

## Dorsal and ventral streams across sensory modalities

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**Abstract:** In this review, we describe the current models of dorsal and ventral streams in vision, audition and touch. Available theories take their first steps from the model of Milner and Goodale, which was developed to explain how human actions can be efficiently carried out using visual information. Since then, similar concepts have also been applied to other sensory modalities. We propose that advances in the knowledge of brain functioning can be achieved through models explaining action and perception patterns independently from sensory modalities.

**Keywords:** sensorimotor integration; action control; perception; dorsal stream; ventral stream; cross-modal

### 1 Introduction

When we feel thirsty, we need to get the glass of water on the dining table, avoiding the obstacles between our hand and the glass, and when we finally grasp the glass we have to bring it to our mouth to drink it. Human actions are often directed towards objects, as in this example, and their final aim is to interact with these objects in the external world to achieve an internal goal.

The aim of this review is to highlight how models of action and perception, first developed to explain the visual guidance of hand movements<sup>[1,2]</sup>, have also been fruitfully applied to other sensory domains, such as audition and touch. Even though some of these “non-visual” action and perception models are still at their beginnings and need further experimental investigation, these first attempts to create a general framework are promising. The models we summarize here suggest that, possibly, the ideal scenario to understand the brain is to consider a perceptual-brain and

an action-brain that, independently from the sensory modality, allow us to respectively recognize a glass of water and to grasp it when we are thirsty.

### 2 Dorsal and ventral streams in the visual domain

Vision has often been compared to the act of “taking a picture of the world”, but research over the past 25 years has emphasized that visual processing involves constructing an internal representation of the external world aimed at interacting with it, rather than being only a passive registration<sup>[1-3]</sup>. Thus, the final goal of vision is not only to recognize objects in the surroundings, but also to translate the visual attributes of an object into the appropriate information used to compute motor outputs for a successful action<sup>[3]</sup>.

The notion that vision is not a unitary process is, however, not recent. Dissociations within visual processing have been observed since the second half of the twentieth century. In rewired frogs, Ingle illustrated segregation between a tectal system that mediates prey-catching, and a pretectal system, for visually-guided locomotion<sup>[4]</sup>. Schneider<sup>[5]</sup> was one of the first scientists to propose a

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distinction between object localization and identification, which subsequently persisted in the description of the functional organization of the visual system<sup>[3]</sup>: Schneider described a ‘dual visual system’ in which retinal projections were deputed to stimulus localization, while the geniculostriate system was responsible for stimulus identification<sup>[5]</sup>. Lately, Ungerleider and Mishkin (1982) developed a “what & where” model, identifying a dorsal stream (posterior parietal cortex) and a ventral stream (inferior temporal lobe)<sup>[6]</sup>. Evidence for this type of dissociation was derived from behavioral experiments on monkeys with lesions to the inferotemporal cortex or the posterior parietal cortex: while the former lesion caused errors in visual pattern recognition, the latter impaired animal performance in tasks requiring the use of a ‘spatial landmark’<sup>[6]</sup>.

However, a model in which disturbances in spatial perception are assumed to be unitary does not exhaustively explain the findings from neurologically impaired subjects. Lesions to the lateral occipital cortex, for instance, have been demonstrated to affect the perception of objects while leaving intact the ability to perform actions towards them<sup>[7]</sup>. Features such as shape and orientation, which are not perceived, are nonetheless used to perform a movement in space<sup>[1,3]</sup>. Similarly, neglect patients, who cannot perceive an object located in the contralesional hemifield, can nevertheless avoid it while performing a grasping movement<sup>[8]</sup>. Assuming that spatial perception (i.e. the decoding of an object orientation) is totally impaired would not predict such a dissociation between abilities (object orientation misperception *versus* orientation-adapted finger position during grasping movements)<sup>[3,7]</sup>.

