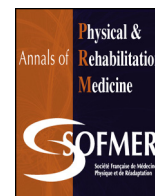




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Update article

Rise and fall of the two visual systems theory



Yves Rossetti^{a,b,*,1}, Laure Pisella^a, Robert D. McIntosh^c

^a Inserm UMR-S 1028, CNRS UMR 5292, ImpAct, Centre de Recherche en Neurosciences de Lyon, université Lyon-1, 16, avenue Lépine, 69676 Bron, France

^b Plate-forme « Mouvement et Handicap », Hôpital Henry-Gabrielle, Hospices Civils de Lyon, 20, route de Vourles, Saint-Genis-Laval, France

^c Human Cognitive Neuroscience, Psychology, University of Edinburgh, Edinburgh, UK

ARTICLE INFO

Article history:
 Received 22 December 2016
 Accepted 15 February 2017

Keywords:

Vision
 Action
 Dorsal
 Optic ataxia
 Visuomotor

ABSTRACT

Among the many dissociations describing the visual system, the dual theory of two visual systems, respectively dedicated to perception and action, has yielded a lot of support. There are psychophysical, anatomical and neuropsychological arguments in favor of this theory. Several behavioral studies that used sensory and motor psychophysical parameters observed differences between perceptive and motor responses. The anatomical network of the visual system in the non-human primate was very readily organized according to two major pathways, dorsal and ventral. Neuropsychological studies, exploring optic ataxia and visual agnosia as characteristic deficits of these two pathways, led to the proposal of a functional double dissociation between visuomotor and visual perceptual functions. After a major wave of popularity that promoted great advances, particularly in knowledge of visuomotor functions, the guiding theory is now being reconsidered. Firstly, the idea of a double dissociation between optic ataxia and visual form agnosia, as cleanly separating visuomotor from visual perceptual functions, is no longer tenable; optic ataxia does not support a dissociation between perception and action and might be more accurately viewed as a negative image of action blindsight. Secondly, dissociations between perceptive and motor responses highlighted in the framework of this theory concern a very elementary level of action, even automatically guided action routines. Thirdly, the very rich interconnected network of the visual brain yields few arguments in favor of a strict perception/action dissociation. Overall, the dissociation between motor function and perceptive function explored by these behavioral and neuropsychological studies can help define an automatic level of action organization deficient in optic ataxia and preserved in action blindsight, and underlines the renewed need to consider the perception-action circle as a functional ensemble.

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Toutes les théories qui servent de point de départ au physicien, au chimiste, et à plus forte raison au physiologiste, ne sont vraies que jusqu'à ce qu'on découvre qu'il y a des faits qu'elles ne renferment pas ou qui les contredisent. Lorsque ces faits contradictoires se montreront bien solidement établis, loin de se roidir, comme le scolastique ou le systématique, contre l'expérience, pour sauvegarder son point de départ, l'expérimentateur s'empressera, au contraire, de modifier sa théorie, parce qu'il sait que c'est la seule manière d'avancer et de faire des progrès dans les sciences. (Claude Bernard, Introduction à l'étude de la médecine expérimentale, 1, II, VI)

1. Context of the theory

Several dissociations have been described within mammalian vision. One can list for example: conscious vs. unconscious vision; focal vs. ambient vision; spatial vs. object vision; egocentric vs. allocentric vision (see [1], for a review). Historically, the focus of these dissociations moved from anatomically-defined distinctions, such as cortical vs. sub-cortical vision [2], towards functional dissociations, such as semantic vs. pragmatic vision [3,4]. It is interesting to consider the development of arguments, stemming from diverse lines of evidence, compiled by several authors during the eighties and nineties in order to propose reconciliations between anatomical, electrophysiological, psychophysical and neurophysical elements (e.g. [3–13]).

1.1. Anatomical context

Visual experience is unitary, but visual anatomical networks are much more complex than a serial hierarchy leading to grand-

* Corresponding author. Inserm UMR-S 1028, CNRS UMR 5292, ImpAct, Centre de Recherche en Neurosciences de Lyon, université Lyon-1, 16, avenue Lépine, 69676 Bron, France.

E-mail address: yves.rossetti@inserm.fr (Y. Rossetti).

¹ www.U864.lyon.inserm.fr.

mother cells of perceptual consciousness. The most apparent division of the retrochiasmatic visual system is that between cortical and sub-cortical visual pathways. Schneider [2] suggested that the geniculostriate pathway of the rodent was essential for visual discrimination, and that the retinotectal pathway corresponded to a system responsible for spatial orientation. He thus introduced the idea of distinct systems specialized to answer the questions “what is it?” and “where is it?”. This distinction was picked-up and developed by several authors.

In humans, lesions of the visual cortex were classically considered to cause complete blindness, though pupillary responses and rudimentary sensitivity to sudden contrast changes might be retained (review: [3]). This opinion was challenged by the observation that monkeys without a striate cortex showed a paradoxical ability to avoid obstacles or grab objects located in their blind visual field [14]. These monkeys lost their residual visual abilities after damage to the areas of the superior colliculi corresponding to their cortical scotoma [15], implicating the retinotectal route as the basis of those abilities. The existence of parallel pathways from the retina through cortical and sub-cortical routes allowed the emergence of one of the most fascinating phenomena in human neuropsychology: “blindsight” [16–18]. Specifically, the observation of “blindsight” in patients with cortical hemianopia reinforced the arguments in favor of the intervention of sub-cortical structures in blindsight [19,20]. The blindsight phenomenon (reviews: [21,22]), especially its relation to visually-guided action [23], will be developed in the last part of this article.

Functional neuroanatomy also unveiled the existence of several visual pathways through which the retina is connected to the cortex (see Fig. 1). This anatomical approach was largely completed and detailed by independent electrophysiological studies of visual areas (review: [24]) and cortical substrates of the action (review: [25,26]). First of all, several exploratory experiments on the visual brain showed the extreme parcellation of the visual cortex into multiple functional areas ([27] and their famous figure 4; [28]). Famous experiments performed on monkeys allowed the identification of two principal cortical pathways of vision [29]. One of the pathways, the occipitotemporal or ventral stream, links the prestriate areas to the inferior temporal cortex. The interruption of this pathway inhibits the visual discrimination of objects without affecting the perception of spatial relationships between them (relative positions). The other pathway, the occipitoparietal or dorsal stream, leads to the posterior parietal cortex (PPC). The interruption of this pathway causes spatial disorientation, characterized by a deficit in the perception of relative positions [29] and a deficit of localization observed during goal-directed actions [30]. These patterns of deficit, observed through surgical disconnection studies in monkeys, suggest that these two divergent ventral and dorsal streams correspond to two different functions: processing the “what” and the “where” (see Fig. 1).

