# The Multiple Pathways Model of Visual System. A Review

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## ABSTRACT

Although seeing is commonly experienced as a unitary activity, the scientific description of vision resists such an intuitive account. Both psychologists and neuroscientists are in agreement with the idea that the elaboration of visual information is distributed across several different routes provided with different functions. Importantly, these routes can be mapped onto well-identified anatomical subdivision of the visual system. Crucially, although originally based on the assumption that different visual information are elaborated via different neural channels, such a model is nowadays used as a tool for indicating a common neural basis between action and perception. The present review is aimed at providing a description of how the modular model of visual system has developed from a model where action and perception are considered as segregate to a model where action and perception are considered ass two labels of the same concept.

KEYWORDS: Perception; Action representation; Space representation; Visual pathways; Ballistic pointing.

## Introduction

Traditionally, perception and action have been considered as two separate and serially organized domains. Accordingly, individual first perceive, and then act. To this functional separation is supposed to correspond an anatomical segregation. Parietal cortex and occipital cortex mediate perception while motor cortex mediates action by peripherally sending the order of execute a

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motor plan. This dichotomy has been criticized by authors who have stressed the logical difficulty of considering action and perception as two completely different functions. For example, Sperry has defined perception as "an implicit preparation to respond" (Sperry, 1952).

In more recent times, such a critique has been empirically corroborated by the contribution of several relevant studies. In the present paper I will review the main theoretical steps towards the development of the nowadays accepted modular model of visual system that takes in account such an overlap between action and perception. More precisely, in section 1, I will describe the original model proposed by Ungerleider and Mishkin (1982), where the two visual streams were devoted to elaborate perception. In section 2 I will describe the model described by Milner and Goodale (1995), where one of the two streams was devoted to elaborate perception and the remaining one to prepare action. In section 3 I will focus on the relation between a specific perceptual activity, namely the process of visually localizing an object in the surrounding space, and a specific motor task like approaching to it with a ballistic pointing movement. The reason of choosing ballistic pointing is twofold. First, since it requires only the computation of spatial relation between the hand and the target to be planned, ballistic pointing is here supposed to be the simplest reaching movement. Accordingly, ballistic pointing can be considered as the purest example of how tight the relation between perceptual and motor operations can be. Second, since ballistic pointing is – by definition – a pointing movement, the focus on ballistic pointing makes this paper fit with the general aim of this volume, which is aimed at discussing pointing. In this sense, however, it should be noted that while other papers in this volume are related to the analysis of pointing behavior in general, this paper is focused on the particular category of ballistic pointing. While in the former case pointing is aimed at solving communicative/declarative functions, the latter kind of pointing is aimed at reaching targets. Finally, in section 4, I will describe a model of the visual system which is articulated in three streams, that can provide perception and action with a common basis.

## 1. Ungerleider and Mishkin: (one) vision for (two kinds of) perception

Although seeing is commonly experienced as a unitary activity, the scientific understanding of human vision has radically challenged such an intuitive view. Nowadays, both neuroscientists and psychologists consider that the processing of visual information is distributed across several different routes which eventually reach different functional outcomes, and that these processing routes can be mapped onto well-identified anatomical subdivisions of the visual system. This general idea finds support in the anatomical organization of the visual system in all the vertebrate species that have been studied over the last hundred years, where the retina projects onto many different cortical and subcortical relays. For example, Ingle (1982) has demonstrated that in amphibians prey-catching behavior is mediated by a particular set of retinal projections onto the optic tectum, while another visual operation like the visual control of the external environment is mediated by a second set of retinal connections with pretectal nuclei. Similarly, Schneider (1969) has demonstrated that a mammalian with a cerebral lesion located in the superior colliculus is able to discriminate vertical from horizontal objects, but could not use the visual information coming from the external environment for navigating in it. Conversely, a second animal with a damaged visual cortex could efficiently move in the environment but not do recognition. Since these evidence came from the study of animals provided with a little visual cortex, this model of visual system stressed the contrast between a first visual processing controlled by peripheral/subcortical structures and a second visual processing controlled by central/cortical structures.

The first step from this idea to the nowadays accepted model of the visual system was due to Ungerleider and Mishkin (1982), who shifted the core nucleus of this dualism entirely at a cortical level. More precisely, they studied the selective effects of some cortical lesions of monkey brain on two different behavioral tasks. In the first task the monkey was required to discriminate between two covered wells on the basis of their proximity to a landmark. The second task consisted in requiring the monkey to discriminate two objects with different features like colors, shapes and textures. Interestingly, the performances of the monkeys varied according to the localization of the brain injuries: a lesion in the posterior parietal cortex severely impaired the animal in the landmark task but not in the object-discrimination task, while a lesion selective to the inferotemporal cortex induced the opposite impairment.