Consequently, the earlier model of a stream devoted to the identification of stimuli and a stream involved in spatial localization<sup>[6]</sup> has been modified in recent years, considering a different frame of reference: the action and perception frame<sup>[1]</sup>. In this conceptual perspective, instead of considering inputs, the focus is shifted to the outputs of the streams<sup>[1]</sup>: perception of the external world has the final goal of establishing an interaction with environmental stimuli rather than of providing a description of them.

Therefore, perception of objects is seen as a complex

chain of transformations of visual stimuli, and if the goal is to perform an action, it involves the activation of a dorsal visual stream devoted to the programming and online control of motor acts<sup>[1]</sup>. For instance, reaching and grasping a glass requires, among other elements, coordination between fingers, hands, and eyes as well as the computation of glass size, its distance from the hand and its weight. Instead of only providing the spatial localization of object, the dorsal stream computes more complex features of the environment: it elaborates the object position in terms of egocentric coordinates<sup>[9]</sup>, as movements need to be planned according to a dynamic world in which targets and obstacles are moving<sup>[10]</sup>; furthermore, the dorsal stream acts in an automatic fashion, characterized by unawareness, and very rapidly, to provide efficient actions<sup>[11]</sup> and online movement control<sup>[12]</sup>. On the other hand, the ventral stream brings awareness information of objects to identify and memorize them<sup>[1]</sup>. Consequently, the ventral stream is not concerned with object orientation changes<sup>[13]</sup> but has a modulation in activation if the subject’s task is to discriminate between object sizes<sup>[14]</sup>.

Much evidence for this new interpretation comes from a study on patient D.F. (Table 1), whose brain was damaged by carbon-monoxide-induced anoxia<sup>[2]</sup>. Although showing a severe form of visual agnosia following brain damage, D.F. was still able to correctly pick up objects that she could no longer identify (for example, opening her fingers correctly to grasp a block without being able to discriminate its dimensions)<sup>[7,15,16]</sup>. D.F. showed quite diffuse brain damage, involving a region now known to be fundamental in visual recognition, the lateral occipital cortex, while her primary visual cortex was largely spared<sup>[17]</sup>. Patients with lesions in the superior regions of the posterior parietal cortex, such as those with optic ataxia (Table 1), show a behavioral pattern opposed to that of D.F.: difficulties in reaching visually-presented objects, but spared perception<sup>[1,3,18]</sup>. Other evidence in favor of a dorsal stream devoted to action control comes from blindsight<sup>[1]</sup> (Table 1), a neurological syndrome due to extended lesions of the primary visual cortex, causing cortical blindness for part of the visual field. This blindness, usually investigated

**Table 1. Summary of neurological cases as a function of the stream affected by the lesion. Only visual and somatosensory modalities are presented, as no clear patient data are yet available for the auditory domain**

Perception – Ventral stream			
Sensory modality	Reference frame	Disease	Lesion
Visual	external	visual agnosia	lateral occipital cortex - patient D.F.
	external	blindsight	primary visual cortex
Somatosensory	external	tactile agnosia	posterior parietal cortex, insula, retroinsular cortex
	internal	body image impairment	infarction of supply area of left middle central artery - patient J.O.
Action – Dorsal stream			
Sensory modality	Reference frame	Disease	Lesion
Visual	external	optic ataxia	superior regions of the posterior parietal cortex
Somatosensory	external	tactile apraxia	posterior parietal cortex
	internal	body schema impairment	lesion in right central posterior lateral nucleus - patient K.E.

“External” refers to sensory processing information concerning objects; “internal” refers to processing pertaining to the body.

through perceptual reports (“Can you see this light?”), is nonetheless accompanied by a pupillary reflex and galvanic skin responses to the visual stimulus<sup>[19]</sup>. More importantly, in blindsight, visually-guided movements are preserved even though the patients cannot identify the objects they reach<sup>[20,21]</sup>.