The exploration of cortical substrates of action, performed with lesions or electrophysiological recording of the parietal cortex of the monkey, confirmed the importance of the PPC in guiding goal-directed movements (e.g.: [31,32]). These results strongly supported the specialization of the dorsal visual system for goal-directed actions (reviews: [4,13,25,33–36]). These findings were complemented by electrophysiological studies on the latency of visual areas, which revealed a rapid processing pathway (the dorsal stream), and a slower one (the ventral stream) [37–39], compatible with the idea of a dorsal stream enabling fast action responses [40]. Furthermore, human clinical data corroborated the importance of parietal areas in action-guidance [3,41,42], followed by functional imaging data published after Faillenot et al. [43].

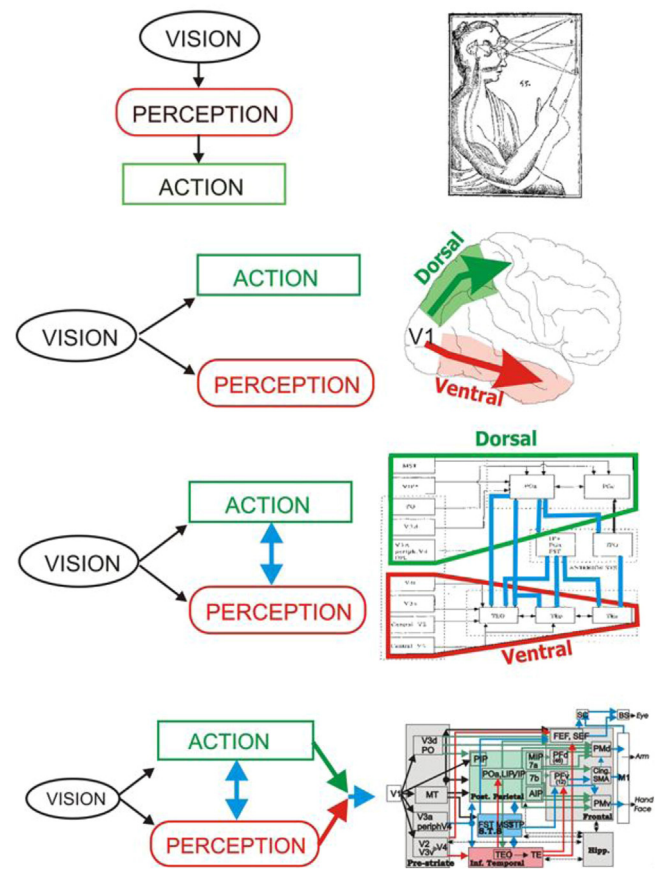


Fig. 1. Representation of the evolution of the visual theories for action. The upper row represents the intuitive concept of vision according to which our actions are preceded by conscious awareness of perception. This serial conception is illustrated by Descartes' drawing. The second row illustrates the duplex notion according to which the visual system is divided into two parts, dorsal and ventral, which are respectively responsible of action and perception, and projected onto the human brain. The third row illustrates the fact that interactions can be described between the two anatomical pathways and perceptive and motor visual functions (data issued from study on the primate's brain) (from [39]). The fourth row illustrates the observation that anatomical projections reaching the primate primary motor cortex, are all subjected to prior interconnections (blue) between dorsal (green) and ventral (red) pathways, suggesting that motor actions could result from several interacting visual processing pathways, converging before the motor exit (from [38,39,49]).

1.2. Psychophysical context

A second methodological approach was based on experimental protocols combining perceptual and motor psychophysics [44]. Variations on the visual “double-step” paradigm proved especially fertile. This paradigm refers to experimental conditions in which a visual target is presented to a subject (1st step: between the initial fixation point and the position of the target), and then moved during the subject's response (second step: between the target's first position and the second one). An interesting variation of the task is one in which the second step is made during a saccade directed towards the first target position. Since small target displacements are not perceived if they occur immediately before or during a saccade (saccadic suppression of image displacement: [45]), a subject's awareness of the displacement in double-step tasks can be eliminated by synchronizing the second step with the increase in eye velocity at saccade onset (e.g. [46]). In the original experiment conducted to evaluate the consequences of this deficient perception on arm movements, Bridgeman et al. [47] asked subjects to make an eye movement and also to move their

hand to the target. Surprisingly, saccadic suppression was not associated with oculomotor or manual performance costs; pointing movements were adjusted normally to take account of the target displacement, even though the displacement went unnoticed.

Subsequently, a now-famous series of experiments was initiated by Prablanc and colleagues, to explore the motor control of rapid movements. In a first work, Pélisson et al. [46] and Goodale et al. [48] asked healthy subjects to direct their eyes and hand towards targets presented in the dark (synchronised with the disappearance of the fixation point). These targets could be jumped to a nearer or further location during the subject's saccade, so that the arm movement, already initiated at the time of the jump, had to be updated to reach the target's second position. Similarly to the findings of Bridgeman et al. [47], subjects were able adjust the arm movement even whilst unaware of the target displacement. Another striking observation was that subjects did not detect their own trajectory corrections, suggesting that these did not give rise to any unusual proprioceptive sensations, [46,48]. These experiments suggest that two visual systems could be differentiated at a psychophysical level; a system involved in the sensorimotor response (i.e. manual vision [49]), and a system participating in the cognitive processes related to conscious perception.

Bridgeman also made use of the original Roelofs effects and the induced Roelofs effects [50]: when a frame of reference is moved during the fixation of a small visual target, a displacement of the target is perceived in the opposite direction. The phenomenon can be observed for slow displacements (induced movements) or discontinuous ones (induced displacements). Bridgeman et al. [5] compared the amplitude of the perceptual illusion with the pointing responses executed by subjects after the target was extinguished: the motor response was much less affected than the perceptual response by the apparent displacement. Their conclusion was that the apparent displacement only affected perception, whereas the real position only affected the motor behavior; the

demonstration was initially proposed as an argument in favor of a dissociation between sensorimotor and cognitive visual functions (see [6,8]). Further studies made it clear that this apparent dissociation could not be taken as an argument for a dissociation between perception and action, as the absence of effect in the visuomotor condition can be explained by the addition of two effects: a perceptual [51] and a remapping component [52]. Further dissociations have subsequently been reported, whereby different visual illusions affect primarily the perceptual or the visuomotor responses as described further below.

