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Claudio Galletti, Patrizia Fattori

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Review for the **Special Issue** of Goodale et al.: **Where to go now with the “What & How” pathway model.**

Title: **The dorsal visual stream revisited: stable circuits or dynamic pathways?**

Authors: Claudio Galletti and Patrizia Fattori

Affiliations: Department of Pharmacy and Biotechnology, University of Bologna, 40126, Bologna, Italy.

Contact

Patrizia Fattori, Dept. of Pharmacy and Biotechnology, University of Bologna, Piazza di Porta S. Donato, 2, 40126 Bologna, Italy. E-mail: patrizia.fattori@unibo.it.

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Abstract

In both macaque and human brain, information regarding visual motion flows from the extrastriate area V6 along two different paths: a dorsolateral one towards areas MT/V5, MST, V3A, and a dorsomedial one towards the visuomotor areas of the superior parietal lobule (V6A, MIP, VIP). The dorsolateral visual stream is involved in many aspects of visual motion analysis, including the recognition of object motion and self motion. The dorsomedial stream uses visual motion information to continuously monitor the spatial location of objects while we are looking and/or moving around, to allow skilled reaching for and grasping of the objects in structured, dynamically

changing environments. Grasping activity is present in two areas of the dorsal stream, AIP and V6A. Area AIP is more involved than V6A in object recognition, V6A in encoding vision for action. We suggest that V6A is involved in the fast control of prehension and plays a critical role in biomechanically selecting appropriate postures during reach to grasp behaviors.

In everyday life, numerous functional networks, often involving the same cortical areas, are continuously in action in the dorsal visual stream, with each network dynamically activated or inhibited according to the context. The dorsolateral and dorsomedial streams represent only two examples of these networks. Many others streams have been described in the literature, but it is worthwhile noting that the same cortical area, and even the same neurons within an area, are not specific for just one functional property, being part of networks that encode multiple functional aspects. Our proposal is to conceive the cortical streams not as fixed series of interconnected cortical areas in which each area belongs univocally to one stream and is strictly involved in only one function, but as interconnected neuronal networks, often involving the same neurons, that are involved in a number of functional processes and whose activation changes dynamically according to the context.

Highlights

- Area V6 distributes visual motion information to both dorsolateral and dorsomedial visual streams.
- Reaching and grasping are not strictly segregated between medial and lateral parts of the dorsal visual stream
- Area V6 subtracts self motion signals from the entire visual field to detect object motion.
- Area V6A encodes both reaching and grasping information for prehension.
- The dorsal visual stream consists of several neuronal networks dynamically recruited according to context.

Visual information flows from the primary visual cortex to several areas of the extrastriate visual cortex along two separate channels called the 'dorsal' and 'ventral' visual streams (Ungerleider & Mishkin, 1982). In the dorsal stream, visual information flows directly from V1 to both MT/V5 (Maunsell & van Essen, 1983; Ungerleider & Desimone, 1986) and V6 (Galletti et al., 2001), that are two retinotopically-organized areas of the extrastriate cortex (Galletti, Fattori, Gamberini, & Kutz, 1999; Gattass & Gross, 1981). According to Rizzolatti and Matelli (2003), visual information from MT/V5 and V6 flows quite separately through two channels, the ventro-dorsal (v-d) and the dorso-dorsal (d-d) channel, that involve visual areas of the IPL and SPL, respectively (Fig. 1A). According to Galletti et al. (2001), however, visual information from V6 takes two different paths (Fig. 1B), one towards MT/V5 (which represents the strongest cortical connection of V6) and other areas of the extrastriate visual cortex (MST, V3A, V4T, LIPv), and the other towards the visuomotor areas of SPL (V6A, MIP, VIP). These two pathways were given the names 'dorsolateral' and 'dorsomedial' visual streams, respectively (Galletti et al., 2001). The information sent by V6 to MT/V5 and V6A is certainly visual in nature, area V6 being a 'pure' visual area, but it is likely different in content because MT/V5 is an area involved in the analysis of visual motion (Desimone & Ungerleider, 1986; Lagae, Maes, Raiguel, Xiao, & Orban, 1994; Maunsell & van Essen, 1983; Sunaert, Van Hecke, Marchal, & Orban, 1999; Watson et al., 1991; Zeki, 1978; Zeki et al., 1991; see Zeki, 2015 for a review), whereas V6A is a visuomotor area involved in the online control of prehension (Galletti, Kutz, Gamberini, Breveglieri, & Fattori, 2003; Gamberini, Galletti, Bosco, Breveglieri, & Fattori, 2011; see Fattori, Breveglieri, Bosco, Gamberini, & Galletti, 2015 for a review). The two following sections of this review will analyze how the visual information coming from V6 could be used by the cortical areas of the dorsolateral and dorsomedial streams, and will suggest the functional roles of the two streams on the basis of data from human and non-human primates.

Figure 1

Functional role of the dorsolateral visual stream: analysis of visual motion

In both human and non-human primates, area V6 is retinotopically organized and represents the entire contralateral visual hemifield, in particular the lower part of it, up to the very far periphery (Galletti, Fattori, Gamberini, & Kutz, 1999; Pitzalis et al., 2006). In the macaque, area V6 is a motion area whose neurons are extremely sensitive to the moving visual stimuli, to their speed, and to the direction of stimulus movement (Galletti, Fattori, Battaglini, Shipp, & Zeki, 1996). Like the macaque V6, the human V6 is extremely sensitive to the movement of visual stimuli (Pitzalis et al., 2010; von Pförtl et al., 2009), to the speed and direction of stimulus movement, and to the optic flow (Pitzalis et al., 2010; Pitzalis et al., 2006).

As recalled above, V6 is strongly connected with area MT/V5 and other areas of the extrastriate visual cortex, in a pattern of connections called the 'dorsolateral visual stream' (Galletti et al., 2001). Interestingly, a similar pattern of connections has been recently described also in humans (Tosoni et al., 2015). Area MT/V5 is the most known visual motion area (Desimone & Ungerleider, 1986; Lagae, Maes, Raiguel, Xiao, & Orban, 1994; Maunsell & van Essen, 1983; Watson et al., 1991; Zeki, 1978; Zeki et al., 1991; see Zeki, 2015 for a review). Besides the strong input from V6, MT/V5, like V6, also receives a direct input from V1 and the extrastriate areas of the occipital pole (Ungerleider & Desimone, 1986; Zeki & Shipp, 1988). Neurons of MT/V5 are highly sensitive to visual stimuli in motion, to their speed and to direction of movement (Zeki, 1974; Zeki, 1978; Albright, 1984; Maunsell & van Essen, 1983; Van Essen, Maunsell, & Bixby, 1981). In both human

and non-human primates, area MT/V5 is retinotopically organized and represents the central part of the contralateral visual field (Desimone & Ungerleider, 1986; Gattass & Gross, 1981; Kolster, Peeters, & Orban, 2010).

Among the other areas directly connected with V6, area MST contains many direction-selective neurons (Desimone & Ungerleider, 1986; Eifuku & Wurtz, 1998; Tanaka et al., 1986; Van Essen et al., 1981), it represents a large part of the visual field (Desimone & Ungerleider, 1986) and is activated by stimulus motion (Sunaert et al., 1999), in particular by egomotion-related visual stimulations (Duffy & Wurtz, 1991, 1995; Morrone et al., 2000; Pitzalis et al., 2013; Tootell et al., 1995).