Nowadays, neuroimaging studies have provided evidence for further division of “sub-streams” inside the two major action & perception streams. It has been proposed that inside the dorsal stream there may be diverse circuits mediating different components of movement control<sup>[22-24]</sup>. For instance, a dissociation has been suggested between a dorsomedial stream, which is automatically involved in the processing of grasping visuospatial parameters, regardless of viewing conditions or object characteristics, and a dorsolateral stream that integrates perceptual information processed in the ventral stream into the prehension plan for adaptation of motor behavior to the current conditions<sup>[22]</sup>. Another example is from the differential activations found in the parietal cortex for arm transport and grip formation in reach-to-grasp action, which confirm Jeannerod’s dual channel hypothesis<sup>[25]</sup>. Although all are part of the dorsal stream, the superior parieto-occipital cortex and the rostral superior parietal lobule are devoted to the transport com-

ponent, while the anterior intraparietal sulcus bilaterally and the left ventral premotor cortex are specialized for the grip component<sup>[23]</sup>. Nevertheless, the conceptual division between the dorsal and the ventral streams remains valid and useful for understanding the brain’s relation with the environment, thanks to the great amount of evidence derived not only from the dissociation between optic ataxia and visual agnosia but also from studies on healthy subjects<sup>[3]</sup>.

### 3 Dorsal and ventral streams in the auditory domain

The auditory and visual systems have many features in common. For instance, rods and cones in the visual system and hair cells in the auditory system all release transmitters instead of firing action potentials; the medial geniculate nucleus of the thalamus is a close neighbor of the lateral geniculate nucleus, involved in visual processing; and finally the inferior colliculus is similar in location and function to the superior colliculus<sup>[26]</sup>.

With the great anatomic similarity between the two systems, it has therefore been proposed that their functional organizations could also be similar<sup>[27-30]</sup>. Rauschecker and Tian have developed a model for a dorsal/ventral stream

dissociation in auditory processing, domain-specific for spatial ('where') and non-spatial ('what') information<sup>[28]</sup>, inspired by the vision field<sup>[2]</sup>. In this model, a 'belt' area surrounds the primary auditory cortex and is bordered by a 'parabelt' area<sup>[27]</sup>. The 'belt' and 'parabelt' areas respond more to complex auditory stimuli, like vocalization and bands of noise, while the core area, namely the primary auditory cortex (A1), responds to simple stimuli. Beginning at the level of the belt area, caudal regions are sensitive to sound localization, while rostral regions are not<sup>[32]</sup>. This "what & where streams" hypothesis is supported by previous electrophysiological studies on *Rhesus* monkeys, revealing a tonotopic organization of auditory areas. A rostral region, named area R, shares its borders with A1 in its low-frequency region, while a caudal area (CM) shares its borders with A1 in its high-frequency region. These two areas appear to be mirror-symmetric with respect to A1<sup>[28]</sup>: while A1 and area R receive inputs from the ventral part of the medial geniculate nucleus (MGN), CM receives its inputs from its dorsal and medial parts; inputs from the ventral part of the MGN reach CM only through A1. In *Rhesus* monkeys, A1 and R work in parallel, while CM information processing appears to be serial<sup>[28]</sup>.

Recently, a number of studies have been conducted to confirm the presence of a "what & where" auditory system also in humans<sup>[30,33-35]</sup>. Several studies behaviorally explored the link between the sound of objects and their features, such as shape and size, focusing on perceptual judgments<sup>[37-40]</sup>. Those few studies exploring the link between auditory processing and action control have highlighted that touch-related sounds, produced when an object is manipulated in the hand, can be used to infer object properties that are useful for manipulation<sup>[41]</sup>; moreover, impact sounds, generated when an object is placed on a surface, allow subjects to estimate the object size to guide grasping movements in the absence of vision<sup>[42]</sup>.

Taken together, these lines of evidence strongly suggest that the dual-route pathway of visual information processing also exists for the processing of auditory information. However, further studies should make efforts to develop more homogeneous experimental paradigms, as

the present results are a mixture of "what & where" (referring to the Ungerleider and Mishkin's model)<sup>[6]</sup> and "action & perception" (in this case adopting Milner and Goodale's distinction)<sup>[1,2]</sup> theories and paradigms. Moreover, future research also needs to address the complicated question of stream cross-talk, a topic neglected in auditory action and perception research.