1.3. Neuropsychological context

A third, human neuropsychological approach to visual modularity combines anatomical and functional aspects and is rooted in clinical traditions [3,13,53]. In addition to the knowledge acquired in non-human primates, the observation of clinical cases validated the modularity of the human visual cortex, adding to the distinction between cortical and sub-cortical vision as explored by the works on blindsight. The observation of multiple clinical pictures of visual agnosia implied the existence of specialized modules for the analysis of shapes, color, recognition of objects, and even specific categories of objects (review: [54]). Other patients presented specific impairments of visual motion detection (akinetopsia) or impairments in directing their gestures towards a visual object (optic ataxia). The former impairments resulted from damage to the occipito-temporal junction through to the temporal pole, and the latter from damages to dorsal occipito-parietal regions (see Fig. 2).

1.4. Optic ataxia

The effects of neurological lesions involving a limited part of the posterior parietal cortex were described in groups of patients by Jeannerod [41] and Perenin and Vighetto [55]. These patients presented difficulties in directing their actions toward objects

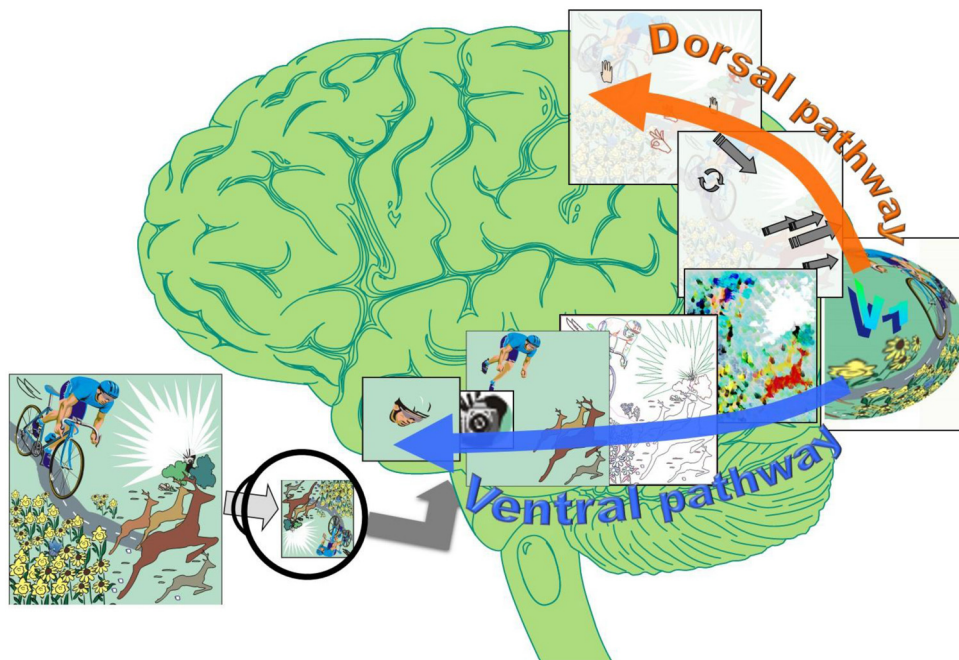


Fig. 2. Functional specialization of the human visual system. Neuropsychology offers the description of specific visual impairments, supporting the existence of specific visual information processing centers, damage to which could lead to visual impairments in seeing shapes (agnosia), colors (color agnosia or central achromatopsia), more or less specific objects (e.g. animal or manufactured objects agnosia) or faces (prosopagnosia), localized in the ventral pathway, movement vision (akinetopsia) or directed movements (optic ataxia), associated to the dorsal pathway. This figure illustrates the information processing of a visual scene (on the left side) in the visual areas processing information received by the primary visual cortex (V1).

presented in their peripheral vision, even though they had no deficits in object recognition. This neurological deficit, optic ataxia, is observed after a lesion of the posterior parietal cortex (see [56–58]) (Pisella et al., 2017: <http://dx.doi.org/10.1016/j.rehab.2016.01.003>). Movements directed towards peripheral visual targets are imprecise, and most often deviated towards the side of the lesioned hemisphere [58–62]. These disruptions become especially obvious when the vision of the hand is prevented before and during the movement. In the presence of visual feedback, the precision is improved but movements remain slower than normal [41]. Distal components, such as hand shaping to grasp objects, are also disrupted by the posterior parietal damage. During grasping gestures, patients opened their hand very widely, presumably in order not to miss the object, and made no appropriate adjustments to their grip aperture until there was tactile contact with the object [41,59,63,64]. Patients who were asked to insert the hand into a slit with a variable orientation did not direct their hand accurately towards the location of this visual goal, but also did not rotate their wrist to the correct orientation [55,59,65]. However, these patients seemed to retain the ability to indicate the orientation of a stimulus with a wrist movement not directed towards the stimulus itself, as seen in matching tasks (see [59,66]). These results suggest that the posterior parietal cortex plays a crucial role in spatial vision (position coding) or object vision (size or shape coding) in the context of goal-directed action (see [3,33,40,49]). The duplex theory interprets optic ataxia as one side of a major dissociation between vision-for-perception and vision-for-action, in which “action” is defective but “perception” is preserved [13,67].

1.5. Visual agnosia

The complementary dissociation profile to optic ataxia yielded important arguments in favor of the notion of a perception-action dissociation. Following a bilateral lesion of the occipito-temporal cortex due to carbon monoxide poisoning, a patient (DF) presented with visual agnosia of shapes [68]: she was unable to recognize the size, shape, or orientation of objects, whether her method of report was verbal or manual (e.g. indicating size by spacing out the fingers, or orientation by rotating the wrist) [69]. However, when she was asked to reach for the object with a grasping action, or to ‘post’ an object through an oriented slit, her accuracy and precision were remarkably increased, even apparently normal. These observations suggested that during goal-directed movements, DF could access visual properties of the object that she could not consciously recognize or report on. This remarkable pattern, then, suggested another dissociation, in which perception was deficient and action control was retained. The contrast of these results with those observed in optic ataxia suggested that deficits in visual recognition of objects and goal-directed action were fully, doubly, dissociable.

1.6. Formulation of the duplex theory

The scientific works on these different approaches published between the 1970s and the 1990s allowed the development of rich knowledge of the anatomical and functional organization of the human visual system. The experimental effervescence was initially organized around the notion of a dissociation of anatomic origin described by Schneider [2] in rodents (tectum/cortex) then by Ungerleider and Mishkin [29] in primates (dorsal/ventral). Despite their very different anatomical bases, the terms proposed to describe these two identified visual sub-function were identical: “what?” vs. “where?” Thus, the visual function is defined by the visual attribute processed. But this criterion of the visual attribute, became progressively insufficient to describe the complexity of clinical observations. Instead, the critical importance of the

behavioural function subserved by the visual processing was underlined, from the beginning of the nineties [3,6,11], giving rise to several independent formulations, including the duplex theory of Milner and Goodale [13].