Area V3A too, strongly and directly connected with V6 (Galletti et al., 2001), is considered a motion area in humans, because it is well activated by moving stimuli (Sunaert et al., 1999) and is involved in extracting form from motion (Orban et al., 2003). In the macaque, on the contrary, V3A is not considered a motion area because it is not activated by the same moving stimuli that activate human V3A (Orban et al., 2003; Tootell et al., 1997). However, we believe that this point of view should be revisited, because neurons in macaque V3A are well activated by the movement of simple visual stimuli, about 30% of them are direction-selective neurons (Galletti, Battaglini, & Fattori, 1991), and about half of V3A neurons encode real motion of visual stimuli in the visual field (Galletti, Battaglini, & Fattori, 1990), all indices of an involvement of the area in the analysis of visual motion. Certainly, it is possible that the involvement of macaque V3A in the analysis of visual motion is different from that of human V3A. This point should be analyzed in specific experiments.

In summary, based on their functional properties, the four areas of the dorsolateral visual stream, V6, MT/V5, MST, and V3A, could all be considered as motion areas. Interestingly, all these areas contain a particular type of cells closely involved in encoding movement in the visual field

(Erickson & Thier, 1991; Galletti et al., 1990; Galletti & Fattori, 2003; Thiele et al., 2002), the ‘real motion’ cells (Galletti, Battaglini, & Aicardi, 1988; Galletti et al., 1990; Galletti, Squatrito, Battaglini, & Maioli, 1984), i.e. cells activated by the actual movement of an object in the visual field, but not by the movement of its retinal image self-induced, for instance, by the eye movements. We suggested (Galletti & Fattori, 2003) that the real motion cells are interconnected in a specific neuronal network (the dorsolateral visual stream) involved in the detection and recognition of object motion in the visual field. A large amount of experimental human data supports this view. For instance, cerebral lesions affecting the lateral temporo-occipital cortex (likely including area MT/V5) produced permanent severe impairment in detection of movement in the visual field (Shipp, de Jong, Zihl, Frackowiak, & Zeki, 1994; Zihl, von Cramon, & Mai, 1983). In addition, moving sensations were evoked by electrical stimulation of the basal temporo-occipital and the mesial parieto-occipital regions (Lee, Hong, Seo, Tae, & Hong, 2000), two cortical regions that likely include areas MT/V5, MST, and V6 (Pitzalis et al., 2010). Furthermore, a lesion of the extrastriate cortex affecting the dorsal parts of Brodmann’s areas 18 and 19, and the cortex in and around the intraparietal sulcus, which is a lesion likely including areas V3A, V6, MT/V5, and MST, produced very selective impairment in motion detection (Haarmeier, Thier, Repnow, & Petersen, 1997). In this case, the patient was unable to judge whether a retinal slip was self-induced by the eye movement or was due to an actual movement of an object. He interpreted any retinal image motion as object motion, even when it was due to his pursuit eye movements. In other words, it looked as if he had lost the output of his real motion cells.

Why several motion areas within the dorsal visual stream?

An interesting question arising from the above reported considerations is why visual motion is processed by several cortical areas (for a recent list of the cortical motion areas see Orban & Jastorff, 2014). A comparative analysis among all the motion areas of the brain is beyond the scope of this review, but to try to give an answer to the above question, we compared the functional properties of the two most studied motion areas, MT/V5 and V6. The information regarding motion flows in parallel from the occipital cortex to MT/V5 and V6 (Pitzalis, Bozzacchi, et al., 2013) so that the response timing in these areas is similar and very precocious (Pitzalis, Bozzacchi, et al., 2013; von Pfösti et al., 2009). The two motion areas have different outputs: while MT/V5 has dense connections with the inferior parietal cortex (Rozzi et al., 2006), which in turn is connected also with areas of the ventral stream, area V6 is mostly connected with the superior parietal cortex, which is not directly connected with the ventral stream (Galletti et al., 2001). MT/V5 and V6 show many functional similarities (direct input from V1, retinotopic organization, motion sensitivity, direction selectivity, presence of real motion cells). The major functional difference between them seems to be the extent and organization of visual field representation: V6 represents the entire visual field up to the very far periphery without a central magnification (Galletti, Fattori, Gamberini, et al., 1999), whereas MT/V5 represents the central 30°-40° of the visual field, with a clear foveal magnification (Desimone & Ungerleider, 1986; Gattass & Gross, 1981). V6 may thus be helpful in detecting visual motion everywhere in the visual field, and in detecting and interpreting the optic flow, that typically involves the entire visual field (global vision); MT/V5, instead, may be engaged in the analysis of visual motion occurring around a particular location that we are looking at (local vision) (Galletti & Fattori, 2003). In other words, as suggested by human data, MT/V5 is likely involved in the analysis of object motion, and V6 in the recognition of both object motion and self motion (Cardin, Hemsforth, & Smith, 2012; Pitzalis et al., 2010; Pitzalis, Sdoia, et al., 2013). In good agreement with this hypothesis, V6 is strongly

activated by optic flow, whereas MT/V5 is not (Cardin & Smith, 2010, 2011; Pitzalis et al., 2010; Pitzalis et al., 2006). Interestingly, global processing of optic flow information is shown to play a fundamental role in the recovery of object movement during ego movement (Warren & Rushton, 2009). The primate visual system is proficient in this job, and when we move about in the environment we have no doubts about who and what is moving in our field of view (Fig. 2A). V6, but not MT/V5, seems to be well equipped to perform this job. Area V6 could be involved in 'subtracting out' self motion signals across the entire visual field and in providing information about moving objects (see Fig. 2B-D), as originally suggested by our group in both monkeys and humans (Galletti & Fattori, 2003; Pitzalis et al., 2010). Since global and local vision are highly integrated processes in everyday life, and since we correctly and concurrently perceive both self motion and object motion, V6 and MT/V5 should interact with one another, and to do this they must be closely interconnected, as in fact they are, and must exchange the motion information they process, as they most likely do.

Figure 2.

Interestingly, a very recent report (Layton & Fajen, 2016) suggests a similar model in which the above described process of visual motion analysis is performed by areas MT/V5 and MST. According to this model, the self motion signals processed by area MST interact with the object motion signals processed by area MT/V5 to provide correct object motion perception during self motion. It may be that both V6 and MST interact with MT/V5 to analyze object motion (and heading) during self motion, but the reason why two cortical mechanisms are involved in this process is at present unknown and should be the topic of future studies.

The above reported data and considerations lead to the conclusion that a functional role of the dorsolateral visual stream is the recognition of object motion and self motion. This is not to say that this is the only role that the areas of this stream play. Area MST, for instance, is connected with several areas of the inferior parietal lobule (Rozzi et al., 2006) which in turn receive afferents from the superior temporal polysensory area (Rizzolatti & Matelli, 2003), an area processing the visual information concerning space and biological motion (the recognition of body movements where the form of the body is defined only by the movements of lights positioned at joint angles (see Bruce, Desimone, & Gross, 1981; Oram & Perrett, 1994; Perrett et al., 1989). It is therefore plausible that the dorsolateral visual stream is also involved in the analysis of biological motion, as already suggested by Rizzolatti and Matelli (2003). To take another example, area V3A contains plenty of neurons sensitive to the form of visual stimuli (S. M. Zeki, 1978) as well as neurons sensitive to stimulus movement (Galletti, Battaglini, & Fattori, 1990), so this area could be involved in the extraction of form from motion, as suggested by Vanduffel et al. (2002). Overall, we suggest that each single area of the dorsolateral visual stream is involved in the analysis of different aspects of visual motion, and together these areas provide information about the real motion, the biological motion, the form of moving objects, the detection and recognition of object motion and self motion, and likely also other aspects of visual motion not yet studied so far. Hence, instead of imagining the dorsolateral visual stream as a neuronal network with a specific functional role, it is better to imagine it as a network of interconnected areas whose neurons show multiple functional properties. Each area, and even each type of neurons within an area, analyzes different aspects of motion. Conversely, each aspect of motion is analyzed in different areas by a network of neurons showing that specific functional property –such as the real motion property, for instance- and the chain of neurons with that property allows a progressive refinement of the specific encoding process. The different neuronal chains are dynamically activated -or not-

according to the context and task demands, and the output of this process is provided to other cortical regions for different functional purposes.