Accordingly, Ungerleider and Mishkin (1982) identified two different cortical pathways involved in the elaboration of different features of the observed objects. The former neural channel is centered on area V4 and is aimed at transmitting information about object properties to the inferotemporal lobe. For this reason, such a stream – located ventrally through the cerebral cortex – has been defined as the "what" stream of vision. Differently, the other cortical channel is centered on area MT/V5 and is aimed at transmitting information concerning the spatial position of the observed objects. Accordingly, this channel has been labeled as the "where" stream of vision. Moreover, since this second pathway is located dorsally in the cerebral cortex, it usually indicated as the dorsal stream of vision.

Crucially, in this model the two streams are not supposed to be different with respect to the function they have to solve. Indeed, in the experiment reported by Ungerleider and Mishkin (1982), monkeys were tested only in perceptual task, where monkeys were required to discriminate which of two objects is located closer to a visual landmark by performing an irrelevant motor task like pressing a lever. Accordingly, the authors hypothesized that both the streams were supposed to be aimed at elaborating perception, so that the only difference assessed between them was related to the kind of perceptual information – descriptive vs. spatial – transmitted by each of the two streams.

The pivotal ideas that inspired this early model, namely that vision is not a unitary process and that different visual information are processed along different cortical pathways, are nowadays largely shared. However, the particular claim that these pathways are both devoted to the elaboration of perception has been strongly criticized during the last decade of the 20th century, thus leading to a model characterized by a dualism between perception and action.

## 2. Vision for perception Vs vision for action

At the beginning of 1990's, the claim that *both* the ventral stream and the dorsal stream are aimed at providing a perceptual representation of the external environment, has been radically questioned by a series of studies (Goodale & Milner, 1992; Milner & Goodale, 1995) conducted on a set of double dissociations provoked in humans by selective brain lesions. A double dissociation is constituted by a couple of disturbances that are a) provoked by distinct/independent lesions and b) associated to opposite behavioral effects. In such a case, while lesion 1 induces an impairment in the first behavioral task by leaving unaffected the second task, lesion 2 provokes an impairment in the second task by leaving unaffected the first task. Stated the difficulty of performing single-cell studies in humans, double dissociations constitute a very powerful investigatory tool for neuropsychological research in humans.

The topic of how the human visual system is supposed to be articulated is an exemplar case of such a relevance.

Lesions located in the dorsal stream provoke optic ataxia (De Renzi, 1982; Perenin & Vighetto, 1988). Typically, patients suffering from optic ataxia are impaired in reaching – via the performance of a ballistic pointing movement – and grasping for visual objects with both hands in their contralesional visual field. Moreover, they usually show a lack of anticipatory hand shaping during grasping movements and a difficulty of coherently orienting spatial attention. By contrast, they are almost normally able in identifying and recognizing surrounding objects. The clinical case reported by Milner and Goodale (1995) was in line with these general characteristics. Indeed, their patient was capable of recognizing common objects when presented either physically or by an image, but was severely impaired when an effective interaction with the objects was required. For example, when the task consisted in reaching for a small wooden block that varied in size from trial to trial, there was little relationship between the magnitude of the grip aperture and the effective size of the block. Not only did the patient fail to show normal scaling of the grasping movement, but he also made more adjustments than normal subjects. According to these results, Milner and Goodale (1995) suggested that damage to the parietal lobe can impair the ability of using information about the size and orientation of an object to control the hand aperture during a grasping movement, even though the very same information can still be used to identify and describe the target objects.

The second clinical case that has inspired the Milner and Goodale's model (1995) was the case of patient D.F. an old woman that after a damage on the ventral stream of vision suffered from visual form agnosia (Farah 2004; Himmelbach et al. 2012). Contrarily to optic ataxia, visual agnosia affects the conscious recognition of an observed object while preserving the capacity of efficiently interacting with it. For example, D.F. showed a great difficulty in indicating the orientation of an observed letterbox. Nevertheless, she was normally efficient in reaching out and in appropriately placing her hand. An analogous set of responses was recorded with regard to his ability of recognizing the size and shape of observed objects. When presented with a pair of rectangular blocks of the same or different dimensions, she was unable to distinguish between them. However, when the patient was asked to simply reach out and pick up the block, the grip aperture changed systematically in agreement with the width of the object, just as in normal subjects. Broadly speaking, D.F. revealed herself as able to scale her grip to the dimension of the target object, even though she appeared unable to perceptually elaborate those dimensions.