As reported above, neuropsychological observations conducted on optic ataxia and visual agnosia suggested that the dorsal-ventral distinction could in reality correspond to the dissociation between the knowledge of the “what” and the organization of the “how” to direct the action [3,4,11,70]. This new interpretation of the parallelism between the two visual systems, which dominated a large part of the scientific literature these past 20 years, takes a lesser consideration of the passive aspect of vision (“what” and “where”) in favor of the use of the stimulus, dependent on the response produced by the subject (“what” and “how”).

In light of the scientific context that attributed a key role to the posterior parietal cortex in guiding movements, the initial study by Goodale et al. [69] that described preserved motor abilities in a patient (DF) presenting with agnosia of visual shapes, supported a theory based on the opposition between visuomotor grasping and visual recognition of objects. As we will see, it is essentially the visuomotor abilities of visual agnosia, used to build this theory, which were experimentally explored, although the first detailed study of DF was focused on perceptual functions [71]. For a long time the other side of the theory, object recognition, or “perception”, was not evaluated in controlled conditions identical to sensorimotor testing ones. The keystone of the duplex theory is unquestionably the existence of a double dissociation, key concept of neuropsychology (see [1]), between optic ataxia and visual agnosia (see [72]).

1.7. The duplex theory

Optic ataxia and visual agnosia have been very often considered as representing dissociations between perception and action, as the two components of a double dissociation between “perception” and “action” (see [13,40]). The duplex theory brought forward by Milner and Goodale was not exclusively based on the contrast between these two neuropsychological pictures, but it drew much strength from this contrast. This argument did have the advantage of identifying a link between some behavioral dissociations and certain anatomical concepts of the visual system. Specifically, the formulation of this theory brought some sense to the increasingly complex anatomical networks described in primates. It triggered a considerable number of behavioral studies that explored the visuomotor functions, leading to numerous new empirical findings, even if some purely behavioural findings were inappropriately interpreted on an anatomical level in light of the duplex notion of an anatomical/functional equivalence (Table 1).

Several dissociations were described in DF or in patients with optic ataxia, shedding light on the functions of the human dorsal and ventral streams. The majority part of these studies explored grasping gestures, pointing movements and visual perception in these patients (review: [4,13,40,49]). Patients with optic ataxia showed a paradoxically improved performance with the introduction of a delay between stimulus presentation and the motor response [64,73,74], whereas DF showed a deterioration of her visuomotor abilities in a few seconds [75]. Perceptual and motor versions of an obstacle-avoidance task completed these descriptions. A great number of studies on the motor and perceptual effects of visual illusions, even though they brought no anatomical results, were also interpreted within this theoretical framework. Goodale and Milner proposed over time several rather stable versions of their theory [67,76–78], and popularized the idea that the visual system is divided in two independent parts dedicated to perception and action respectively, illustrated and validated by a dual neuropsychological dissociation.

Table 1
Dissociations related to the perception-action dissociation of the duplex theory.

Perception		
Sub-cortical vision	Cortical vision	Cajal [133]
Tectal vision (Where?)	Cortical vision (What?)	Schneider [2]
Ambient vision	Focal vision	Threvarthen (1968), Humphrey [134]
Localization	Identification	Paillard (1983)
Locus-specific information	Global-feature or figural information	Held [135]
Spatial	Object	Ungerleider and Mishkin [29]
Response		
Action	Experiential	Goodale [136]
Motor	Cognitive	Bridgeman [135], Bridgeman [6]
Sensorimotor	Cognitive or representational	Paillard [9], Paillard [10]
Implicit	Explicit	Weiskrantz et al. [18]
Action (How?)	Perception (What?)	Goodale and Milner [11], Milner and Goodale [13]
Pragmatic	Semantic	Jeannerod and Rossetti [3], Jeannerod [12]
Direct parameter specification	Conscious representation	Neumann and Klotz [137]
How?	Where?	Rossetti et al. [138,139]
Automatic	Voluntary	Popular
Reflex eye movement	Voluntary eye movement	Gabersek and Jobert [140]
Elicited extension	Guided placing	Wolgin et al. [141]
Ballistic movement	Terminal guidance	Paillard [10]
Reaching channel	Grasping channel	Jeannerod [142]
Automatic	Conscious	Péllisson et al. [46]
Egocentric reference frame	Exocentric reference frame	Bridgeman [6], (2006)

This non-exhaustive list of distinctions picked-up in the literature concerns the domains of perception and action. If there are some major overlaps between several of these distinctions, they can nevertheless be reduced to one. Several reviews of these parallel or successive proposals have been published [3,4,13,23,40].

2. Deconstruction of the theory

This theoretical description of a double dissociation between optic ataxia and visual agnosia contrasts sharply with the clinical picture, if one asks which patient is more disabled in the actions of daily life. To the extent that patients with agnosia cannot identify objects, they cannot select appropriate goals for their actions, and are functionally incapacitated. By contrast, patients with optic ataxia execute actions fluently in central vision (unless the ataxia is bilateral), so suffer very little loss of autonomy in daily life [56,58,79]. As a striking example, one of the patients we followed became a taxi driver after his vascular stroke. So how did we come to formulate and disseminate so widely a theory suggesting the contrary of this clinical reality? Let's review some of the key anatomical and functional data, to deconstruct this theory [60].

First of all, a critical data figure reproduced by Milner and Goodale [13], to illustrate the proposed dissociation between

perception and action, comes from works by Vighetto and Perenin [55,59]. The figure selected by Milner and Goodale illustrates the number of motor errors made by 10 patients with right or left optic ataxia in simple reaching (Fig. 3). We can observe on this figure that patients make most errors (corrected and uncorrected) in the contralesional visual hemifield. However, the version of the figure presented by Milner and Goodale selectively omitted the central panel, which showed that patients made hardly any errors in the central part of their visual field, except for one patient (No. 3) who presented with multiple associated impairments ([55], Figure 4). The text from the original article also described the absence of motor errors when patients visualized the target in foveal vision ([55], Table 9.4), and the existence of errors for perceptual responses (see [60], Figure 10.2). This aspect was not mentioned by Milner and Goodale [13], but has been validated by several subsequent publications (e.g. [74,80–83]), and is illustrated in Fig. 4.