Functional role of the dorso-medial visual stream: vision for action

While the input of area V6 to MT/V5 and to the other motion areas of the dorsolateral visual stream is evidently useful in the analysis of visual motion, what is not so obvious is the role that V6 input could play for the areas of the dorsomedial visual stream, namely V6A, MIP, VIP, which are not classic motion areas, but receive, overall, about 40% of total V6 projections (Fig. 2B; Galletti et al., 2001). As reported above, the V6 input is a visual motion signal coming from the entire visual field. Since the VIP neurons have very large visual receptive fields showing direction selectivity (Colby, Duhamel, & Goldberg, 1993; Duhamel, Colby, & Goldberg, 1998), are activated by optic flow, and encode heading direction (Bremmer, Duhamel, Ben Hamed, & Graf, 2002), the direct connection between V6 and VIP has a strong functional logic. But what can be the role of visual motion input to cortical areas that are involved in the control of arm-reaching movements and object prehension like V6A and MIP? (Colby & Duhamel, 1991; Fattori et al., 2015; Snyder, Batista, & Andersen, 1997). To answer this question we have to bear in mind that for successful action planning and execution, the visuomotor system must first know the spatial location of the object to be grasped. Crucial to this concept is the output of the so-called 'real-position' cells, found in the parietal areas V6A and VIP (Duhamel, Bremmer, Ben Hamed, & Graf, 1997; Galletti, Battaglini, & Fattori, 1993) and in premotor cortex (Fogassi et al., 1992, 1996; Graziano & Gross, 1998). The visual receptive fields of these cells do not move with the eyes, but remain anchored to the same spatial location regardless of the direction of gaze. Neurons of this type encode the visual space directly, and can continuously provide the spatial location of graspable objects to the motor

system that controls arm movement (Galletti et al., 2003). But for successful action planning and execution, the visuomotor system must also recognize whether the object to be grasped is moving, because in this case it will continuously change its spatial location. To do this, the system must recognize the direction and speed of motion of the object, both encoded by V6 and by many cells of V6A (Galletti et al., 1996), but first of all the visuomotor system must recognize whether a shift of the retinal image of the object is caused by self motion or to real motion of the object. The recognition of these two types of motion, obtained thanks to the output of 'real motion' cells highly represented in V6, is essential for planning and executing reaching for and grasping of nearby objects, stationary or in motion, as well as for the avoidance of obstacles, in particular during walking in a structured environment like that usually found in everyday life. We suggest that the real motion signals (i.e. the V6 output) ensure a stable and correct perception of the external visual world, necessary to orchestrate eye, arm, and body movements, and to navigate in a complex and dynamic environment, like the orangutan swinging from branch to branch depicted in Fig. 3.

Figure 3.

We have claimed above that V6A and MIP are visuomotor areas involved in the control of arm reaching movements and prehension. But to understand the functional role(s) played by these areas, hence the role(s) played by the dorsomedial visual stream, we have to analyze the functional properties of their neurons in detail. The entire extent of area MIP has not yet been studied in detail, the only study involving most of this area being the one by Colby and Duhamel (Colby & Duhamel, 1991). This study showed that MIP neurons are modulated by reaching activity, by somatosensory stimulations and, in the deepest part of the intraparietal sulcus, by visual

stimulation, but we have no details about these neural modulations. Intense single cell recordings have involved the dorsal part of MIP and the adjacent visual cortex in the caudal SPL, mostly referred to as PRR, parietal reach region. The PRR was not defined on an anatomical basis, but on a functional basis as a cortical region containing neurons that show reach-related discharges (Snyder et al., 1997). Therefore, the extent and location of the PRR is not clearly identifiable, nor are the areas of the SPL that could be included within the PRR, though it is well accepted that it likely includes area MIP (Gail & Andersen, 2006). Many papers describe the functional properties of reaching neurons in area PRR (e.g. Chang & Snyder, 2010; Hwang, Hauschild, Wilke, & Andersen, 2014; Kuang, Morel, & Gail, 2016; Snyder et al., 1997). These reaching neurons encode the direction of reaching movement, as well as the intention to move the arm, but nothing has been reported, to date, about a putative grasping activity of PRR neurons. Area V6A, instead, has been proved to be involved in both reaching and grasping activities (Fattori et al., 2009, 2010; Fattori, Breveglieri, Amoroso, & Galletti, 2004; Fattori, Kutz, Breveglieri, Marzocchi, & Galletti, 2005). V6A is a visuomotor area that contains about 65% of visual neurons (including about 10% of real-position cells), and about 30% of somatic cells (see Gamberini et al., 2011 for a review). The visual neurons represent the contralateral hemifield up to the far periphery and, partly, the ipsilateral visual field (Galletti, Fattori, Kutz, & Gamberini, 1999); the majority of visual neurons are orientation and direction-selective (Gamberini et al., 2011). The somatosensory neurons almost exclusively represent the arm (Breveglieri, Kutz, Fattori, Gamberini, & Galletti, 2002). Most somatosensory neurons are modulated by joint stimulation and a minority by skin stimulation; in both cases, the proximal part of the arm (shoulder) is more represented than the distal part (wrist/hand; (Breveglieri et al., 2002; Gamberini et al., 2011). Most of the neurons of area V6A show motor-related properties, being modulated by reaching and grasping movements (Gamberini et al., 2011). In reaching neurons, the neural discharge is tuned by the direction of arm

movement (Fattori et al., 2005) and by the distance reached by the hand (Hadjidimitrakakis et al., 2014; Hadjidimitrakakis, Dal Bo', Breveglieri, Galletti, & Fattori, 2015), as can be seen in the example shown in Fig 4. In grasping neurons, instead, neural activity shows a strong modulation according to the orientation of the wrist/hand while grasping (Fattori et al., 2009)(Fig. 5A) and the grip used by the animal to grasp the object (Fattori et al., 2010; Fattori, Breveglieri, Raos, Bosco, & Galletti, 2012)(Fig. 5B). Several V6A neurons are tuned by both reach direction and wrist orientation (Fattori et al., 2009), indicating their involvement in both proximal and distal components of prehension.

Figure 5.