To sum up, such data suggest that damage to the dorsal stream of vision can impair the ability to use information about the size, shape and orientation of an object to control the hand during grasping movements, even though the very same set of information can be used to classify the observed objects. Conversely, damage to the ventral stream can induce an impairment in the capacity of recognizing observed objects while preserving the capacity of planning coherent interactions with them. In line with these considerations, Milner and Goodale (1995) proposed to relate the ventral stream to the processing of those visual information that are useful for the elaboration of perception, and the dorsal stream to the processing of those visual information required by the visual control of goal-directed movements like pointing movements. In analogy with the Ungerleider and Mishkin's model, Milner and Goodale (1995) labeled the ventral stream as the "what" stream of vision. However, since the dorsal pathway was supposed to be aimed at controlling actions rather than at simply providing general spatial information, the dorsal stream was labeled as the "how" stream, rather than as the "where" stream. It should be noted that in this classification, information concerning the spatial features of observed objects are not treated as useful for building a perceptual image of it, but as an expression of how the object can be reached. In other words, in this conceptualization, it doesn't matter where the target is, but only how it can be reached by the observing subject. Such a theoretical shift is probably due to the discovery of the existence of visuo-motor neurons in the motor cortex of monkey brain. Rizzolatti et al. (1988) showed that premotor area F5 of monkey brain, a motor area involved in controlling manual movements (Rizzolatti & Luppino, 2001), contains not only motor dominant neurons, but also neurons (the so-called canonical visuo-motor neurons) that discharge both during the act of grasping a tridimensional object and during the simple fixation of the very same target. Crucially, the visual specificity of F5 neurons is congruent with their motor specificity, so that these neurons respond to the act of performing a particular grasping and to the presentation of a tridimensional object compatible with such a grasping and not to the visual presentation of targets incompatible with it (Murata et al. 1997). To observe an object can thus be considered as a potential way of interacting with it, so that its spatial position is coded in terms of a potential ballistic pointing movement (see section 3 for further debate).

Further evidence for this updated dual model of vision comes from the investigation of humans responses to illusory displays. For example, in front of a Titchener disk illusion, subjects judged that the diameter of a disk is larger when the disk is surrounded by an annulus of smaller circles than when it is surrounded by an annulus of larger circles. However, when subjects were asked to grasp the central disk, the measurement of their maximum grip aperture showed that the visuomotor computation of the target is not affected by the illusion (Haffenden et al. 2001).

## 3. Space representation and ballistic pointing movements

Recent theories on motor control claim that the central nervous system control bodily movement by elaborating some action models that synthesize the motor commands required to execute the selected action (Blakemore et al. 2002; Haggard, 2005). To do so, the pragmatic characteristics of the perceived target object must be computed and transformed in motor terms as action possibilities, i.e. affordances, via a series of sensorimotor transformations. Since this review is aimed at considering the relation between vision and action, in the present paper I will focus only on visuomotor transformations. However, to compute a set of affordances is not sufficient to enable the acting subject to perform a successful interaction. Indeed, since no interaction can be performed at distance, every successful interactive operation requires as a preliminary condition that the target object is localized and reached. Crucially, since ballistic pointing requires only the computation of the spatial relation between the pointer's hand and the target object, here I suggest to consider ballistic pointing movements as the simplest form of reaching movements. Although commonsense judgments describe localizing something in the surrounding space and reaching it as two radically different processes two decades of experimental data have largely showed that such an intuitive view should not be accepted as valid. Since the former process is supposed to be purely perceptive and the latter purely motor, to clearly highlight the reason of such an inconsistency will provide a first argument in favor of the idea according which perception and action should be considered as bound together.

The key element of the reasoning discussed here is the existence, in the monkey brain, of a parieto-frontal neural network involved in the control of proximal reaching movements as the one involved in defensive behavior, namely the VIP-F4 network. Crucially, these reaching movements largely consist in ballistic pointing movements directed to specific position in space.

A parietal area generally emphasizes sensory or representational processes or attention. By contrast, a motor area generally emphasizes motor output. The point is that in the case of the neural network involving VIP and F4 these functions overlap extensively, so that no clear distinction can be made between a purely sensory area and a purely motor area. Area VIP, which is located in the dorsal stream of vision, is a region of convergence of multimodal sensory input. Accordingly, most neurons in VIP are multimodal, responding to visual and tactile stimuli. Tactile receptive fields of these neurons are distributed on the head, chest, arm and on the hand (Colby et al. 1993; Duhamel et al. 1998). Visual receptive fields are spatially anchored to the corresponding tactile receptive field, so that the visual properties of these neurons are independent from the direction of gaze (Duhamel et al. 1997). More recently, Schlack et al. (2002) have reported that a high percentage of neurons in VIP responded also to auditory stimuli, thus suggesting that VIP neurons encode the locations of objects in a multimodal fashion that integrates vision, touch and audition.