#### 4 Dorsal and ventral streams in the somatosensory domain

Just as for the visual and auditory domains, somatosensory perception has also been recently regarded as a process allowing representation of external stimuli with which humans have to interact rather than being only a passive registration<sup>[1,2]</sup>.

Consequent to this change of viewpoint, Dijkerman and De Haan<sup>[43]</sup> proposed a two-route model for the somatosensory system, based on a distinction between perception-centered and action-centered processes. Importantly, this model specifically concerns touch discrimination and proprioception and does not yet incorporate nociception, temperature or other somatosensory-related functions. It has also to be noted that a division of labor between "what" and "where" pathways in touch had already been proposed<sup>[44,45]</sup>, but Dijkerman and De Haan<sup>[43]</sup> are the first to systematize the available knowledge in a coherent theoretical frame.

The tactile perception-ventral stream is thought to originate from secondary somatosensory cortex (SII) and project into the posterior parietal cortex (PPC) and the insula, allowing haptic/tactile object recognition; this stream contains a static representation of the body, available to consciousness, and allows an integrated sense of one's own body in a dynamic environment (corresponding to the classical concept of body image<sup>[47,48]</sup>). Specifically, the right inferior PPC is thought to be specialized in spatio-temporal integration of conscious tactile perception and object recognition<sup>[43]</sup>. It has to be noted that the term "perception" used in this model refers to the final point of a recognition process and to a conscious experience, rather than to perception of physical aspects as classically used in the visual science<sup>[49]</sup>. The tactile action-dorsal stream, on

the other hand, is supposed to send efferences from SII to the PPC, providing information essential for exploratory hand movements toward objects. The action-dorsal stream is also responsible for the construction of a dynamic representation of one's own body (known as body schema<sup>[46-48]</sup>), through tactile and proprioceptive information.

Like the visual and auditory correspondences, the tactile perception and action streams are not encapsulated, but rather cross-talk<sup>[49]</sup>: information provided by one stream can be communicated to the other through the anterior intraparietal area (AIP). In this model, it is specifically assumed that the AIP plays a crucial role as "interlocutor" between (insular) perceptual and (parietal) action-related processes, since often exploratory movements are necessary to recognize an object<sup>[43]</sup>. Interestingly, in the macaque visual dorsal stream AIP is concerned with motor planning, such as wrist orientation for grasping movements<sup>[50-52]</sup>, and the human homologous AIP appears to be involved in object size processing when this feature is relevant to grasp planning<sup>[14]</sup>. Thus, in the visual dorsal stream, the AIP does not seem to mediate processing between the two streams. Nevertheless, it has been demonstrated that the AIP has major direct connections with the inferotemporal cortex, the superior temporal sulcus, the middle temporal gyrus, the premotor area F5 and prefrontal areas 46 and 12<sup>[53]</sup>, supporting Dijkerman and De Haan's assumption<sup>[43]</sup> on at least the tactile modality<sup>[53]</sup>.

Taking for granted a constant interaction between the somatosensory streams, Dijkerman and De Haan hypothesize that deficits in one stream can affect the other, but also that a selective compromise of one of the two can take place<sup>[43]</sup>. Even though few studies of pure selective deficits in tactile object recognition or exploratory hand movements have been reported, those described in the literature support a dissociation between tactile agnosia and tactile apraxia (Table 1). Tactile agnosia is a condition in which an object cannot be recognized through exploratory hand movements, in the absence of more basic somesthetic dysfunctions<sup>[57,58]</sup>. Tactile apraxia, on the other hand, is characterized by an isolated disturbance of hand movements used to interact with objects, while movements that do not

require an interaction with an object, repetitive movements or gestures, are preserved<sup>[59]</sup>. These two neurological deficits are the behavioral correspondents of a selective lesion in one of the two streams<sup>[43]</sup>. When the target of the action is an external object, tactile agnosia is a specific deficit of the perception stream, since solely tactile object recognition is impaired<sup>[43]</sup>; conversely, tactile apraxia directly refers to an action stream deficit because hand movements for object exploration are impaired. This dissociation between tactile agnosia and tactile apraxia nicely parallels the distinction between visual agnosia and optic ataxia that concur with blindsight data in the formulation of the action and perception streams in the visual domain.