The sensitivity for the direction of reaching movements is not a specific property of areas MIP and V6A, but is typical of many areas of the posterior parietal cortex (PPC), as documented by many reports since the seminal work of Vernon Mountcastle in the 70's (Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975; see for a review Andersen, 2015). Since then, neurons encoding spatial signals for reaching have been found in many areas of the dorsal visual stream. (Battaglia-Mayer et al., 2001; Fattori et al., 2005; Ferraina et al., 1997; Hwang et al., 2014; McGuire & Sabes, 2011; Piserchia et al., 2016; Snyder et al., 1997). On the contrary, it has been well known since the 90's that grasping neurons represent a specific property of a region of the lateral bank of the intra-parietal sulcus called area AIP (anterior intraparietal area). This area hosts neurons tuned for the grip type and the hand shape used when grasping an object (Murata, Gallese, Kaseda, & Sakata, 1996; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Sakata, Taira, Murata, & Mine, 1995; Taira, Mine, Georgopoulos, Murata, & Sakata, 1990). As a spatial tuning for AIP grasping activity was not reported, the hypothesis of two parallel channels in the PPC for the control of prehension was proposed, a medial one specific for reaching and a lateral one specific

for grasping (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). This model had a counterpart in the premotor cortex, with the dorsal premotor cortex involved in encoding directional signals for reaching, and the ventral premotor cortex involved in the control of the hand shape to match the objects to be grasped (Caminiti, Ferraina, & Johnson, 1996; Kurata & Tanji, 1986; Luppino, Murata, Govoni, & Matelli, 1999; Pesaran, Nelson, & Andersen, 2006; Riehle & Requin, 1989; Weinrich & Wise, 1982; Wise, Boussaoud, Johnson, & Caminiti, 1997; Hoshi & Tanji, 2007; Weinrich, Wise, & Mauritz, 1984). This model had considerable influence in the neuroscience community in the last few decades, and is still reported in the main neuroscience text-books (see Fig. 6), but the finding that grasping movements modulated the neural activity of an area of the 'reaching' network (area V6A; Fig. 5, 7A) questioned the existence of separate reaching/grasping channels (Fattori et al., 2010, 2004; Galletti et al., 2003). Grasp-related modulation found in the dorsal premotor area F2 (Fig. 7B; (Raos, Umiltá, Gallese, & Fogassi, 2004), another area of the putative 'reaching' network, and directional signals related to arm reaching movements found in the 'grasping' areas AIP and ventral premotor PMv (Fig. 7C, D; Lehmann & Scherberger, 2013; Stark, Drori, Asher, Ben-Shaul, & Abeles, 2007) supported the view that, instead of being segregated in two separate circuits, reaching and grasping activities are actually distributed across many areas of the posterior parietal and frontal cortices.

Figure 6.

Figure 7.

Lesion studies in humans support the hypothesis that grasping is not segregated in a specific circuit of the dorsal stream. Indeed, although SPL lesions have traditionally been recognized to be responsible for optic ataxia (Perenin & Vighetto, 1988), a neurological condition where the patient

has difficulty in reaching toward visual objects presented in the peripheral visual field (Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003; Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006), the careful analysis of errors of optic ataxia patients showed that most of these patients exhibit deficits also in the grasp component (Jeannerod, 1986; Pisella et al., 2006). Grasping deficits consisted in impairments in orienting the wrist so to match the orientation of the object to interact with (Perenin & Vighetto, 1988), abnormal finger opening while grasping an object, and failure to scale the grip aperture to the object size (Jakobson, Archibald, Carey, & Goodale, 1991; Jeannerod, 1986), exactly as observed after selective lesions of the macaque area V6A (Battaglini et al., 2002). Interestingly, the grasping deficits in humans were present after medial PPC lesions that spared the AIP but included a region of the brain that likely contains area V6A (Pisella et al., 2006; Pitzalis et al., 2013). In other words, it seems likely that as in the macaque V6A, both reaching and grasping activities are represented in the human V6A too.

Brain imaging studies using multi-voxel pattern analysis and adaptation paradigms (Gallivan, McLean, Valyear, Pettypiece, & Culham, 2011; Monaco et al., 2011) converge in attributing a grasping role to the part of human SPL corresponding to monkey V6A (Pitzalis et al., 2013; Tosoni et al., 2015). Indeed, these imaging studies found that the cortex around the dorsal-most part of the parieto-occipital sulcus plays a role in processing wrist orientation and grip formation (Gallivan et al., 2011; Monaco et al., 2011), thus confirming a role for the dorsomedial PPC in the control of reach-to-grasp actions (see Fattori et al., 2015 for a review on this particular aspect).

Why two grasping areas within the dorsal visual stream?

The data summarized above suggest that two areas of the PPC are involved in the control of grasping, areas AIP and V6A. A way to understand the likely different role(s) played by these two areas is to compare their anatomical connections and functional properties. Figure 8 summarizes the main cortical connections of AIP and V6A. The two areas share many targets, but the connections with most of them were strikingly different in proportion. In the frontal lobe, area AIP has preferential connections with PMv and prefrontal cortex, whereas area V6A is connected with PMd. The inferior temporal cortex is connected with AIP but not with V6A. Conversely, the mesial cortex is connected with V6A but not with AIP. The inferior temporal input to AIP is likely useful to provide object information to generate object-oriented actions (Borra et al., 2008; Rizzolatti & Matelli, 2003), while the mesial cortex input to V6A is likely useful to coordinate arm movement and grasping during navigation (Hutchison, Culham, Flanagan, Everling, & Gallivan, 2015; Kravitz, Saleem, Baker, & Mishkin, 2011). Moreover, the IPL is closely connected with AIP (about 70% of AIP connections), but much less with V6A (about 15% of V6A input). Conversely, V6A receives important inputs from extrastriate visual cortices (nearly 40%) and from other areas of the superior parietal lobule (about 30%), whereas AIP is practically devoid of inputs from these two cortical sectors. In summary, while AIP receives visual input from the ventral and dorsolateral visual streams (Borra et al., 2008), V6A receives information from the dorsomedial and dorsolateral visual streams and the mesial cortex, but not a direct input from the ventral visual stream (Gamberini et al., 2009; Passarelli et al., 2011). Finally, it is worthwhile noting that areas AIP and V6A are reciprocally connected, so a direct transfer of grasping information can occur between the two areas (Borra et al., 2008; Gamberini et al., 2009; Passarelli et al., 2011). Interestingly, recent imaging works indicate an interplay between the two areas also in humans (Verhagen, Dijkerman, Medendorp, & Toni, 2012, 2013).

Figure 8.

Why does the brain host two circuits for grasping? Functional data and anatomical connections suggest that the use of visual information by AIP during grasping is different with respect to that of V6A. For instance, in AIP, grasping in light activates the cells more than grasping in darkness, whereas in V6A about half of the neurons are inhibited by the vision of grasping (Fig. 9B; Breveglieri, Bosco, Galletti, Passarelli, & Fattori, 2016). While cell activation by vision of grasping suggests a use of the visual feedback as supplemental information to control grasping movements, the cell's inhibition is difficult to interpret. The V6A cells are inhibited not only during grasping in light, but also as soon as the object is presented to the animal, and during the subsequent movement preparation (see Fig. 9B). It could be that those V6A cells are silenced to prevent an arm movement, but the discharge that they show during preparation when grasping is performed in darkness (see Fig. 9A) seems to contradict this hypothesis. It could be that the higher activity observed in darkness is due to other factors related to the absence of visual feedback, such as the higher level of attention required for grasping objects in the dark. If this is the case, what seems to be 'inhibition' observed in light could simply be a lack of this attentional enhancement (Breveglieri et al., 2016; Breveglieri, Galletti, Dal Bò, Hadjidimitrakis, & Fattori, 2014). This hypothesis seems to be reliable because a clear effect of attentional level on the activity of V6A neurons has been proved (Galletti et al., 1996; Galletti et al., 2010), but specific experiments are required to verify this hypothesis.

Figure 9.

A second difference between AIP and V6A concerns the sensitivity to visual stimulations performed outside the grasping context. While the overwhelming majority of neurons in AIP (90%)

are sensitive to simple visual stimuli, like fragments of shapes, presented to the animal without any request for interaction with them, including grasping (Romero, Pani, & Janssen, 2014), only a minority of V6A neurons (about 30%) respond to simple visual stimuli passively presented to the animal (Fattori et al., 2015; Galletti, Fattori, Kutz, et al., 1999; Gamberini et al., 2011). Interestingly, AIP is connected with the ventral visual stream whereas V6A is not (see Fig. 8; Borra et al., 2008; Gamberini et al., 2009; Passarelli et al., 2011), and it has been recently reported that V6A neurons are activated by the affordance evoked by the object presented to the animal, irrespective of its visual features (Breveglieri, Galletti, Bosco, Gamberini, & Fattori, 2015). Taken together, these data seem to reflect a deeper involvement of AIP with respect to V6A in object recognition, and conversely a deeper involvement of V6A in encoding vision for action.

