 2006). Spatial remapping mechanisms operate at a fraction of a second, when WM is thought to operate at the timing scale of a second or a minute. Future studies are needed to establish what are the relationships between these levels of a same functional network.

4. Conclusion

The present review suggests that it is necessary to move beyond a crude dichotomy between perception and action, supported by two streams of visual processing. Several neurological conditions have been long viewed as unified models for specific visual or visuo-motor deficits, but deeper analyses demonstrate that this view is problematic. A challenging issue is whether it is reasonable to try to establish a perfect match between unitary functions (when identifiable) and specific brain areas and processing streams. Visual processing pathways can be characterised by specific neuronal resources and specific functional properties. On the other hand, these resources are embedded within a complex cerebral network, and their contributions are ultimately determined by the dynamics of the network. Accordingly, the study of temporal constraints such as those recently investigated in OA may reveal important characteristics of these interactions between specific neuronal resources and larger cerebral networks. We also wish to emphasise the differential roles of the ventro-dorsal and the dorso-dorsal pathways by highlighting their different WM capacities. The dorso-dorsal stream has a very limited WM, while the ventro-dorsal streams have a significantly larger WM storage and exchange information with the temporal lobe. This large WM in the ventro-dorsal pathways could function as an integrator that is combining the different sensory inputs into more complex representations of movements or space. In contrast to the SPL, the IPL could thus have an important integrative function in the higher motor and space processing.

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