A paradigm that proved to be effective for investigating the dual-route processing of touch in normal subjects is the rubber hand illusion (RHI)<sup>[60]</sup>. The RHI is a phenomenon in which a tactile sensation is referred to an alien limb after synchronized haptic stimulation of a visible rubber hand, while the real hand is out of sight. Subjects classically report the curious feeling that the rubber hand is their own hand<sup>[60]</sup>. This illusion has a stronger effect on the perceived hand position than on motor localization responses<sup>[61]</sup>; moreover, in order to induce the illusion, information about body representation (related to the somatosensory perceptual stream) must be available and intact<sup>[61,62]</sup>. Thus, it has been suggested that the RHI is based on body segmentation into parts, allowing the distinction of each part of the body, even in semantic terms<sup>[63]</sup>. However, this local body representation is not useful during actions: since a global body representation is required for appropriate complex movements to be performed, coherent knowledge of action functional units provided by the body schema is used<sup>[64]</sup>.

Separation between streams in the somatosensory domain is also confirmed by the dissociation between reference frame coordinates also characterizing the visual action and perception streams. Hach *et al.*<sup>[65]</sup> borrowed the classical experimental methodology from the visual domain, in which a delay between the input and the subject's answer is introduced in order to provide a switch from the dorsal-action representation to the ventral-perception one<sup>[1,2]</sup>. Using this methodology, the authors provide evi-

dence on the distinction between egocentric and allocentric references even in somatosensory spatial representations<sup>[65]</sup>. Specifically, the execution of pointing movements either backward towards pre-defined landmarks on the subject's own body (egocentric reference frame) or to a forward projection of the body (allocentric representation) does not result in performance changes if a delay is introduced; conversely, accessing an allocentric representation of one's own body results in performance changes if the pointing is immediately executed.

Even though at first glance the analogy with Milner and Goodale's two streams visual system<sup>[2]</sup> is immediately apparent, Dijkerman and de Haan also embody other theories in their model, such as Paillard's concept<sup>[56]</sup> about body schema and body image dichotomy<sup>[43]</sup>. Particularly, Paillard has the merit of being the first author to theoretically describe a dissociation between a body schema as an internal representation for action and a body image involved in perceptual identification of body features<sup>[47,56]</sup>. More recently, Anema *et al.*<sup>[66]</sup> have provided evidence favoring this theoretical distinction (Table 1), describing a double dissociation in two neurological subjects on two tactile localization tasks: the pointing-hand task in which the two patients were requested to point directly to the positions receiving tactile stimuli on their own hands, and the pointing-map task in which they were asked to identify the locations of tactile stimuli in a drawing of their own hand<sup>[66]</sup>. The results showed that one patient had impaired performance when locating tactile stimuli on his own hand but better performance in the map hand task, while the other showed an opposite pattern. These data suggest a deficit in body schema for the first patient, and a deficit in body image for the second<sup>[66]</sup>.