To speculate, we could hypothesize that when we want to grasp an object, areas AIP and V6A are both, though differently, activated according to the type of object and the context in which grasping has to be performed. If for instance we want to grasp a delicate and fragile object, V6A would be involved in directing the hand toward it, a movement based on visual cues and somatosensory signals from the arm, and in grasping it with the correct hand orientation and grip aperture; meanwhile, AIP should be activated too, being however more involved in evaluating the fine structure and fragility of the object to be grasped and therefore in how to approach it with caution. If, on the contrary, we want to grasp an object of similar size and features but robust and of low value, V6A would remain involved as before in guiding the hand to grasp the object whereas AIP should be less activated. We could also speculate that if the object (of either high or low value) suddenly drops down from a table, most of the work to rapidly grasp it would be done by V6A, because this area can intervene more rapidly since it is directly connected with the frontal cortex (Galletti et al., 2001; Galletti, Fattori, Gamberini, & Kutz, 2004) and shows visual responses with very short latencies (von Pfösti et al., 2009). The existence of a fast control mechanism of

reaching and its dependence on the medial PPC was first reported by Pisella and coworkers (Pisella et al., 2000) and indicated by Rizzolatti and Matelli (Rizzolatti & Matelli, 2003) as a typical activity of the d-d stream. We too suggested that V6A is an area directly involved in this fast control mechanism (Galletti et al., 2003), but direct experiments aimed at testing this thesis have not yet been carried out.

Summary and Conclusions

Visual motion information leaving area V6 flows to the areas of the PPC through two pathways, called the dorsolateral and dorsomedial streams. While the areas of the dorsolateral stream use visual information to recognize object motion and self motion, and in particular the movement of objects during ego movements, those of the dorsomedial stream use visual motion information to continuously monitor the spatial location of stationary and moving objects while we are looking at them and/or moving around, to allow skilled reaching for and grasping of objects around us even in dynamic contexts.

In line with other reports (Grol et al., 2007; Pisella et al., 2006; Rizzolatti & Matelli, 2003), we propose that in the dorsal stream the area AIP, that receives direct information from areas of the ventral stream, provides the ventral premotor cortex with detailed information on the qualities and visual features of the objects to be grasped, whereas area V6A provides the dorsal premotor cortex with basic information like object size, orientation and position of graspable objects, and is preferentially involved in the control of prehension acts when temporal constraints are imposed (Galletti et al., 2003). Notably, area V6A receives not only visual information, but also somatosensory information from the upper limbs (Gamberini et al., 2011). Since the lesion-deficit

and imaging results provide evidence that the posterior part of the PPC in the region of the superior parietal lobule and intraparietal sulcus is critical for the selection of biomechanically viable grasp postures (Wood, Chouinard, Major, & Goodale, 2016), we suggest that V6A, which in humans occupies this region of the brain (Pitzalis et al., 2013), plays a critical role in this process.

The present review, like many other works in the last few decades, suggests that cortical areas with similar functional characteristics, connected to one another, may work together to perform specific brain processes, like the analysis of some aspects of visual motion or the provision to the motor centers of the elements needed to interact with the objects around us, as described here. Many other cortical networks (streams) could be described that make it possible to analyze other aspects of vision or visuomotor processes, or even other types of brain processes. But the discovery of an increasing number of functional streams should not conceal the fact that the same cortical area, and even the same neurons within an area, are not specific for just one functional property, as often seems to be the case in the literature, but are able to encode multiple functional aspects. This means that an area with a single functional property does not exist, and the subdivision of cortical areas into streams in which each area belongs univocally to one stream is an oversimplification. Different types of information are concurrently propagated to a multiplicity of brain areas according to the demands of the task. The single functional properties are encoded by neuronal networks that involve some neurons (not all) of different areas, but these same neurons could also be parts of other functional pathways. Therefore, circuits encoding different functional properties can involve the same area, and even the same neurons within the area. If this is the case, we should expect to find plenty of functional networks in the so called dorsal visual stream, each one of them dynamically activated or inhibited according to the context: the dorsolateral and dorsomedial streams would represent only two examples of these networks.

This view is in good agreement with the different functional roles suggested for the dorsal visual stream, originally described as involved in the analysis of space (Ungerleider & Mishkin, 1982) and visual motion (Desimone & Ungerleider, 1986), then in action preparation (Goodale & Milner, 1992), fast form and motion analyses (Galletti et al., 2001), space and action perception (Rizzolatti & Matelli, 2003), online control of reaching (Rizzolatti & Matelli, 2003; Galletti et al., 2003), etc. Actually, all these functions are undertaken by different neuronal networks which often involve the same occipital and posterior parietal areas and provide information to the premotor frontal cortex. All these networks, together, represent the so called 'dorsal visual stream'.

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Captions:

Figure 1. Visual streams and cortical connections of area V6 in the macaque brain.

A. Lateral view of the macaque brain highlighting the Dorso-dorsal ('d-d'), Ventro-dorsal ('v-d'), and Ventral visual streams according to Rizzolatti and Matelli (2003).

B. Posterolateral view of a partially dissected macaque brain showing the cortical connections of area V6 (modified from Galletti et al., 2003). The inferior parietal lobule and the occipital lobe of the right hemisphere have been cut away to show the cortex of the medial bank of the intraparietal sulcus and that of the anterior bank of the parieto-occipital sulcus. The mesial surface of the left hemisphere is depicted in grey. Arrows are used to indicate the flow of visual information from occipital to posterior parietal cortices, though originally all connections were reciprocal (Galletti et al., 2001).

V1, V2, V3, V3A, V4, V4T, MT/V5, LIPv, MIP, MST, PEc, PEip, V6, V6A, VIP, 7m: cortical areas V1, V2, V3, V3A, V4, V4T, MT/V5, MST LIPv, MIP, MST, PEc, PEip, V6, V6A, VIP, 7m. IPL: inferior parietal lobule; SPL: superior parietal lobule. PMd: dorsal premotor cortex. PMv: ventral premotor cortex.

Figure 2. Flow Parsing Hypothesis (modified from Fig. 1 of Warren & Rushton, 2009).

A. View of a corridor: imagine that an observer is walking forward while fixating the end of the corridor. Note that a ball is falling vertically downwards on the left.

B. Pattern of retinal motion associated with forward motion down the corridor shown in A. Note the retinal motion of the walls, floor, and ceiling, which are scene-stationary, and the inappropriate oblique retinal trajectory of the ball.

C. Warren and Rushton (2009) proposed that the flow parsing mechanism identifies and subtracts the optic flow associated with observer movement. For the movement in B, this is equivalent to adding the motion field shown. Note the ringed vector to be added at the location of the ball.

D. Perceived motion under the flow parsing hypothesis (obtained by adding the motion field in C to that in B). Note that the mechanism has solved the problem of perceptual stability (walls, floor, and ceiling are perceived as stationary) and the physical trajectory of the ball has also been recovered.

Figure 3. Orangutan moving in the jungle.