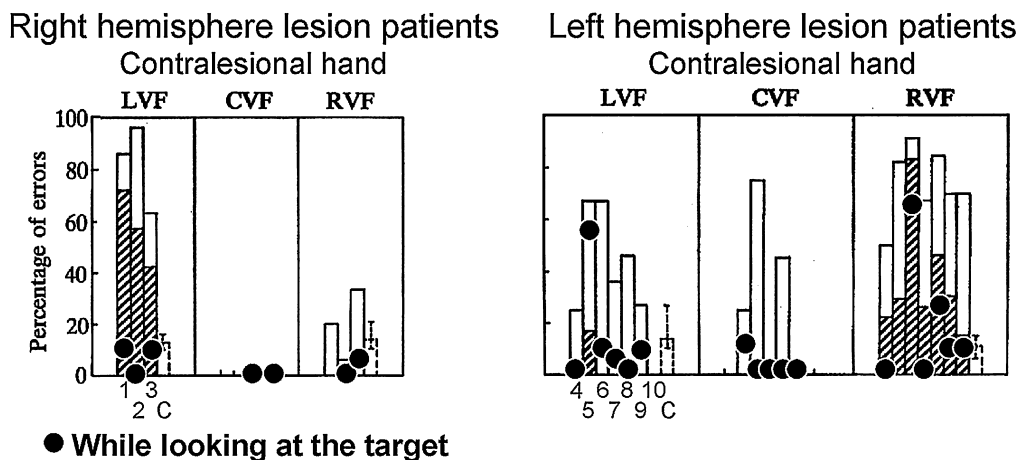


Fig. 3. Performances of ten patients presenting with optic ataxia. Three patients with a right hemisphere lesion (No. 1 to 3) and seven patients with a left hemisphere lesion (No. 4 to 10) were tested in the left (LVF), central (CVF) and right (RVF) areas of their visual field for grasping movement directed towards an object in the CVF condition, objects were presented in the central area of the visual field, but not specifically on the fixation point. The performances of five control subjects are presented in the dotted line bar graphs. This figure only presents the movements performed with the contralesional hand. Errors analyzed on a video recording were classed as corrected when the patient reached his or her goal (white bar graphs) or not corrected (striped bar graphs). In addition, performances of patients when they actually stare at an object in foveal vision are represented in black dots (not illustrated on the original figure). This figure reveals that movements in foveal vision are normal, and that corrected but essentially non-corrected errors appear in the contralesional peripheral vision. Notice that the figure reproduced by Milner and Goodale [13] in their book (part 4.2.1.) takes out the central areas (CVF) of the original figures (from [55]).

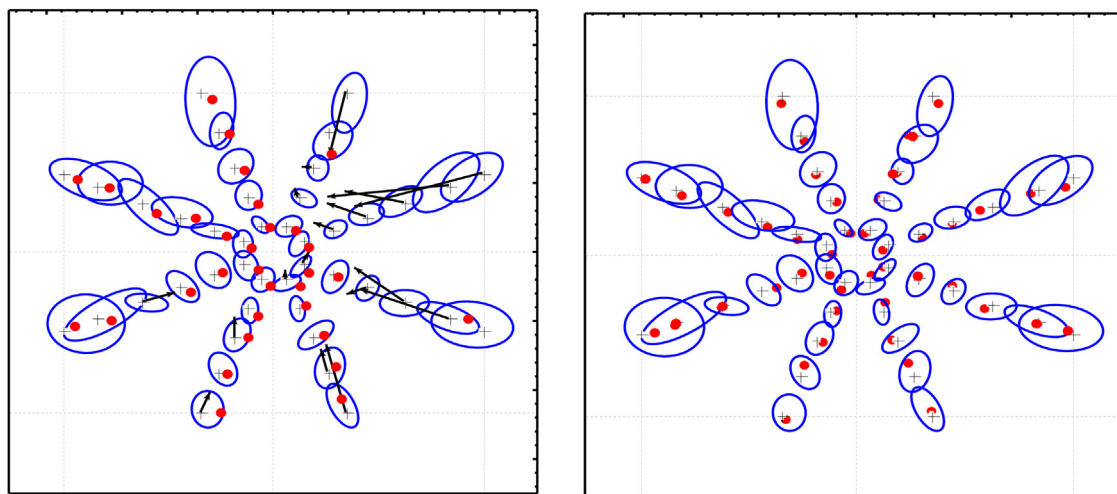


Fig. 4. Visuomotor field test. Pointing tasks performed by a patient with unilateral optic ataxia. The test was performed in peripheral vision during central visual fixation (left image) or in central vision when the patient can freely move the eyes (right image). Crosses represent the locations of all targets aimed at, and confidence ellipses describe the confidence interval of the performance of healthy subjects. Red points represent mean errors made by the patient and are associated with an arrow when they are larger than those made by healthy subjects. We notice that significant errors (which can exceed 10 cm) are only observed in contralateral peripheral vision of the patient (from [60]).

If we review the data available in publications concerning optic ataxia and visual agnosia, it appears that (1) the arguments in favor of a dissociation between perception and action in optic ataxia are decidedly weak, and (2) the conditions used to contrast visuomotor performance in DF (central vision) and in patients with ataxia (peripheral vision) are not comparable, rendering evidence for a double dissociation inadequate. Patients with optic ataxia make substantial errors only in the peripheral visual hemifield, validated by pointing and grasping tasks [55,59,64,73,74,84,85], whereas the absence of perceptual impairments has largely been demonstrated in central vision only. Where it has been specifically assessed, perceptual impairments have in fact been found in peripheral vision [60,74,86–88]. Some patients studied specifically in the context of optic ataxia [73,89], have even have been studied by others authors chiefly with regard to their prominent perceptual impairments (e.g. [86,90]). Thus, the existence and nature of the single dissociation in optic ataxia is uncertain, and the famous double dissociation with visual agnosia even more so [79].

Regarding visual agnosia, the fact that Goodale and Milner's portrayal was based on the study of a single patient showed theoretical but also statistical weaknesses. Revisited and considered in a comprehensive manner, the classical dissociation between impaired perception and preserved action in patient DF may be more accurately viewed as a pattern of relative preservation of visuomotor function, without normal performance in either domain (a strong rather than a classical dissociation; e.g. [91]), thereby reducing the inferential significance of these results [92,93]. Even more dramatic, recent results have revealed that DF actually presents a pointing pattern in peripheral vision similar to the one that characterizes optic ataxia [94,95]. The updated analysis of this patient's brain imaging confirms dorsal stream damage, in both hemispheres, that would be consistent with a co-existing diagnosis of optic ataxia. This striking observation, of co-existing visual agnosia and optic ataxia, even if they have discrete anatomical bases, fundamentally undermines the prior claim that DF's behavior can be taken as one half of a double dissociation between these conditions. Such considerations have led several authors now to suggest that we reconsider the duplex theory of Milner and Goodale [4,79,85,93,96,97].