The somatosensory model by Dijkerman and de Haan<sup>[43]</sup> is challenging, as it encapsulates not only the notion of "action & perception" but tries to include also "body schema & body image" concepts. The model's extensions should include nociception, temperature and other somatosensory processes such as itch perception, in addition to proprioception and touch: these functions might be essential for guiding motor actions, particularly in the

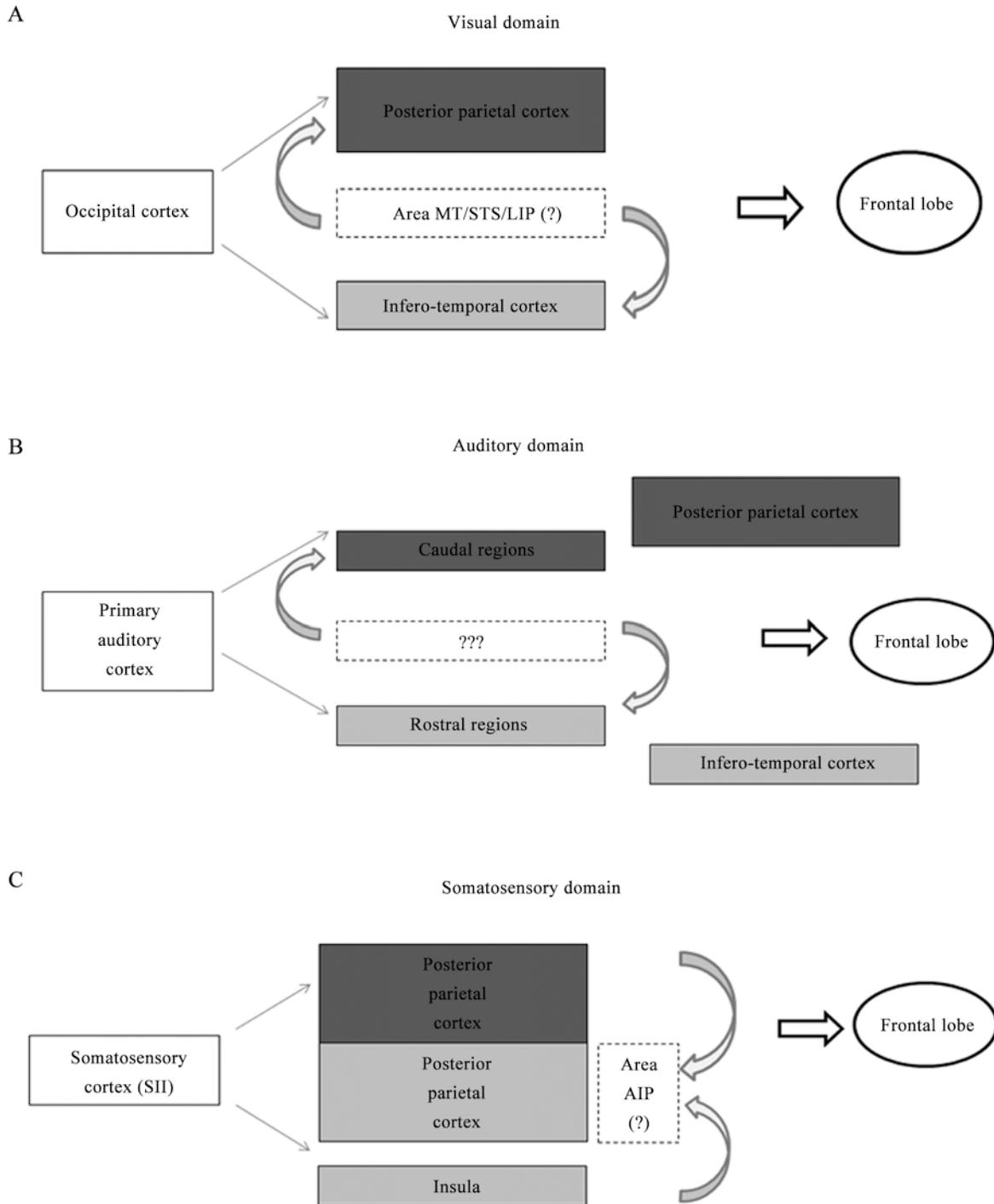
absence of other information and when actions are directed to the body itself<sup>[67]</sup>. Furthermore, the model may benefit from addressing or at least clarifying inconsistencies with the visual correspondence, especially those that concern the anatomical substrates.