This is an example of a situation requiring the activity of the dorsomedial fronto-parietal circuit for controlling grasping actions. When grasping lianas in the forest, the monkey needs information on the spatial location of lianas while their retinal images are continuously in motion thanks to both eye movements and self motion. The high sensitivity of V6 to wide patterns of coherent motion that mimic the continuously changing optic flow stimulation experienced during spatial navigation, together with the output of real motion cells, allows V6 to process visual ego motion signals and any other motion signal present in the field of view to extract useful information on object position and movement (see text; see Fig. 2). The close interconnections between areas V6 and V6A and the characteristics of the two areas led us to propose that the dorsomedial visual stream is particularly indicated to transform visual information about an everchanging visual scene into appropriate input to control hand actions.

Figure 4. Spatial signals for reaching in the medial posterior parietal area V6A.

Left: experimental set-up used for testing reaching discharges when the arm is directed towards different directions and depths (different colors). Eye and hand movements are performed toward one of the 9 targets located at eye level at different depths and directions.

Right: Example neuron with depth tuning in several epochs. From top to bottom in each panel: spike histograms, version (1st trace) and vergence (2nd) eye traces. The 9 panels illustrate neural responses and eye signals for the 9 target positions arranged in 3 directions (columns) and 3 depths (rows). Vertical bars indicate the alignment of neural activity and eye traces at the start of arm movement. In color: the epochs coincident with the execution of reaching:

red is the farthest, blue the nearest. Spatial modulations occur during both planning and execution of arm movement, showing a preference for reaches towards targets near the body.

Scales: version, 60° per division; vergence, 20° per division. Modified from Fig. 3 of Hadjimitsakis et al., 2014.

Figure 5. Distal arm movements modulate neural discharges in area V6A of the dorsomedial visual stream.

Two examples of cells modulated by wrist orientation (A) and finger prehension (B). All grasping are performed in darkness.

A. Top: tested wrist orientations. Middle and bottom: Peri-event time histograms, time epochs, raster displays of impulse activity, and recordings of horizontal and vertical components of eye positions. Long vertical ticks in raster displays are behavioral markers, indicating from left to right: go-signal, onset of arm movement, end of reach-to-grasp movement, cue to release the handle, handle-release, home-button press. Activity is aligned with the onset of reach-to-grasp arm movement. Scales: vertical bar on histograms, 75 spikes/s; eye traces, 60°/division. The cell has a clear preference for grasps performed with the wrist in a neutral position, intermediate between pronated and supinated. Modified from fig. 2 of Fattori et al., 2009.

B. Top: tested grip types. Scale: vertical bar on histograms 150 spikes/s. All other conventions are as in A. The unit shows a stronger activation for grasping and holding the handle (left) rather than the cylinder (right).

Figure 6. Widely-accepted view of the division of labor of two substreams of the dorsal stream (modified from Kandel et al., 2013 Principles of Neural Science. Columbus, OH, USA: McGraw-Hill).

Lateral view of the macaque brain: left hemisphere, caudal is on the right. The areas located within the intraparietal sulcus are shown in an unfolded view of the sulcus.

A. Circuit proposed to control reaching actions. It links superior parietal cortex (areas V6A, PEc, MIP) with dorsal premotor cortex (area F2).

B. Circuit proposed to control grasping actions. It links inferior parietal cortex (areas AIP, PFG, PF) with ventral premotor cortex (area F5).

PEc, PF, PFG: parietal areas PEc, PF, PFG.

Other abbreviations as in Fig. 1.

Figure 7. First evidence of grasp-related activity in the dorsomedial fronto-parietal network (A-B) and of directional tuning of grasping activity in the dorsolateral fronto-parietal network (C-D).

A. Top: neural activity of a superior parietal cell (area V6A) during three successive episodes of grasping. Vertical bars are action potentials recorded in the audio band of a videoclip. Different types of lines under the neural trace indicate different behavioral periods: thin lines mark periods of feeding, dotted lines the movement time, and thick lines the occurrence and duration of grasping movements, from food touching to the onset of backward arm movement. Letters α - δ below the neural trace indicate the times of occurrence of the digital frames reported below. Bottom: frames from a digital TV camera illustrating an episode of grasping food. The sequence of frames shows arm movement towards the food (α), food grasping (β , γ), feeding after backward movement to the mouth (δ). Modified from Fig. 7 of Galletti et al., 2003.

B. Example of a neuron selective for grip type recorded in dorsal premotor cortex (PMd, area F2). The two panels show neural activity recorded when the monkey grasped a cube in a fissure (left) and on a plate (right) performing two types of grip. Rasters (top) and histograms (bottom) are aligned (vertical bar) with the beginning of grasping movement. Modified from Fig. 5 of Raos et al., 2004.

C. Example of a neuron modulated by spatial factors recorded in an area of the lateral parietal cortex (area AIP). The monkey performed a power grip to grasp a handle directing the action to the left (black trace), straight ahead (dark grey) or to the right (light grey). Vertical lines indicate the onset and offset of the task epochs: fixation, cue, planning, hand movement. All trials are threefold aligned to fixation onset, cue offset, and go cue. Averaged firing rates are

shown in different levels of grey for each condition, as indicated by the inset with arrows on the left. Modified from Fig. 3D of Lehamn and Scherberger, 2013.

D. Directional tuning of grasps of a unit recorded in ventral premotor cortex (PMv). Each response in each tested direction is shown as mean firing rates and raster displays. In each panel, neural activity is fourfold aligned to Go Signal, Movement onset (M), Grasp (Gr), Hold (H). Modified from fig. 5B of Stark et al., 2007.

Figure 8. Cortico-cortical connections of the lateral (AIP) and medial (V6A) parietal grasping areas.

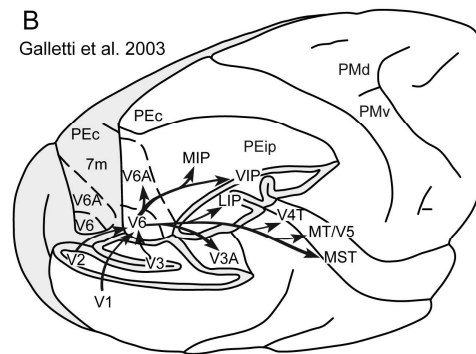
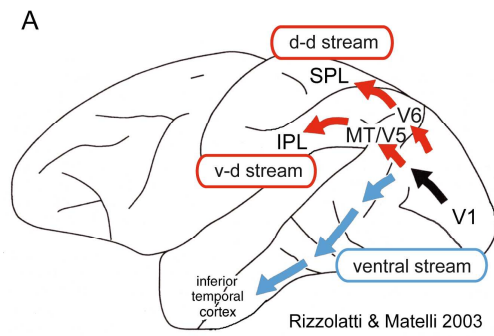
Columns show the Incidence of V6A (black) and AIP (white) connections with different regions of the cortical mantle. Extrastriate: extrastriate cortex (areas V2, V3, V4, MST, V6). SPL: superior parietal lobule. Mesial: areas of the mesial surface of parietal lobe. IPL: inferior parietal lobule. Inf.temp: interior temporal cortex. PMd: dorsal premotor cortex. PMv: ventral premotor cortex. PFC: prefrontal cortex.