2.1. Rich and interconnected anatomical networks

In spite of this emphasis on the dissociations within the visual system, an integrated behavior must necessarily involve

projections onto motor structures from both the dorsal and ventral pathways. The projections from the ventral system onto the motor areas of the frontal cortex, less direct than those from the dorsal system, can involve the sub-cortical structures (basal ganglia); and the TE areas project onto the prefrontal cortex, and then on the motor areas (see Fig. 1). These two anatomical projection systems may be articulated with behavioural arguments in favor of a duality of visuomotor actions [98]. The famous figure 4 of Felleman and Van Essen [27] listed more than 30 cortical areas that receive retinal projections, organized in a rich network within which more than 300 reciprocal connections were described. Given the extreme complexity of interconnection within this more exhaustive representation of the visual network, one can understand that academics preferred a version that simplifies to three [24] or even two very distinct pathways [13]. This simplification can be a helpful aid to theorizing, but the reality remains that there are many interconnections within the visual system ([37], Figures 1 and 2) as well as within the visuomotor projections [4,99]. It is interesting to underline that certain sub-cortical visual networks also project on prestriate visual areas (see [100,101]).

The inferior row of Fig. 1 ([49]) presents a review of the neuroanatomical projections of dorsal and ventral systems connecting primary visual entrances (V1) with primary motor exits (M1). The connection network obtained via a review of the literature on primates reveals a multitude of 'through-routes' between V1 and M1. Beyond gross distinctions between cortical and sub-cortical vision, between ventral and dorsal visual pathways, or between the two occipitofrontal pathways, the obvious conclusion is that these sub-systems are densely interconnected, providing much scope for visuoperceptive and visuomotor functions to interact [40,102].

A recent re-evaluation of dorsal cortical visual networks [103] proposed three major systems differentiated beyond posterior parietal cortex: a parietal-premotor system for goal-directed action (eye, arm and hand movements) with the main pathway linking V6a and MIP to the PMd, but also including a pathway between the VIP and the PMv; a parietal-mediotemporal system linking the caudal intraparietal sulcus (IPS) to the mediotemporal lobe, including the hippocampus, the posterior cingulate cortex and the retrosplenial cortex, for orientation and spatial navigation; and a parietal-prefrontal system having for its sources LIP, VIP, MT, MST and projecting on the FEF (area 8a and area 46) for voluntary

control of eye movement and spatial working memory. This new interpretation of visuomotor networks highlights the existence of several anatomo-functional systems involved in visuomotor organization.

2.2. The anatomical illusion

Functional dissociations observed in the healthy subject are also potentially informative regarding sensorimotor organization. Prominent among these dissociations is the very appealing claim that contextual visual illusions have a greater impact on perceptual responses than on motor ones, suggesting different underlying visual representations for these classes of response. However, some major objections can be applied to using this argument to defend a perception-action dissociation mapped onto ventral and dorsal streams.

A first consideration is that the motor responses used in this type of experiment are quite basic (reaching or grasping gestures) and the action parameters used to characterize the response correspond to motor variables, such as grip aperture, controlled in an automatic manner. In a highly influential experiment, Aglioti et al. [104] used the Ebbinghaus size-contrast display, in which a graspable central chip is perceived as smaller when surrounded by large circles, and as larger when surrounded by small circles. The authors reported a clear biasing effect of the surrounding circles when subjects were asked to direct their grasp to the chip that appears larger (or smaller), but little effect upon the grip aperture [104,105]. The conclusion drawn was that, contrarily to perception, action is not affected by the illusion. But this implies a very narrow definition of 'action', specifically the automatic control of some action subroutines, within a wider context in which the intentional directing of the grasping response was influenced by the illusion. Thus, even if the basic result is accepted (see below), the dissociation indicated would be between the automatic control of the grasp and a higher level of control of intentional action.

Second, many have contested the basic result (see [106], for a recent pre-registered re-examination of the immunity of grasping to the Ebbinghaus illusion), and it is certainly the case that the motor system is not, in general, immune to optical illusions. Some illusions can have effects that are identical for perceptual and motor responses (e.g. [107,108]), or even more pronounced for motor responses [109]; the pattern of results obtained may depend critically upon the particular stimulus and response conditions employed, and do not indicate any general dissociation between perception and action responses (e.g. [110–112]). Particular patterns of dissociation that may be observed empirically need to be explained in terms of the particular combinations of cues used in forming different responses.

Third, particular patterns of dissociation cannot be mapped on to the anatomical distinction between dorsal and ventral streams, in the absence of relevant experiments. Coello et al. [113] initiated the exploration of anatomical supports for perceptual and motor effects of visual illusions. According to the prediction stemming directly from the theory of two visual systems, a patient with a bilateral lesion of the dorsal pathway should inevitably differentiate herself from healthy controls and show a similar effect of the illusions on perceptual and motor responses (Fig. 5). In fact, both the perceptual and the motor responses of this patient were totally similar to those of healthy controls free from brain lesions, and this for the size-contrast illusion as well as the two other illusions (sagittal and frontal Roelofs effects). The conclusion validated by this study is that the behavioral dissociation initially observed in healthy subjects cannot be related to the two dorsal and ventral visual pathways, and that the organization of action also depends on other visual pathways. This conclusion completes the following arguments: on the one hand the duplex model is too narrow to

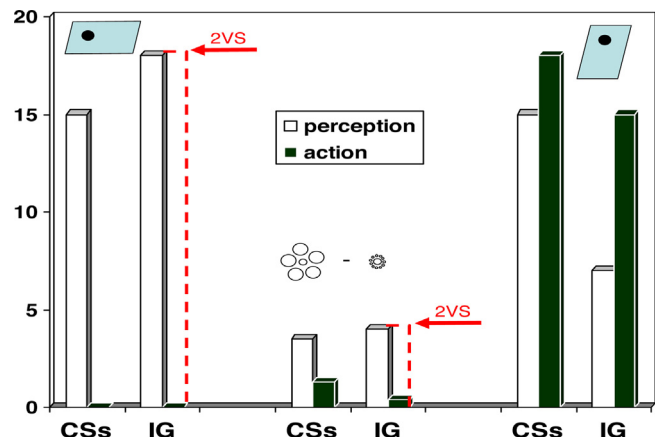


Fig. 5. Perceptive (white) and manual (black) responses to three visual illusions. Visuoperceptive and visuomanual responses of healthy subjects (CSs) were tested in three mock situations. For the Roelofs effect on the frontal plane (on the left side), healthy subjects presented a strong perceptual illusion but no motor error. For the illusion of size-contrast (in the center), the effects of the illusion are greater for the perceptual responses (white) than motor ones (black). Finally, for the deep Roelofs illusion, healthy subjects reveal errors of the same order for the two types of responses. Predictions of the duplex theory for a subject without a dorsal pathway are represented by broken red lines. In reality, performances of a patient presenting with a bilateral lesion of the dorsal pathways were similar to those of controls, for the three illusions tested. None of the situations evaluated yielded an argument in favor of a key role of the posterior parietal cortex in visuomanual responses performed like here in central vision (from [113]).

account for behavioural dissociations and absence of dissociations, and on the other hand the perception itself does not depend solely on the ventral pathway processes (e.g. [114–118]).