## 5 Conclusion

Several types of information obtained from different sensory modalities are used in order to achieve a successful interaction with the environment<sup>[42,68]</sup>. The final and common goal of different cognitive processes is to provide a stable, exhaustive and comprehensive multimodal representation of ourselves as active agents in the world<sup>[3]</sup>.

A pattern of organization, similar across different sensory modalities, may be considered a parsimonious and strategic evolutionary solution. From this point of view, the hypothesis about different sensory modalities organized in a similar dual-stream pattern is reasonable (Fig. 1). Similar to what happened for the visual domain, in which scientific studies shifted from inputs to outputs, leading to the first formulation of the "action & perception" model<sup>[1]</sup>, a shift from exploring and detailing a single sensory modality (either visual, auditory or somatosensory) to a more general notion of searching for "action & perception" patterns about brain functioning might be profitable to achieve further knowledge of human interactions with the environment.

Research on touch and audition has recently started to move in this direction. First models are promising, but further knowledge is necessary to detail the functioning of these sensory modalities, as now the dorsal and ventral visual streams hypothesis remains the one with the greatest and more convincing amount of evidence. Genetic approaches, such as the topographic mapping of receptive fields or connective strength that have been recently used in dissecting circuit connectivity in animals, could help in clarifying the neural mechanisms underlying the anatomical and functional segregation between ventral and dorsal streams in the brain, especially the exact circuit connective pattern. For example, Wang *et al.*<sup>[69]</sup> demonstrated the existence of ventral and dorsal streams in rodents by applying



**Fig. 1.** Dorsal and ventral streams across sensory modalities. Dorsal and ventral streams in the visual (A), auditory (B) and somatosensory (C) domains. While in all streams the final efferences are directed towards the frontal lobe, the starting points and the intermediate stations of each stream are different. In all modalities, dark grey boxes indicate areas belonging to the dorsal stream; light grey boxes indicate areas belonging to the ventral stream; boxes with broken lines indicate putative areas that allow intercommunication between the ventral and dorsal streams. Question marks indicate areas devoted to cross-talk between streams that are still not known or under debate. For the auditory domain (B), caudal and rostral regions refer to areas surrounding the primary auditory cortex. MT, medio-temporal area; STS, superior temporal sulcus; LIP, lateral intraparietal area; AIP, anterior intraparietal area.

multidisciplinary approaches: the authors established a foundation for future work to better detail the operating rules of dorsal and ventral streams and to identify brain areas that are devoted to intercommunication between streams.

Furthermore, despite the accumulating evidence supporting the anatomical and functional separation between the ventral and dorsal streams, there are still pieces missing from the puzzle that question this approach. For instance, several studies in diverse domains, ranging from macaque electrophysiology<sup>[70,71]</sup> to emotion recognition in humans<sup>[72]</sup>, highlight that the medio-temporal area MT, which is usually considered part of the ventral stream, also processes visual motion-related information. This area contains cells that respond to moving and static stimuli, and that are sensitive to three-dimensional structure from motion<sup>[71]</sup>. Moreover, cells in the parahippocampal gyrus encode speed, acceleration, or direction of hand movements only during visuomotor tasks and not during visual- or motor-only tasks<sup>[70]</sup>. Given all these results, most recent hypotheses try to accommodate these findings into the “dorsal & ventral streams” model and suggest that the medial-temporal lobe may serve as an integration node between the two processing streams<sup>[70]</sup>, since its characteristics are compatible with both streams. Another possible candidate for cross-talk between the ventral and dorsal visual streams is the lateral intraparietal area<sup>[3]</sup>, an area known to be involved in attentional tasks that could transmit information about relevant objects in the environment, i.e. the target of the action, to the ventral stream. Subsequently, the same information could be retransmitted to the dorsal stream to be used for planning movements<sup>[3]</sup>. Further studies should directly corroborate these assumptions, by designing experiments aimed at testing where cross-talk occurs in the brain and whether different modalities have different cross-talk areas, as seems to be the case from the results obtained so far.

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