However, recent data show that area VIP is not involved only in perceptual localization, but also in a motor activity like the planning of ballistic movements. For example, the electrical stimulation of neurons in VIP evokes defensive-like behavior whereas simulation of surrounding areas does not (see Stepniewska et al. 2005 for a review). More precisely, this defensive behavior largely consists in a series of ballistic pointing movements that a) were aimed at reaching the portion of visual space occupied by the visual receptive fields of the stimulated neurons and that b) resembled the defensive movements spontaneously evoked as reactions to tactile stimulation of the monkey's bodily surface.

Odological studies have shown that the parietal area VIP is strongly connected with the motor area F4 (Gentilucci et al. 1988; Rizzolatti & Luppino, 2001). The dorsal half of area F4 is occupied by the so called polysensory zone (PZ), that contains neurons with multimodal properties (Graziano & Gandhi, 2000). As neurons in VIP, neurons of PZ respond to visual, tactile and auditory stimuli (Fogassi et al. 1996; Graziano et al. 1999). Additionally, neurons in PZ have tactile receptive fields located on the head, the chest and the upper limbs, and their visual receptive fields are spatially anchored to the corresponding tactile receptive field (Graziano & Gross, 1998). Electrical stimulation of sites within PZ produces a constellation of movements of the bodily part where the tactile receptive field is located (Cooke & Graziano, 2004a; Graziano et al. 2002). Crucially, stimulation of non-polysensory sites around PZ does not evoke such movements, thus suggesting a specific role of PZ in eliciting defensive behavior like reaching – as well as pointing – movements. Some additional data come from a study where Cooke and Graziano (2004b) disinhibited neuronal activity of PZ by injecting bicuculine and inhibited the activity of PZ by injecting muscimol. After the injection of bicuculine, not only the local neuronal activity increased, but the neurons also began to fire in intense spontaneous bursts of activity, followed by the standard set of defensive-like behavior. Additionally, bicuculine also exaggerated the monkey's actual defensive reaction to a stimulus. By contrast, the injection of muscimol provoked a reduction in the muscular activity associate to defensive reactions.

Taken together, these neurophysiological data argue against the commonsense intuition that treats the perceptual task of localizing an object in the surrounding space and the motor activity of approaching to it with a ballistic pointing movement as two completely distinct processes. Data concerning the VIP-F4 network, namely a network connecting a parietal area located in the dorsal stream of vision with the motor cortex, indicate the existence of a neural basis which is common to both processes, thus suggesting an analogy between observing an object in a certain position in space and reaching it with a pointing movement.

## 4. The triadic model: how to bind together perception and action

In the hands of Jacob and Jeannerod (2003), the distinction between two visions, the former for perception and the latter for action, become the distinction between two different *ways of seeing*. On the one hand, by processing iconic information concerning qualitative features of surrounding objects, the ventral stream has been defined as the channel of the semantic vision. Its function consists in elaborating information useful for the recognition and classification of what is observed, that are at the service of the elaboration of a subject's belief. On the other hand, by permitting the elaboration of visuo-motor transformations, the dorsal stream of vision becomes the channel of the pragmatic vision. In such a dualism, while the semantic vision is supposed to be at the service of the elaboration of subject's beliefs, the pragmatic vision is supposed to be at the service of promoting an agent's intention (Jacob & De Vignemont, 2010).

Although at a first sight such a dualism seems very close to the model outlined by Milner and Goodale (1995), a deeper analysis shows a significant difference between them. Indeed, while Milner and Goodale explicitly moved from the conviction that the two streams evolved because perception and action require quite different transformation of visual signals, the model proposed by Jacob and Jeannerod (2003) does not rely on this premise. In this sense, this model represents a significative step towards a model of visual system that can take into account a common basis, instead of a radical opposition, between perception and action.

However, the most important argument for a modular model of the visual system capable of binding together perception and action has been provided by Rizzolatti and Matelli (2003) at the beginning of the 21th century. By moving from anatomical and odological studies conducted on monkey brains, the authors have first challenged the idea that the visual streams are only two in number and, second, used these data for providing a new conceptual interpretation of the above described model proposed by Milner and Goodale.