2.3. Are there only perception and action?

Another approach to the question of perception-action dissociations as related to the anatomical dorsal/ventral distinction, consists in comparing precisely the perceptual performances of subjects with optic ataxia in the experimental conditions where they show a sensorimotor deficit, i.e. with fixation maintained throughout and all targets presented extra-foveally. The first observation of this type was made in a fortuitous manner during an experiment using delays during which the visual target could be displaced without the knowledge of patients [74]. With each displacement of the targets, pointing movements were initially directed towards the target's first position, suggesting that these subjects acted "with a delay", consistent with the duplex theory. But a side observation during this study was that the two patients were apparently also very poor at detecting target displacements, even when asked to make a perceptual report about whether the target had moved during the delay. Following this observation, we started more formally studying the perceptual responses of patients with unilateral optic ataxia for stimuli presented in their ataxic hemifield. Responses obtained were impaired for the two dorsal-related visual qualities, position and orientation [60].

To meticulously explore the possibility of a deficit common to action and perception, McIntosh et al. [88] adapted the double-step paradigm in a patient presenting with bilateral optic ataxia, requiring either manual pointing responses, or a simple discriminatory button-press to report the detection of target jumps. Visuomotor and perceptual responses were collected for target jumps between different parts of the visual field. The close correlation between perceptual and motor deficits, across the various jump configurations (Fig. 6), strongly suggest that these two deficits result from the same primary functional disorder [56,57].

In conclusion, it seems that the idea of a dissociation between optic ataxia and visual agnosia should be rejected, at least on present

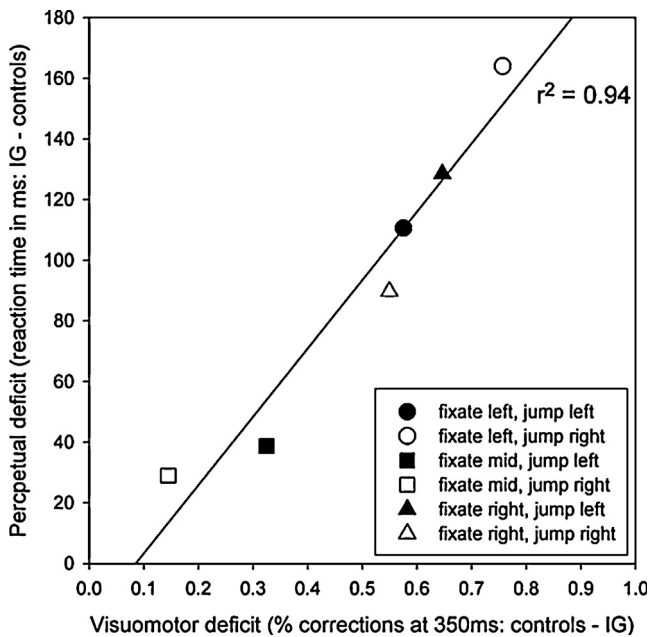


Fig. 6. Correlation between perceptual and motor deficits in optic ataxia. This figure represents visuoperceptive performances (measured by the increased reaction time vs. controls) of patient IG (bilateral optic ataxia) according to her visuomotor performances (expressed in percentage of correction vs. controls). The correlation between these two measures is excellent (from [88]).

evidence. We have also argued that the alleged dissociation between perception and action does not accurately match the experimental conditions used and is far from reflecting the complexity of the entire visual system. It consists only in object recognition and goal-directed action, i.e. only two of the multiple functions of the visual and visuomotor systems. The duplex theory did strongly promote the study of the visuomotor tracking function as an integral aspect of visual processing, but its dichotomy simplified too far the complexity of the anatomical networks, as well as overstating the divisions between visual and visuomotor functions, which might be better described as gradients rather than rifts [4].

3. Rebuilding after the theory

The simplicity of the duplex theory has proven powerfully seductive of scientific and philosophical minds. Countless works were conducted within this theoretical framework, or referenced it. This theory generated few data on the nature of visual perceptual processing, and we saw that the action-dedicated vocabulary was usurped to describe the lower level motor function to which this two visual systems' theory refers. One main contribution of works on this theme has been to refine and even move the frontier between visuoperceptive response and visuomotor response. Goodale and Milner adopted the matching task used by Vighetto [59] and Perenin and Vighetto [55] to discriminate between these two levels. The matching task used a manual response to communicate the conscious perception of a stimulus, so here the visual information processing had a descriptive goal, but the manual response itself was differentiated from the visuomotor task only because the hand was not directed towards the stimulus. This seemingly modest difference in protocol can in fact produce startling differences in performance, revealing that only the action performed directly towards the stimulus could be distinguished from the verbal response. A similar approach could also help differentiate between two very close responses such as locating a tactile stimulus and reaching it [119]. The goal of this distinction was to highlight the specificity of the immediate target-directed

motor response vs. all responses involving an additional mediation between the stimulus and the response, such as a delay, spatial separation, or verbalization [4,120,121].

The comparison between perception, a cognitive function related to consciousness, and visuomotor tracking, a sub-function or module of the sensorimotor organization of action, is not balanced in terms of theoretical 'weight' or complexity. Visuomotor tracking is by nature a smaller functional element, easier to define and isolate for study, which may help explain why most publications dedicated to the two visual systems have focused on this side of the distinction. We want to propose here that this sensorimotor module corresponds in reality to the parietal automatic pilot evidenced in healthy subjects, and in patients with "action blindsight".