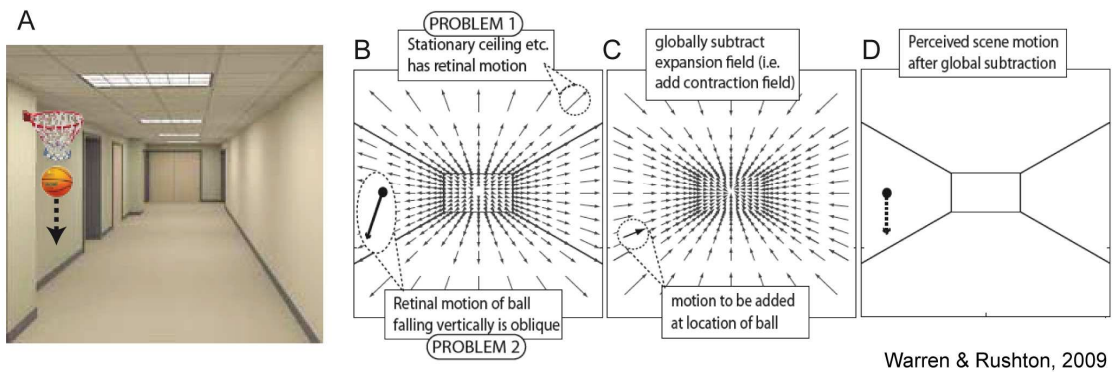
Data derived from Borra et al., 2008 and personal communication; Gamberini et al., 2009; Passarelli et al., 2011.

Figure 9. Inhibition of grasp-related discharge in V6A when grasping is performed in light.

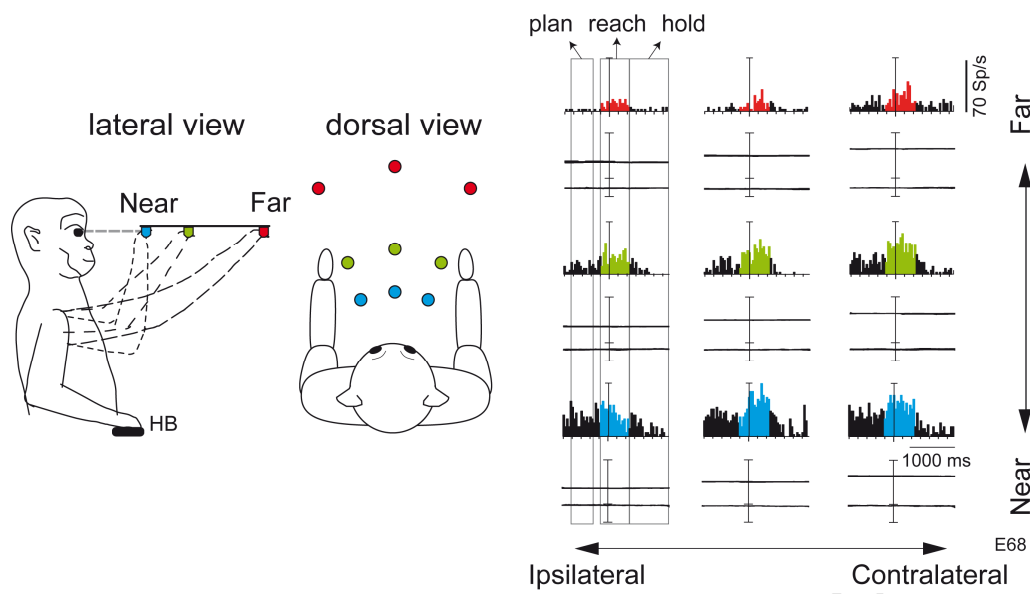
Activity modulation of a V6A grasping neuron when the animal performed an advanced precision grip in darkness (left) and in light (right). Neuronal activity is expressed as peri-stimulus time histograms and raster displays of impulse activity. Neural activity and recordings of horizontal and vertical components of eye position are aligned twice (long vertical lines across histograms), first on the illumination of the fixation light, and then on the onset of the reach-to-grasp movement (see arrow). Long vertical ticks in raster displays are behavioral markers, indicating from left to right: fixation light onset, go signal, movement onset, object pull, cue to release the object, object release, end of return movement, end of trial. Scales: vertical bars on histograms, 120 spikes/s; eye traces, 60°/division.

Note that in light the cell was inhibited not only during movement execution, but also during movement preparation, the inhibition starting just after the beginning of fixation. This means that the cell inhibition was not the result of the vision of the object to be grasped (since it was visible to the animal before fixation without affecting the cell's activity), nor the result of the vision of grasping, because it started well before it. See text for an alternative explanation.

