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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

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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.

> *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-

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[*] 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.

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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 geniculo-striate 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 occipito-temporal 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 occipito-parietal 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].

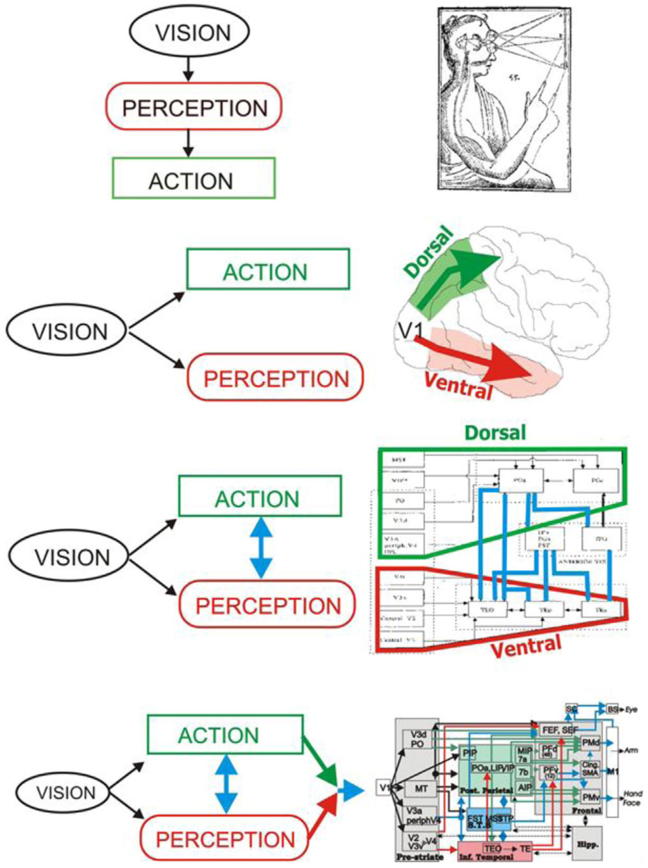

Fig. 1. Representation of the evolution of the visual theories for action. The upper row represents the intuitive concept of vision according to which our actions are preceded by conscious awareness of perception. This serial conception is illustrated by Descartes' drawing. The second row illustrates 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

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