3.1. Blindsight in action

The "blindsight" oxymoron represents another interesting neurological deficit to consider in regards to the theoretical framework of dissociations between implicit and explicit sensory processing. Within this neuropsychological condition, three major sub-categories have been proposed: action blindsight, attention-blindsight and agnosopsia (object processing without awareness) [23]. The first studies conducted on patients presenting with cortical blindness following a lesion of the visual cortex, showed that in spite of the amputation of a visual hemifield, some of them retained the ability to orientate their eye [16] or hand [18] towards a visual stimulus presented briefly in that hemifield (see [22]). After it was initially interpreted as a residual sub-cortical visual function, this motor ability was subsequently observed in more complex tasks. For example, we showed that patients with blindsight were able to orientate their hand and adapt their grip aperture to visual objects they could not consciously see [40,122]. Similarly to the patient who presented with visual agnosia, this manual ability was only observed in the conditions of a goal-directed action and not in conditions of visual matching tasks. However, we observed a far greater variability with cortical blindness than in visual agnosia (see [4]), which can be easily explained since the occipital lesions responsible for hemianopia are associated with an alteration of occipito-parietal projections. The neuroanatomical substrate brought up today to explain this implicit sensorimotor function is a system of subcortical projections connecting the superior colliculus to the posterior parietal cortex via the pulvinar (see [23,100]). The blindsight phenomenon and particularly its expression in the context of action, was considered as a strong argument for the dissociation between the dorsal (occipito-parietal) and ventral (occipito-temporal) pathways of the visual system (e.g. [3,13,40,49,123]).

3.2. Parietal automatic pilot

We described earlier the existence of visuomotor tracking independent of conscious perception in the experiment conducted by Prablanc et al. (1986). This tracking allows the hand to reach the position of a target that was moved without the subject's knowledge. Afterwards, a series of experiments studied the degree of autonomy of this visuomotor hand tracking, by specifically analyzing the effects of movement duration on this type of control [53,124]. A green target was presented at the beginning of each test and subjects were requested to point to it under different speed constraints. This target remained still in 80% of the tests, or could jump in an unpredictable manner to the left or right side at the beginning of the movement. In the so-called "position-stop" experimental condition, subjects had to systematically interrupt their movement in response to the target jumps. Thus, the direction of the jump was not relevant for this task. A strict respect

of the instructions to stop would mean that subjects reached the first position of the target when their movement was too quick to give them time to process the disruption, or they succeeded in interrupting their movements. Conversely to these predictions, a very significant number of movements were re-directed to the target's second position. These corrections were made in the direction of the target, in spite of the fact that the subject had not been instructed to follow the target. After having touched the second target, subjects most often expressed a strong feeling of frustration, corresponding to the impression that their hand was not responding properly.

A movement time effect was described on the type of response produced by subjects. In healthy subjects, most corrected movements have the same duration as non-disrupted movements. Because they appear in a limited temporal window, escaping the slower processes of voluntary control, the corrections observed can be presumed to result from an inability to inhibit an automatic process of visuomotor tracking of the arm. This "automatic pilot", activated by default during the execution of the movement, induces subjects to make corrections during a narrow temporal window (about 200 to 300 ms), even if they have not been asked to do so. During a portion of this temporal window we observed that the correction rate produced by subjects in the "position-stop" condition could not be differentiated from the rate produced by subjects in the "position-correction" condition, where they had to correct their movement to reach the position of the second target. These fast movements are in fact corrected by the sole action of the "automatic pilot" of the hand movement independent from attention. Only movements with a duration > 300 ms seem to come under the control of voluntary processes.

The study of movements in one patient (IG) presenting with a bilateral lesion of the dorsal pathway (and thus optic ataxia) evidenced the loss of this automatic pilot, whereas the intentional processes of action control were retained [124]. This observation led to the conclusion that fast movements are controlled by a Parietal Automatic Pilot for which the dorsal pathway constitutes a necessary substrate [125]. Slower movements, lasting more than ~300 ms can additionally come under the influence of intentional motor processes that may be largely independent from the posterior parietal cortex. Patients with frontal lesions, tested in the same task, showed a loss of ability to voluntarily inhibit the automatic pilot and thus by extension performed automatic corrections even for their slower, voluntarily controlled movements [121].

These studies complete the results obtained with blindsight [40], numb-sense [120], and optic ataxia (e.g. [64,74]) to extend the need to take into account a major, invisible, functional property of anatomo-functional networks, the temporal dimension.

4. Conclusions

Scientific theories are differentiated from experimental facts by the clarification they bring to the interpretation of empirical data. It is unavoidable for a theory to escape from the mass of data in order to bring some sense to it, but by leading to more studies it may also generate data incompatible with the theory itself. As incompatible observations accumulate, they may outweigh the theory, and impose a more or less extensive reappraisal and reformulation. At the end of this review, it is important to note that the duplex theory has played this role to the fullest: it generated a large number of studies and results, made popular an unknown scientific field of investigation, and produced predictions that were tested by experiment. Like any scientific theory, it needs to evolve in line with the data. The main challenge of this evolution is to rebuild a more nuanced interpretation, based on the rich, multidisciplinary data (during the proof correction of this paper a relevant paper to this debate was published by David Milner: Milner [126]).

We underlined how the anatomical data were less and less supporting the idea of a simple dichotomy of visual brain organization. Several anatomical data were differentiated within the occipito-parieto-frontal and occipito-temporo-frontal networks (e.g. [49,103,127]). Among those an occipito-parietal pathway involving the V6 and V6a areas, lesional location of optic ataxia [56] has been associated to an automatic processing of the "where" and the "how" [103]. This pathway seems to correspond to the one spared in action blindsight [23], enabling us to propose that optic ataxia and action blindsight represent the negative and positive neuropsychological image of this parietal automatic pilot. Specifically, this proposal suggests that automatic correction of reaching behaviour should be demonstrable in blindsight. Although it is interesting to be able to identify this facet of the visual brain on an anatomical and functional level, this visuomotor function remains only a small element of the human visual and motor organization. In the framework of the duplex theory, all other visual pathways were essentially considered in opposition to this automatic visuomotor pathway, as if they represented in a monolithic manner "the perception". The exploration of the visual brain needs to continue to refine the respective contributions of these other processing pathways for retina information, and identify the networks involved in action programming [74,113,121,128], and perception [96,129]. Further studies should also try to understand the role of attention (or attentions) in these sensory and motor processes [56,130] (Pisella et al. [131]; this issue). But above all we must explore the coordination between perception and action in order to account for the most elaborated functions of the perception-action cycle allowing to elaborate, test and update our internal model of the outside world (e.g. [132]).

Disclosure of interest

The authors have not supplied their declaration of competing interest.

Acknowledgements

Authors would like to sincerely thank Alain Vighetto, Fadila Hadj-Bouziane, Hisaaki Ota and Denis Pélisson for their stimulating interactions for this chapter. This work was supported by Hospices Civils de Lyon, Inserm, CNRS, the university of Edinburgh and Labex Cortex (Labex/Idex ANR-11-LABX-0042).

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