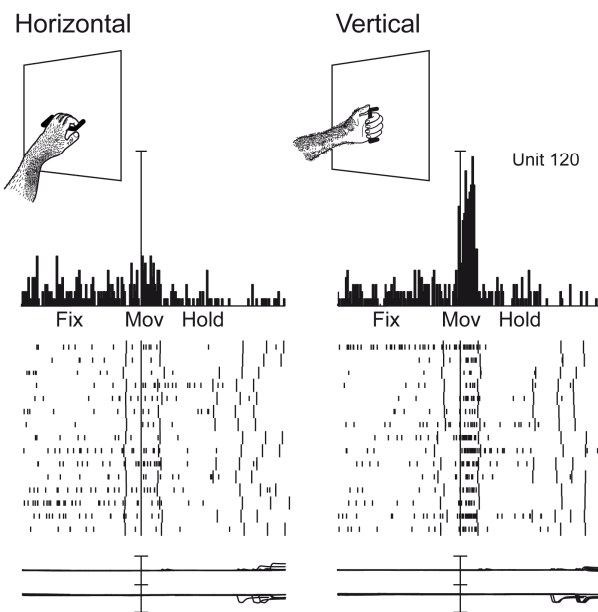




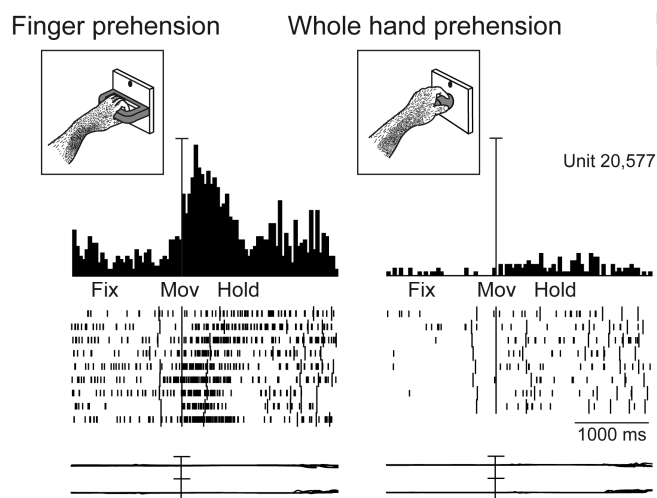




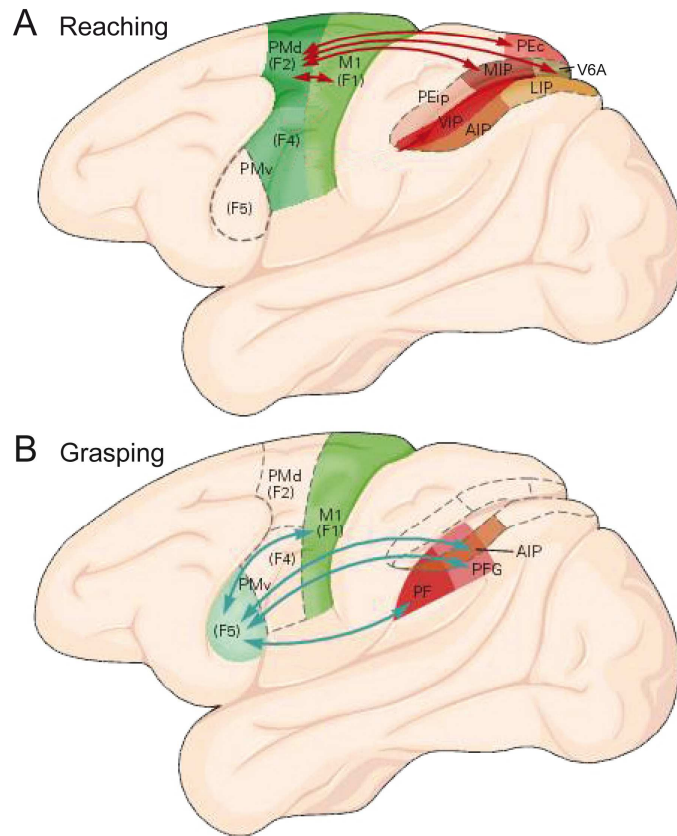
A Different wrist orientations



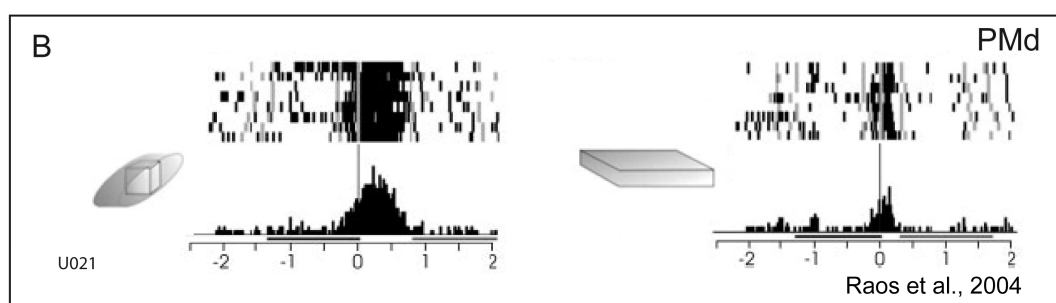
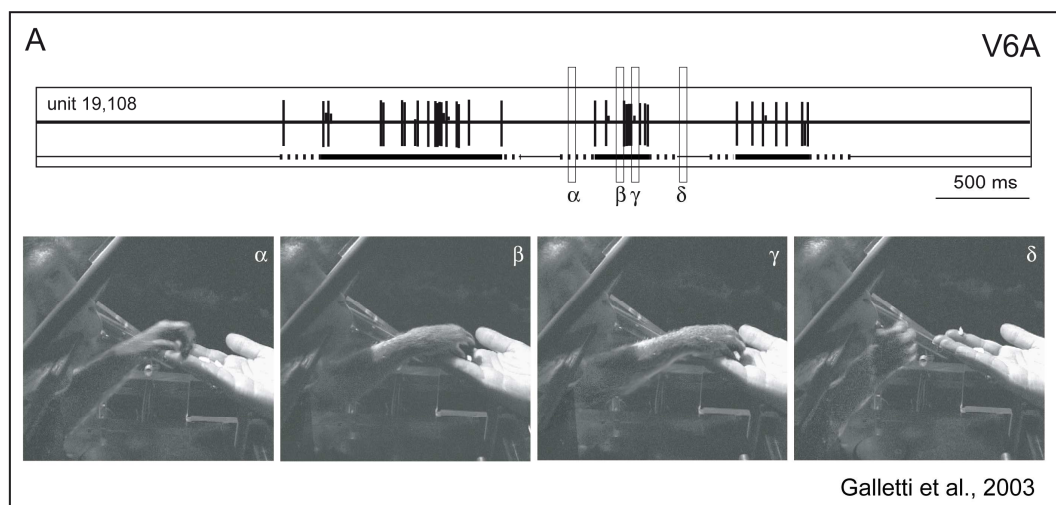
B Different grip types



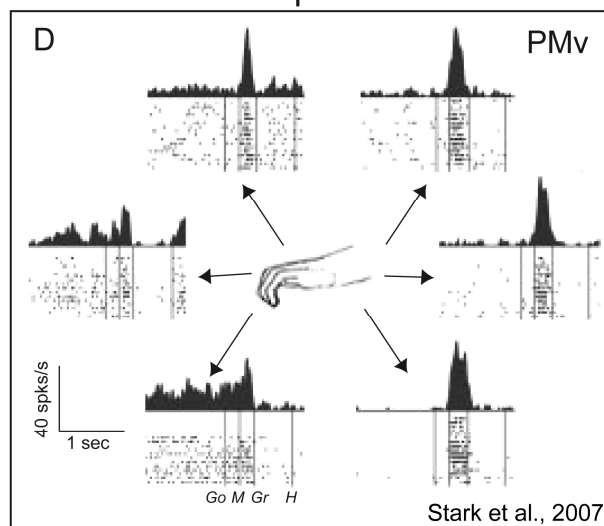
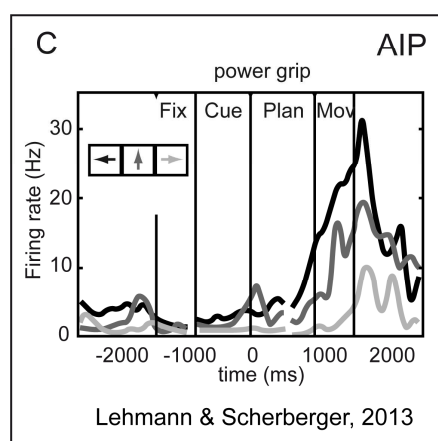
Classic scheme of segregation of reaching and grasping within the dorsal stream

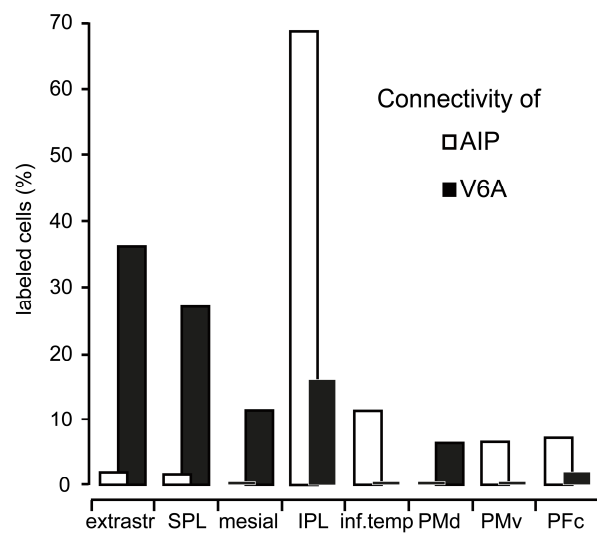


Grasping signals in dorsomedial fronto-parietal stream

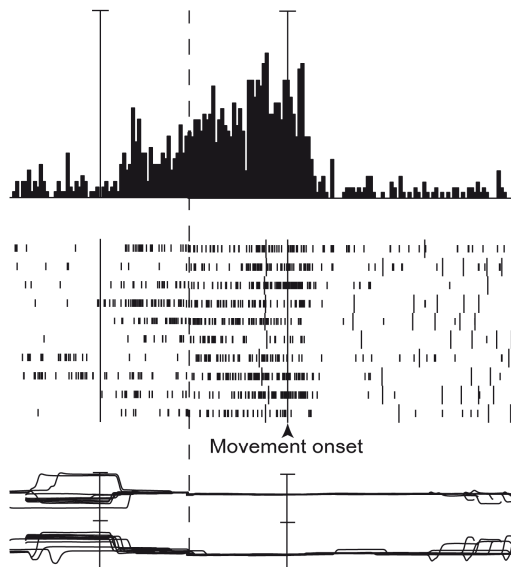
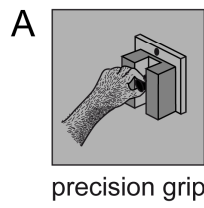


Directional signals in dorsolateral fronto-parietal stream





Grasping in dark



Grasping in light