More precisely Rizzolatti and Matelli (2003) proposed to subdivide the dorsal stream in two functionally different functional pathways: the dorso-dorsal stream and the ventro-dorsal stream. The former pathway is formed by area MIP of the superior parietal lobule, by area V6 and by area V6A. Its major function consists in permitting an "on line" control of performed actions, and its damage leads to optic ataxia. Basically, it overlaps with the classical "how" stream described by Milner and Goodale (1995). The ventro-dorsal pathway is formed by IPL and by area MT. Crucially, while lesions to the dorso-dorsal streams induce optic ataxia, damages on the ventro-dorsal stream provoke in humans ideomotor apraxia, that induces a motor deficit with a dissociation between voluntary and automatic behavior (De Renzi & Faglioni, 1999). Briefly speaking, a subject suffering from ideomotor apraxia is able to perform actions in the presence of the appropriate context, namely in the presence of the target object, but is unable to replicate the very same movements following an explicit command, whether verbal or not.

Additionally, electrophysiological studies conducted on monkey brains, have driven to the conclusion that in contrast with the dorso-dorsal stream, the ventro-dorsal stream is also involved in a) the elaboration of goal directed ballistic pointing movements and b) in the organization of manipulative behavior, like grasping, involving the target object. Ballistic pointing movements, to be efficiently performed, require the computation of the target position in the term of how the hand should be moved in order to reach the target object. As stated in section 3, such a motor transformation is computed by the "reaching circuit" VIP/F4. Interestingly, lesions of area VIP provokes in monkey a disturbance named neglect (Rizzolatti et al. 1983), which induces the tendency of ignoring the contralesional visual hemispace. Crucially, when neglect is mild, motor deficits are absent or at least very weak, thus suggesting that neglect has a perceptual nature.

Manipulative behavior like grasping, to be efficiently performed, require that the size and the shape of the target object are computed in a motor format. The cortical area that plays a pivotal role in processing these transformations, is the area AIP (Sakata et al. 1994), namely an area of the parietal cortex located in the ventro-dorsal stream. Area AIP is reciprocally connected with the prefrontal area F5 (Rizzolatti & Luppino, 2001), thus constituting a "grasping network" where visual information concerning size and shape of observed objects are translated in appropriate motor schemata. This view has been supported also by inactivation studies concerning these two areas (Gallese et al. 1994; Fogassi et al. 2001). According to these data, the ventro-dorsal stream seems to be completely aimed at planning action.

However, area AIP uses information from area F5 also for action understanding. Indeed, F5 contains not only canonical visuo-motor neurons, also another class of visuo-motor neurons: mirror neurons (Di Pellegrino et al 1992; Rizzolatti et al. 1996). The defining functional property of mirror neurons consists in that they discharge both when a certain goal directed movement is performed in first person and during the observation of the very same action performed by another agent. Differently from canonical visuo-motor neurons, mirror neurons do not respond to the object presentation, and the sight of a mimed action usually do not provokes a mirror response (see Rizzolatti & Craighero, 2004 for a review). This is not the right place for an exhaustive description of the theoretical implications of mirror neurons' activation. On the contrary, here it is sufficient to note that, stated their functional properties, mirror neurons are supposed to play a pivotal role in action recognition in monkeys and humans. Briefly speaking, such a comprehension – that is motor rather than inferential – is based on an implicit simulation of the observed action in terms of an activation of the observer's motor system.

Taken together, these findings show that ventro-dorsal stream is involved in two different kinds of processes. On the one hand, as demonstrated by data concerning the "grasping network", it is aimed at elaborating the visuo-motor transformations useful for planning coherent and efficient actions. On the other hand, as demonstrated by the presence of the "reaching network" and by the mirror properties of the grasping network, the ventro-dorsal pathway is involved in *both* perceptual processes like spatial representation (Rizzolatti et al. 2000) and action recognition (Rizzolatti & Sinigaglia, 2008). In this sense, the ventro-dorsal stream is involved in both perceptual and motor activities, thus constituting a neural substrate useful for binding together action and perception.

## Conclusion

The data reviewed in this paper indicate that action and perception are two closely related processes. More precisely, spatial abilities like space representation and action recognition depend on the activity of the same areas that are involved in the control of spatial aspects of motor behavior and in the elaboration of the motor plans for relative first-person execution.

Finally, it should be noted that as proposed by Vyigotsky (1982), the ability of indicating something with the hand is supposed to be derived from the capacity of planning/executing ballistic pointing movements. Accordingly, I see no reasons for excluding that the relation between localizing and indicating something should be treated as analogous to the relation between localizing and reaching something. However, the effective extent of such an analogy is still a matter of debate, since up to now studies have focused only on the relation between observation and the reaching-side of the pointing. In this sense, this paper is also aimed at providing arguments for future empirical researches. For example, it could be interesting to test patients from optic ataxia in tasks where subjects are not required to reach for an object but only to indicate it with their index finger.

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